John Maynard Smith and the Fact(s) of Evolution.
A Study of Scientific Working Life in Post-War Britain.

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John Maynard Smith's family has supported my project by granting me copyright to use material from the archive, by attending one of my public events on Maynard Smith, and my sending me both a photograph and remembrances by friends and colleagues. Strange as it may seem, I also have to thank John himself: for his lucid writing which helped a non-biologist through his work – and, very importantly, for writing "What the SHIT am I DOING??" on his research notes once, as well as for crossing out a whole bit with 'BALLS!' written over it. It's encouraging to know that we all occasionally struggle!

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Abstract

John Maynard Smith (1920-2004) was one of Britain's foremost evolutionary biologists in the second half of the twentieth century. Drawing on his largely unexamined archive at the British Library and additional archival material, as well as on recent scholarship in science communication studies, this thesis offers a thematic study of Maynard Smith's working life as an evolutionary biologist. Three themes in particular are studied throughout. First, and contrary to the route taken in many scientific careers, popular science played a very prominent part in Maynard Smith's early career. He made use of both print and broadcast media to present his neo-Darwinian view of evolutionary science, to defend it against detractors and to advocate for science as both important for and responsible to society. Second, Maynard Smith, a natural communicator, used non-specialist and professional modes of communicating in tandem, exploiting them to his own professional advantage and to further professionalise evolutionary biology as a science. These different layers, and different uses of popular and professional outlets, also become apparent in his involvement in scientific controversies. Controversies – the third theme – become clearly conspicuous in Maynard Smith's later career, notably controversies around scientific conduct and around scientific ideas. In the former, scientific priority was at the centre, with Maynard Smith taking an "attributional" approach. In the latter, he showed a Popperian mindset, with a focus on falsifiability (to distinguish science and from religion) and constant critical testing as the way to move science forward, arguing both for orthodox views (in the punctuated equilibria debate) and against them (suggesting human mitochondrial DNA might recombine).

<u>Keywords</u>

John Maynard Smith; history of biology; science communication; popular science; neo-Darwinism; evolution; science and religion; creationism; scientific priority; scientific controversy; recombination in mitochondrial DNA; William D. Hamilton; Stephen Jay Gould.

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1 Introduction

1.1 John Maynard Smith and his archive

> *John Maynard Smith:* I don't think I have a spiritual existence. I mean I haven't, I suppose, got very much longer to live. I mean I'm now over eighty. […] So, I mean obviously, my expectation of life has to be limited. I don't expect anything after I'm dead […] I don't think I want to live in another realm: I'd love to know what's going to happen about X, you know... But personal things, I'd love to see my grandchildren when they're grown up – well one of them is but... you know, I'd love to see how the people I love get on and I would like to know what happens to science.
>
> *Robert Wright:* And does it help you to be at peace with the prospect of not existing someday to know that you made important contributions to a field that will be ongoing?
>
> *John Maynard Smith:* I think if I'm honest, yes it does. Yes, yes, I think it does. Butler's type of immortality is important to me.[1]

John Maynard Smith (1920-2004) was the 'senior statesman of British evolutionary biology' with a career that spanned the second half of the twentieth century.[2] He was approached by the former British Library Board chairman Sir John Ashworth in 2001, asking if he 'had thought of the ultimate fate of [his] archive(s).'[3] The British Library had, at that point, just acquired the British biologist William D. Hamilton's archive (as a loan) and was in the process of acquiring the American scientist George R. Price's papers as well.[4] Maynard Smith knew both of these men and had collaborated with Price on a seminal paper in the early 1970s.[5] 'I am anxious,' continued Ashworth,

> that the Library build on this nucleus so that we can develop a collection of material relating to the development in the UK and elsewhere of evolutionary studies more generally. You were and are a key person in this intellectual history and it would greatly enrich the national collection if we were able to add your archives to it.[6]

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[1] Maynard Smith and Wright 2001.
[2] Kohn 2003, 36.
[3] Ashworth to Maynard Smith, 21 May 2001. John Maynard Smith Archive (hereafter JMSA) Add MS 86809.
[4] Other archives by twentieth-century biologists held at the British Library are, for instance, those of Anne McLaren, Donald Michie (who later, and more famously, pioneered research in machine intelligence), and Marilyn Monk.
[5] Maynard Smith, J. and Price, G.R. (1973). The logic of animal conflict. *Nature 246,* 15-18.
[6] Ashworth to Maynard Smith, 21 May 2001. JMSA Add MS 86809.

Maynard Smith agreed to leave his papers to the Library which, after his death in April 2004, was confirmed by his son Anthony (Tony) Maynard Smith.[7] And so it came that the donation of the material from Maynard Smith's office at the University of Sussex was effective from 2 August 2004. So far, however, the archive has remained largely untouched.[8] As a hybrid archive, it contains both paper-based material (correspondence, research and lecture notes, computer printouts, manuscripts, offprints and notebooks) and born-digital material (floppy disks containing computer programs and drafts for his last book, *Animal Signals*,[9] as well as two hard drives). The paper-based material is fully catalogued (Add MS 86569-86840); the born-digital elements had not yet been catalogued or explored at the start of this project.

John Maynard Smith entered evolutionary biology only after a different first degree. In the late 1930s and early 1940s he read engineering at Trinity College, Cambridge. During this time he also joined the Communist Party, going almost immediately against the Party line by trying to enlist after the outbreak of World War II. He was rejected because of his bad eyesight, finished his degree and became an aircraft engineer. But Maynard Smith had had a childhood interest in nature and science and had spent much time in the school library at Eton educating himself with books by Charles Darwin, Albert Einstein, Arthur Eddington and J.B.S. Haldane. Haldane proved to be a major influence on Maynard Smith (a fact also represented in the archive). After the war, career prospects in engineering seemed dim and Maynard Smith decided to switch to biology. He wrote to Haldane, then teaching at University College in London (UCL), asking for advice. This marked the start of a fifty-year long career as a research scientist who worked, among other things, on the evolution of senescence, sex, and conflict. Before these mostly theoretical undertakings, Maynard Smith worked as an experimental geneticist in Helen Spurway's laboratory. He published several

[7] Maynard Smith to Summers, 25 June 2001, and Maynard Smith to Leighton John, 28 June 2004. BL Acquisition File "John Maynard Smith".

[8] Oren Harman has drawn upon it in his biography of George Price, one-time collaborator of Maynard Smith. See Harman, O. (2010). *The Price of Altruism. George Price and the Search for the Origins of Kindness.* London: The Bodley Head.

[9] Maynard Smith and Harper 2003.

papers on *Drosophila subobscura*, the European fruit fly, research which will only briefly feature in this thesis.[10]

The fact that Maynard Smith was one of Britain's most eminent evolutionary biologists was recognised multiple times: he became a Fellow of the Royal Society in 1977 and won numerous medals and prizes,[11] along with several honorary science doctorates (universities of Kent, Sussex, Oxford, Edinburgh, Chicago). His working life is defined almost exactly by the second half of the twentieth century: he entered University College London after leaving his previous position as aircraft engineer in 1947 and graduated with a first-class honours degree in zoology in 1950.[12] After graduation, he did not go to Oxford as encouraged by David Lack (and like his friends Aubrey Manning and David Blest did) to study ethology because he felt that he would not be very good at it – he was convinced his bad eyesight would prevent him from doing any proper field work.[13]

Instead he stayed with Haldane at UCL and decided to 'better do the sums', something he had always been good at since his school days.[14] (He went to Eton and would always bemoan the lack of a science education he received there but had to acknowledge that they taught him mathematics very well.[15]) Haldane had been the reason he went to study at UCL in the first place – Maynard Smith had first come across his future mentor's work while a student at Eton:

> I noticed that there was one person who attracted the particular hatred of several of my teachers. This was J.B.S. Haldane, himself an old Etonian, who had betrayed his class and religion, and who lost no opportunity of attacking everything Eton stood for. Thinking that anyone they hated that much could not be all bad, I sought out his books in the school library; it is to Eton's credit that the books were there.[16]

He connected with Haldane via reading his writings, and not knowing about his temperament, wrote him a letter in October 1947 – addressing him as 'Dear Comrade'; they were both members of the Communist Party at the time. After graduation he started a PhD

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10 Kohn 2004, 199-223.
11 Darwin Medal (1986), Frink Medal (1990), Balzan Prize (1991), Copley Medal (1991 or/again 1999), Linnean Medal (1995), Royal Medal (1997), Crafoord Prize (1999, with Ernst Mayr and George C. Williams), Kyoto Prize (2001).
12 Charlesworth and Harvey 2005, 256.
13 Kohn 2004, 214.
14 Kohn 2004, 214.
15 E.g. Maynard Smith 1985.
16 Maynard Smith 1985, 348.

under Haldane's supervision, but in 1951 Peter Medawar offered him a lectureship in zoology. Maynard Smith accepted without any regrets about not finishing his doctorate: he later commented that he was 'one of that distinguished company […] who can afford to remain Mr.'[17] Maynard Smith acknowledged in an interview that Haldane and Medawar were two of his greatest influences (his other heroes included, unsurprisingly for a neo-Darwinist, Charles Darwin and August Weismann): 'I spent my life imitating Haldane'; Medawar was 'the other great figure who influenced me as a scientist.'[18]

Medawar again played a pivotal role in Maynard Smith's next appointment: it was he who suggested Maynard Smith as founding dean at the University of Sussex's School of Biological Sciences. In the planning stages for the new university, James Frederic Danielli – Chair of Zoology at King's College, London, since 1948 and 'a physical chemist who had merely picked up his cell biology along the way'[19] – had originally been approached for the position. '[S]erious planning work began, laboratories were designed, appointments were offered and accepted, and all seemed set for a second flowering of the Danielli school in England.'[20] But around that time Danielli was also invited to the University of Buffalo, and for a while he 'tried to enjoy the best of both sides of the Atlantic by being, simultaneously, Dean of the School of Biological Sciences at Sussex, and Professor of Medicinal Chemistry, and Chairman of Biochemical Pharmacology at Buffalo.'[21] This situation proved unsustainable in the long term. After a phone call with Danielli, Medawar wrote to Sussex's first vice-chancellor, John Fulton, that 'the case is hopeless'.

> May I suggest that at the earliest opportunity you should forthrightly offer the Deanship to Mr. John Maynard Smith, Reader in Zoology in University College London (my old department)?
>
> Maynard Smith would in fact be a much better bet than Danielli. In research he has been an all-rounder, and has reached real distinction in certain aspects of physiological genetics. His Penguin on "The Theory of Evolution" is absolutely first-rate, and I read it from cover to cover. He is also a most devoted teacher, both at undergraduate and at graduate student level. […]

[17] Maynard Smith to Glover, 31 March 1958. Penguin Archives (hereafter PA) DM1107/A433.
[18] Maynard Smith 1988a, 128f.
[19] Stein 1986, 120.
[20] Stein 1986, 121.
[21] Stein 1986, 121.

> I am most enthusiastic about this idea and have not a shadow of doubt that Maynard Smith is the best man going for the job.[22]

Fulton followed Medawar's suggestion and in 1964, Maynard Smith moved to Brighton. He was to stay for the rest of his career, serving as dean from 1965 to 1972 and again from 1982 to 1984. He formally retired in 1985 but continued working and publishing until his death in 2004 (his last book, *Animal Signals*, co-authored with David Harper, was published in 2003). He seems to have been slightly bemused by this retirement that was not a retirement: 'I'm now "retired" (which means they don't pay me, but doesn't seem to have much other effect),' he informed one correspondent in 1988.[23] Two years previously, he had written to John Fulton (now a lord): 'In theory, I retired last September, but it hasn't made much difference. I am even doing some teaching. The best thing is that I don't have to go to any more meetings.'[24] (It has been said that Maynard Smith 'was hopeless at academic politics and never attended committee meetings in London if he could avoid it.'[25])

1.2 To write a biography or not to write a biography?

All this puts Maynard Smith squarely into the recent history of biology in Great Britain. Consequently, his archive opens many opportunities for the study of a post-war scientific working life in evolutionary studies. Why should we care about Maynard Smith and his working life? As highlighted above, he was one of Britain's most eminent and prominent evolutionary biologists. He contributed to several fields of study and was instrumental in establishing evolutionary game theory as a fruitful way of studying animal behaviour. But his archive also reveals the interests and activities that went beyond academic, scientific research: Maynard Smith's working life included a commitment to communicating science

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[22] Medawar to Fulton, 12 December 1963. JMSA Add MS 86575.
[23] Maynard Smith to Fox, 27 July 1988. JMSA Add MS 86575.
[24] Maynard Smith to Fulton, 12 March 1986. JMSA Add MS 86575. Similarly, he declined a request to review a manuscript, pointing out that '[a]fter all, it is five years since I formally retired, so I think I am allowed to please myself' (Maynard Smith to Graham, 23 October 1990. JMSA Add MS 86576). He stayed active teaching, however. In 1980, when the University of Basel started a summer school in evolutionary biology in the Alps, he joined the faculty almost yearly until 2000. ('Faculty of Evolutionary Biology in Guarda', n.d. Thanks to Richard E. Lenski for pointing me to this.)
[25] 'Professor John Maynard Smith' 2004.

widely and to pushing science forwards by being critical and welcoming of constructive controversy.[26]

How to study John Maynard Smith and his working life against the backdrop of twentieth century evolution biology and related themes? A scientific biography would be one obvious way. There most definitely is an interest in scientific biographies of evolutionary biologists active and influential in the twentieth century. George R. Price has recently been featured in an extensive biography, and so have William D. Hamilton,[27] David Lack,[28] and, less recently, J.B.S. Haldane,[29] R.A. Fisher[30] and Sewall Wright.[31] Dawkins has just published his autobiography in two volumes.[32] Further autobiographies exist of Sir Peter Medawar,[33] Edward O. Wilson[34] and Robert Trivers.[35]

Thomas L. Hankins pointed out that biographies need to do more than just 'chart the life or sketch the personality of his subject.'[36] In history of science, biographies can be very useful, but they bring with them a particular set of problems 'because of the great difficulty of integrating science into the rest of human intellectual endeavour.'[37] Scientific biography, for Hankins, needs to first, actually deal with the science, secondly, it must integrate the subject's various interests and activities into a coherent picture (or one as coherent as possible), and finally, while doing all of that, it has to remain readable.[38] One could take

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[26] The main body of primary sources for this thesis is provided by the John Maynard Smith Archive (JMSA) held at the British Library in London. Other British Library collections used are the George R. Price Papers (GPP) and the William D. Hamilton Papers (WHP). The archives of the publisher Penguin (PA), housed in the University of Bristol's Special Collections, and the BBC Written Archives Centre (BBC WAC) in Caversham, Reading, provided additional material. So have the J.B.S. Haldane Papers (JBSHP) in UCL's Special Collections and the Maurice Wilkins Papers (MWP), King's College London Archives; digitisations of some of these latter two archives are available through the Wellcome Library.
[27] Segerstråle, U. (2013). *Nature's Oracle. The Life and Work of W.D. Hamilton.* Oxford: Oxford University Press.
[28] Anderson, T. (2013). *The Life of David Lack: Father of Evolutionary Ecology.* Oxford: Oxford University Press.
[29] Clark, R.W. (1968). *J.B.S.: The Life and Work of J.B.S. Haldane.* London: Hodder & Stoughton.
[30] Box, J.F. (1978). *R.A. Fisher: Life of a Scientist.* New York [etc.]: Wiley-Blackwell.
[31] Provine, W.B. (1989). *Sewall Wright and Evolutionary Biology.* Chicago and London: The University of Chicago Press.
[32] Dawkins, R. (2013). *An Appetite for Wonder: The Making of a Scientist.* London: Bantam Press and Dawkins, R. (2015). *Brief Candle in the Dark: My Life in Science.* London: Bantam Press.
[33] Medawar, P.B. (1986). *Memoir of a Thinking Radish: an Autobiography.* Oxford: Oxford University Press.
[34] Wilson, E.O. (1994). *Naturalist.* [n.p.]: Island Press.
[35] Trivers, R. (2015a). *Wild Life. Adventures of an Evolutionary Biologist.* [n.p.]: Plympton.
[36] Hankins 1979, 1.
[37] Hankins 1979, 2.
[38] Hankins 1979, 7ff.

these points to heart and, following the examples of Harman and Segerstråle, add a full-fledged biography of Maynard Smith to the historiography. However, that is not the aim of this thesis. Maynard Smith's career and work offer such a wealth of possible thematic foci that it would be a shame not to use this as an opportunity to explore a more limited number of related issues in more depth and detail. The thesis will, however, keep the timeline largely chronological from the 1950s up until Maynard Smith's death in 2004 – with, as we will see, a brief foray into the afterlife of one of Maynard Smith's ideas. The chronological approach wedded to three thematic focus sections will be revealing some anomalies in Maynard Smith's working life: his emphasis on science communication to a popular, or non-specialist, audience marked his first decade as a research scientist rather than, as is usually the case, the end of his career.

The three themes, with two chapters each, are as follows: popular science, professional science, and controversial science. While this is a guide to the emphases of the chapters in each theme, it by no means is to suggest that we can draw clear boundaries between them. Rather the opposite: in Maynard Smith's working life, all three aspects often played together. As such, discussions of the professional content of science are important within the first section's focus on popular science; science discussed by and for people beyond the core group of professional experts and controversy feature in the second section's discussion of two major professional concerns of Maynard Smith; and lastly, the scientific controversies of the third section spilled over into the world beyond academia while being very much concerned with the status of the profession's knowledge about evolution.

1.3 Historiography

John Maynard Smith himself has received little focused historical treatment. Marek Kohn provides us with two biographical chapters, also discussing him in chapters on J.B.S. Haldane, William D. Hamilton, and Richard Dawkins.[39] The journal *Biology and Philosophy* edited a special issue on Maynard Smith and his influence on the philosophy of biology and of science, discussing his views on consistency, optimisation, fitness, levels of selection, animal signals, adaptation, and the strategy concept.[40] The *Journal of Theoretical Biology* too

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[39] Kohn 2004, esp. 197-255.
[40] Okasha, S. (ed.) (2005). Special issue on John Maynard Smith. *Biology and Philosophy 20*(5), 931-1050.

published a special issue; like the *Biology and Philosophy* issue it does not focus on historical discussion but instead collects scientific papers on or inspired by Maynard Smith's ideas.[41]

The history of evolutionary biology in the twentieth century, and the British context, however, have been studied in several volumes over the past decades. This literature therefore provides the larger backdrop to the thesis, but as the above mentioned thematic organisation indicates, the historiographical framework is more diverse than this: discussions of science communication in a variety of media form an important part for the first third of the thesis; scholarship related to intellectual property and scientific priority are necessary for the second third; and the thesis' last third will rely on additional literature about scientific controversies. This diversity will structure the rest of the historiographical section in this chapter, before we move on to outline this thesis.

1.3.1 Neo-Darwinism

As a student of J.B.S. Haldane's, Maynard Smith was taught to study evolution from a neo-Darwinian perspective, a theoretical perspective grown out of a period in the history of evolutionary biology known as the modern synthesis – a term coined by Julian Huxley in 1942.[42] The modern synthesis refers to the integration of Mendelian genetics with the Darwinian theory of natural selection. Its founding fathers are commonly cited to be J.B.S. Haldane, R.A. Fisher, and Sewall Wright.[43] Their work, done in the 1920s and 1930s, showed that Mendelian genetics was not incompatible with Darwinian natural selection, as believed by many at the time: the pervading problem was how to integrate the gradualism of Darwinian evolution with the understanding that Mendelian genetics, due to the nature of mutations, necessitated evolutionary change to happen in steps. Establishing the field of population genetics, Haldane, Fisher and Wright brought mathematical thinking to bear on the problem by developing 'formal models to explore how natural selection, and other evolutionary forces such as mutation, would modify the genetic composition of a

[41] Szathmáry, E. and Santos, M. (eds.) (2006). Special issue in memory of John Maynard Smith. *Journal of Theoretical Biology 239*(2), 129-288.
[42] Huxley, J. (1942). *Evolution. The Modern Synthesis.* London: Allen & Unwin.
[43] They were, of course, not the only architects of the synthesis or developers of population genetics. See e.g. Bowler 2003; Cain 2013; Ruse 2013a.

Mendelian population over time.'[44] Population genetics came to be the theoretical cornerstone of the modern evolutionary theory.[45]

The nature and origins of the synthesis are a matter of debate,[46] and the question of the professionalisation of evolutionary biology is often discussed in tandem. Betty Smocovitis, for instance, has studied it in terms of its instrumentalisation for discipline formation, discussing, *inter alia*, the 1959 centennial celebrations.[47] Michael Ruse has emphasised that, outside of the professional writings necessary for discipline formation, there was a carrying over of progressivist ideas from the nineteenth century, discussed in the more popular writings of biologists like Theodosius Dobzhansky or Julian Huxley.[48] (As we shall see, Maynard Smith too used non-specialist writings to make a statement about the professional state of evolutionary biology. However, he did so at the beginning of his career rather than once he was established, and he did not separate it out from his professional life.) Joe Cain further argues that the synthesis concept was useful for constructing an identity in the post-war years but that over time, it has grown into a unified event, a master narrative lacking nuance but in the light of which everything else is being studied.[49] There were, however, many shifts and transitions, such as in focus (from object to process as well as from description and narratives to causes, heuristics and mechanisms) and method (from observational and inductive to analytical and experimental).[50]

For this thesis, the synthesis period and concept are of less importance than these larger discussions and the neo-Darwinian perspective that grew out of the modern synthesis. In the British context particularly, neo-Darwinism has sometimes been characterised as – and criticised for – being focused on natural selection and adaptation. The term "ultra-Darwinism" had been used in the nineteenth century to describe this view, taken up again by Stephen J. Gould in the twentieth century.[51] *A Reason for Everything*, subtitled *Natural Selection and the English Imagination*, provides biographies of the main British

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44 Okasha 2016.
45 See also Depew and Weber 1995; Bowler 2003.
46 Bowler 2003, chapter 9; see also Lennox 2008, esp. from 83 onwards, and Cain 2009, 2013.
47 Smocovitis 1992, 1996.
48 Ruse 1996/2009, 1999.
49 Cain 2009.
50 Cain 2013.
51 Kohn 2004, 13ff.

players in twentieth-century evolutionary biology (it also includes two chapters on Alfred Russell Wallace): Marek Kohn here analyses how British biologists have reacted to and furthered our understanding of adaptation and natural selection, and evolutionary thought more broadly.

1.3.2 Popular science

As mentioned above, the thesis has a layered and thematic approach to studying Maynard Smith's working life. I have mentioned three themes: popular, professional and controversial science. Even a quick glance at the recent literature in science communication studies and studies of scientific knowledge shows that these terms are loaded with pre-conceived notions. A long prominent view of popular science or science popularisation has been what is known as the diffusionist or deficit model, an undynamic view in which scientific elites produce knowledge which, in a simplified way, trickles down to a passive lay public. This model assumes two separate spheres between which scientific knowledge travels one-way only. In a now classic article, Roger Cooter and Stephen Pumfrey pointed out the problems with historians of science's mostly uncritical acceptance of this model and similarly the implied dichotomy of elite versus popular cultures.[52] They called for a re-thinking of the history of popular science, bringing in 'the essentially dialectical basis of the construction of popular culture'.[53] Similarly, Stephen Hilgartner has problematised the diffusionist model; he prefers to think of science popularisation as happening on a continuum and in degrees.[54]

We can indeed go as far back as 1935 for arguments doubting the view that science popularisation is either unimportant to or isolated from professional science. Ludwik Fleck's monograph on the emergence and genesis of scientific facts expressed a view that includes feedback loops between popular and professional science and literature. He stressed the importance of popular literature for the formation of the worldviews of scientists and communication not only between scientists and non-scientists but also between scientists of different (degrees of) specialisations. Popular science thus forms the basis of every person's knowledge. Problematically, however, Fleck also characterised

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52 Cooter and Pumfrey 1994, 248-252.
53 Cooter and Pumfrey 1995, 252.
54 Hilgartner 1990; see also Whitley 1985; Myers 2003; Bucchi 2008.

popular science as defined by loss of detail and controversy, leading to artificial simplification, and simple acceptance or rejection of certain points of view, with the aim to create a worldview.[55] The idea of continuity between popular and professional modes of science communication also informs Cloître and Shinn's 1985 model of four main stages: the intraspecialist, interspecialist, pedagogic (Fleck referred to this as 'textbook science'), and popular level.[56] This too is an idealisation from which actual science communication often deviates.[57] Considering Maynard Smith as a science communicator will complicate and nuance the story further. There is no linearity about where, when and to whom he presented scientific ideas: his 'popular science' occurs at all stages of his career, alongside, intermixed with and before his 'professional science'; ideas are presented simultaneously in different contexts and media, specialist and non-specialist.

The recent criticisms of the concept of popular science and science popularisation itself are therefore relevant. In order to avoid the intellectual baggage of associating popular science with the diffusionist model, James Secord has suggested to reconceptualise popular science as part of a broader "knowledge in transit" category: 'to think, at every point in our work, about science as a form of communicative action—to recognize that questions of "what" is being said can be answered only through a simultaneous understanding of "how," "where," "when," and "for whom".'[58] Jon Topham is moreover keen 'to advocate a closer attention to actors' own categories of the "popular".'[59] In a focus section in *Isis*, introduced by Topham,[60] Andreas Daum pointed to several other problematics, in particular imbalances in scholarly focus. These were emphasis on (natural) science, on English-speaking literature and Britain, and on the nineteenth century.[61] Ralph O'Connor has similarly highlighted the fact that 'the postwar period [is] currently little studied by historians.'[62] The focus on the nineteenth century may at least be partly due to the fact that, as Topham[63] and others have pointed out, this was when popular science emerged, thus

55 Fleck 1935 (English translation 1979).
56 Bucchi 2008, 61.
57 Bucchi 2008, 63.
58 Secord 2004, 663f.
59 Topham 2009a, 5.
60 Topham 2009b.
61 Daum 2009, 322f.
62 O'Connor 2009, 335.
63 Topham 2009a, 6ff.

offering rich case studies about its early stages and development. At the same time, there is a long-standing view that with increasing scientific professionalisation in the twentieth century, popular science lost its standing. But, as Peter Bowler has pointed out, scientists continued to popularise throughout the early twentieth century.[64] This thesis takes up some of these problematics by extending discussions into the post-war period. It highlights science communication as an integral part to Maynard Smith's scientific working life from the very beginning of his career, informing both his own and his discipline's professionalisation.

1.3.3 Scientific priority

In terms of the professional and controversial aspects of science studied, this thesis builds on work on intellectual property and scientific priority as well as on scientific controversies. Assigning scientific priority is generally done based on who has 'done something innovative before others did it'.[65] The public credit a scientist gets for this establishes their intellectual property rights to an idea or discovery. Some of the early work in the field has been done by Robert Merton and Thomas Kuhn.[66] The sociology of scientific knowledge (SSK) and science and technology studies (STS) have furthered the conceptual structures over the last decades, keeping the context of scientific controversy. There are, however, different conceptions about what counts as scientific priority: the point model describes one, the attributional model another; related to that is the difference between unpredictable and predictable discoveries. The point model – the problems of which Kuhn pointed out in 1962 – understands scientific discovery as a "Eureka" moment: who thought of something when is therefore easily pinpointable and priority easily assignable.[67] In 1981, Augustine Brannigan developed a different way of thinking about scientific controversy, the attributional model. Considering the social nature of science, discovery is a process both in terms of the making of a discovery and the recognition of the discovery as having been made.[68]

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[64] Bowler 2009, 2006.
[65] MacLeod and Radick 2013, 190.
[66] Merton 1957; Kuhn 1962.
[67] Kuhn 1962; Pinch 2015.
[68] Brannigan 1981, cf. Pinch 2015.

Kuhn also differentiates between unpredictable and predictable discoveries. The latter are often more straightforward and closer to the point model because people are working towards them and have a sense of what they are looking for. It is thus easier to recognise when they have made a discovery or formulated a solution. Unpredictable discoveries, on the other hand, make it difficult to trace their development.[69] At the same time historians and sociologists of science have emphasised the importance of examining the circulation of unpublished material, informal conversation, and collaboration. All of these imply an exchange of ideas and feedback which may re-shape an idea or re-define a discovery.[70] The process of scientific publishing and the peer-review system play a crucial role but are insufficiently problematised, with the focus mostly being on their role as establishers of priority and as quality control. Marcel LaFollette is one of few scholars discussing referee misconduct, noting that 'suspicions and rumors persist that referees have stolen from manuscripts under review.'[71] Similarly, Jerome Ravetz has highlighted that scientific publishing 'provides no systematic protection for property in the next phase of the development of a problem', that is, after publication, when intellectual property and scientific priority rely on proper citation.[72]

1.3.4 Scientific controversy

As mentioned, priority conflicts form a subset of scientific controversies which can be evident in journals, communications, correspondence, or in the popular media. Controversies have been studied, *inter alia*, in the fields of SSK and STS. Here, Trevor Pinch has identified three themes that have been of interest since the 1960s: controversies in science (and technology) and its relation to society, controversies within science with a focus on their social construction, and most recently a combination of these two earlier strands.[73] In terms of how to understand scientific controversies philosophically, Philip Kitcher has identified a rationalist and an anti-rationalist model. Both have simple and sophisticated versions and are distinguished by their proposition on what settles controversies: rationalists favour 'experimentation, evidence and the exercise of reason',

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[69] Kuhn 1962.
[70] Ravetz 1996; Fleck 1979.
[71] LaFollette 1992, 127.
[72] Ravetz 1996, 225.
[73] Pinch 2015, 282.

whereas anti-rationalists hold that 'context-transcendent canons of reason and evidence have no power to resolve major scientific controversies'.[74] A problem that faces the rationalist model is how to explain why controversies persist if they can reach closure through the means suggested. Closure is a concept developed by Harry Collins, alongside 'interpretative flexibility', a 'core set' of scientists within a controversy, and the 'experimenter's regress'.[75] Interpretative flexibility means that 'scientific findings are open to more than one interpretation.' According to this view, experiments, by themselves, are therefore not able to decide a controversy as rationalists hold: once the definitions of not only test results but also the tests themselves are called into question and discussed from opposing ends of the room, you need a criterion 'independent of the output of the experiment itself' to decide. This and other concepts are connected – and applied – in Harry Collins and Trevor Pinch's *Golem* series, a work aiming to show the 'the golem that is science'.[76]

Science is often controversial. Most importantly, it is in controversy that the workings of science often become most visible and that the notion of "the truth being out there" for science to find is challenged. By studying controversial science, we can learn both 'a little of science' – in the following, of an aspect of human evolution – and 'a lot about science' – how science works, how scientists communicate, and how they deal with new ideas, ideas exciting to some yet uncomfortable for others.[77]

1.4 Thesis plan

Considering the above, how does John Maynard Smith, referred to at one point as the 'senior statesman of British evolutionary biology', fit into post-war evolutionary biology and what role does science communication play in that context? What do his involvements in scientific controversies tell us, first, about his philosophy of science – not in the disciplinary sense but as a personal notion – and the state of evolutionary biology in the second half of the twentieth century? To answer these questions, the above-indicated three-fold thematic

[74] Kitcher 2000, 21.
[75] Pinch 2015, 283; see also David Bloor's "Strong Programme" (e.g. Shapin 2015, 675). Some of these ideas have been taken up by studies of technology, particularly by the SCOT (social construction of technology) approach.
[76] Collins and Pinch 2004, 2.
[77] Collins and Pinch 2004, 2.

yet largely chronological structure will be adopted. The answers to these questions will then ultimately merge into the master narrative of John Maynard Smith and the fact(s) of evolution.

1.4.1 Part 1: popular science

The first part highlights Maynard Smith's activities in "Popular Science", roughly covering the first three decades of his scientific career. Chapter 1 starts in the early 1950s with Maynard Smith's first scientific and non-specialist publications. It introduces us to his monograph *The Theory of Evolution*, published with Penguin in 1958, the centenary of the reading of Charles Darwin's and Alfred Russell Wallace's papers introducing natural selection. The dates are no coincidence and reflect the book's role in the professionalisation of evolutionary biology. At the same time, the chapter addresses his own professionalisation and the role of popular science while complicating the notion of "popular science". Maynard Smith was an early-career scientist, transitioning from engineering into evolutionary biology. He placed himself into a larger historiography of scientists writing for non-specialist audiences and focused on the utility of mathematics for biology.

Chapter 2 moves from non-specialist writings into the world of broadcasting. From the mid-1950s onwards, Maynard Smith was active on radio and television. We will see how he discussed, explained, advocated for, and defended science in general, and the theory of evolution in particular. The different media brought their own challenges and we will see Maynard Smith navigating the BBC's increasing mediation of science. Both the broadcasts and the parallel involvement with the British Society for Social Responsibility in Science highlight Maynard Smith's commitment to the communication of science. They also highlight his left-wing politics which he retained after leaving the Communist Party in 1956.

1.4.2 Part 2: professional science

In the second part we turn towards "Professional Science", focusing on the two decades from the early 1960s to the early 1980s. Chapter 3 takes us into the world of the origins and developments of scientific ideas, linked to issues of priority and intellectual property. It follows the story of biological altruism as developed by William Hamilton (under the name "inclusive fitness"). Hamilton accused Maynard Smith of first, not crediting him with the idea, even stealing it (by publishing a similar idea and calling it "kin selection"), and later, of shifting the priority to J.B.S. Haldane. A citation analysis helps understand the long-term fate of inclusive fitness versus kin selection and the 1964 papers in which they were introduced. The conflict highlights the different understandings of scientific priority Hamilton and Maynard Smith had (point model *vs.* attributional model), influenced by their reading it in different contexts (validation of early-career work *vs.* combating group selection).

Chapter 4 brings us to the scientific contribution for which Maynard Smith is most famous: evolutionary game theory and evolutionarily stable strategies (ESS). Inspired by a draft manuscript, written by George Price, Maynard Smith acquainted himself with economic game theory and translated it into biological terms to study animal behaviour. A possible priority conflict with Price was averted by collaborating with him on the seminal 1973 paper 'The logic of animal conflict', which included early use of computer simulation in theoretical biology. This chapter will have one of the clearest examples of non-specialist and specialist, or popular and professional, science interacting in Maynard Smith's working life: the concept of the ESS was introduced in an essay aimed at non-specialists, was immediately covered in more popular science magazines after publication in a scientific journal and further broadcast in the *Horizon* episode based on Richard Dawkins' *The Selfish Gene* (in itself in part based on Maynard Smith's work).

1.4.3 Part 3: controversial science

Lastly, the third part on "Controversial Science" will take us from the 1970s through to Maynard Smith's last years, including a short turn back to the 1960s and a look at the fate of one of the controversies beyond Maynard Smith's actual working life. Chapter 5 presents Maynard Smith with two challenges – external and internal to science – that were put to neo-Darwinism: creationism and punctuated equilibria. Although the focus lies in the late 1970s and 1980s moving into the early 1990s, previously voiced thoughts on religion from the 1960s provide us with an invaluable understanding of Maynard Smith's Popperian understanding of science. This frames his public interactions with creationism as well as his initially welcoming attitude to the punctuated equilibria challenge, a theory used by creationists to discredit neo-Darwinism.

Chapter 6, finally, puts us firmly into the last decade of Maynard Smith's working life. Representing the orthodox side in a scientific controversy in the previous chapter, we now find him – together with colleagues – suggesting an unorthodox theory: that human mitochondrial DNA (mtDNA) might recombine. This suggestion had huge implications for the story of human evolution, especially for research on when and where anatomically modern human beings first arose. Tracing the controversy beyond Maynard Smith's involvement to the present day allows us to draw further conclusions on the nature of closure, namely that some ideas take on an 'undead' life. The suggestion of recombination in human mtDNA is persistent despite efforts to proclaim it impossible and undeniably disproven.

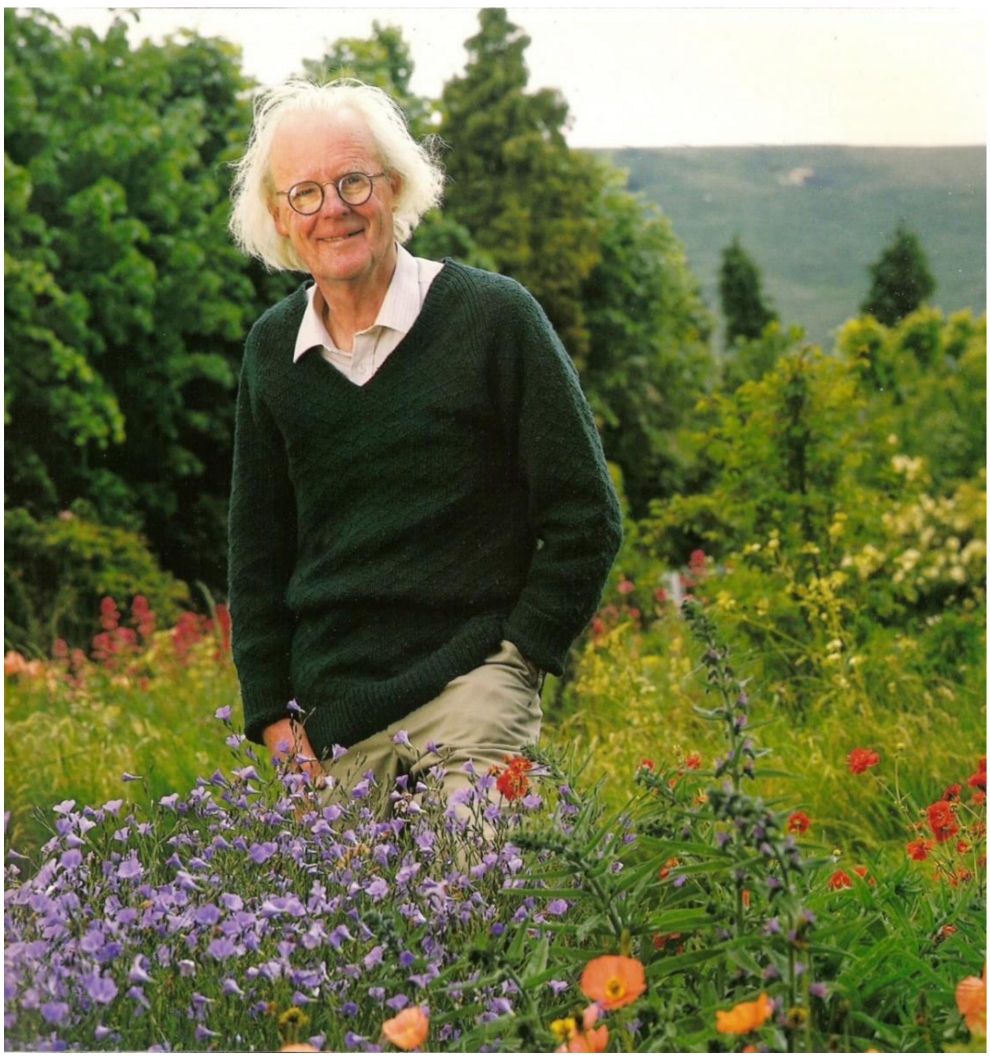

Figure 1. John Maynard Smith. Sussex, 1989. © Anita Corbin and John O'Grady. Courtesy of John Maynard Smith's Estate.

PART 1: POPULAR SCIENCE

The John Maynard Smith Archive holds material between 1948 and 2004 with a focus on the 1970s to the 1990s. When Maynard Smith discussed the donation of his papers to the British Library, he had noted that he 'tend[ed] to throw things away'.[1] Yet that does not mean that we cannot look at his early working life: there is some material from the 1950s and 1960s, and triangulation with other archives such as the Penguin Archive and the BBC Written Archives helps fill in the picture. In this first part of the thesis, we therefore meet up with Maynard Smith after graduating from University College in 1950 and follow him into the late 1960s, early 1970s. Communicating science to wider, non-specialist audiences, starts very early in Maynard Smith's career, making it our first focus. Throughout his working life, he spent time writing non-specialist science books and essay reviews as well as appearing on radio and television.

In Chapter 1, I discuss Maynard Smith's earliest work of science communication, with a particular focus on his book *The Theory of Evolution* (1958). The development of his "little Penguin", as he liked to refer to it (calling to mind his publisher, Penguin), is important on two accounts. First, it marks Maynard Smith's first book publication as a popular publication which found widespread use across audiences (specialist and non-specialist as well as intermediary). Second, it sets out his general biological outlook as neo-Darwinian (an outlook he would follow throughout his five-decade long career) at a pivotal time for the Darwinian theory of evolution: its centenary.

Moving into the 1960s and from print media onto the airwaves, Chapter 2 widens Maynard Smith's outlets, audiences, and topics of science communication. We will see him explain, defend, and promote science in general, and (neo-Darwinian) evolutionary biology in particular, by analysing some of his programmes. This part of Maynard Smith's working life is also indicative of wider interests in the social responsibilities of science. These interests were in a sense limited to the late 1960s and early 1970s, at least in terms of explicit engagement, but we do find them return implicitly in the late 1970s and early 1980s when Maynard Smith debated evolution with creationists.

[1] Maynard Smith to Ashworth, 11 June [2001]. BL Acquisition File "John Maynard Smith".

2 *The Theory of Evolution:* the story of a little Penguin

2.1 Introduction

In 1959, the centenary of the publication of *The Origin of Species*, Harvard historian Donald Fleming noticed that Charles Darwin appeared not to be a universal hero. In a survey of centennial literature, he found that in fact many historians were pointing to failures in Darwin's theory, or were putting the emphasis on predecessors in evolutionary thinking. It were biologists, contributing in a variety of works to the Darwinian literature, who seemed to have done a better job than the historians at evaluating Darwin and his work historically.[1] One of those biologists was John Maynard Smith, who in 1958 published a volume entitled *The Theory of Evolution* with Penguin. It might be surprising to start the description and analysis of a scientist's working life with that part of his work which is directed not at other scientists but intended from its inception for a non-specialist public. But as Bernhard Haubold's obituary pointed out, Maynard Smith was remarkable not only for his research – and more about this in later chapters – but also for his style of doing research. 'His great talent was to track down the core of a complex biological process and characterise it elegantly with language and mathematics.' What is more, for Maynard Smith 'science is a social activity. These two aspects, the restless desire to get to the bottom of things, combined with the will to embed any made discoveries into the discourse of a community as broad as possible, were the motivating forces behind his constant work in popular science.'[2] Maynard Smith did not wait until the end or even the middle of his career to start engaging with the public. Less than a decade after his graduation from UCL he had published an article in a journal committed to bringing a range of biological topics to a wider audience, and shortly after, his first popular science book, *The Theory of Evolution*, made its way into bookstores and from there into homes. He had already taken first steps into science broadcasting (see Chapter 2).

[1] Fleming 1959.
[2] Haubold 2004, 537 (my translation).

The present chapter reflects the multi-faceted nature of 'one of biology's best explainers'[3] as well as the interconnectedness between Maynard Smith's research and science communication activities. From the very beginning of his career, these were integrated and the boundaries between them often fluid.[4] As we shall see, Maynard Smith's involvement with Michael Abercrombie, the series editor bringing him to Penguin Publishing House, began with an article published in the publisher's *New Biology Series* in 1953,[5] which was based on previous work published in *Evolution* in 1952[6] and presented at an undergraduate conference at Oxford.[7] These first two articles also provide continuity from his previous career as an aircraft stressmann, neatly combining engineering – where he had been 'working mainly on structural design, strength and performance calculations'[8] – and aerodynamics with biology. In a lecture given in 1997, Maynard Smith came full circle, presenting the work of his first scientific publication to a small audience for a science masterclass.[9] The chapter also places Maynard Smith and his book in the wider context of the state of Darwinian theory one hundred years after its first publication. As Fleming has pointed out, Maynard Smith was one of those authors providing the public, and indeed other (evolutionary) biologists, with an overview of Darwin's theory, both scientifically and historically.

In order to establish Maynard Smith's role – and that of his writing – as science communicator within and between the worlds of the non-scientist and the scientist, we will proceed chronologically from his first specialist and first non-specialist publications to *The Theory of Evolution*, his "little Penguin". The latter works will be placed in relation to the aims

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[3] Dennett 2004, 307.

[4] In 1982, Maynard Smith edited a volume to commemorate another Darwin-related anniversary, his death. *Evolution Now. A Century after Darwin* collects a variety of scientific articles, grouped thematically. Maynard Smith wrote a general introduction, including a brief history of evolutionary biology and introduced each group and the ideas expressed in the articles with an accessible comment. 'First, I explain how the topic is related to Darwin's ideas. Second, I have tried to help non-specialists to find their way through papers which are sometimes rather technical. […]' (Maynard Smith 1982a, 5). He was thus aware of the possibility that 'the lay reader will find it hard going' (Lewontin 1983) but still successfully opened up specialists' topics and concerns to non-specialists, whether they were scientists from other disciplines or non-scientists willing to engage with science.

[5] Maynard Smith, J. (1953). Birds as aeroplanes. *New Biology 14*, 64-81.

[6] Maynard Smith, J. (1952). The importance of the nervous system in the evolution of animal flight. *Evolution 6*(1), 127-129.

[7] Kohn 2004, 214.

[8] Maynard Smith to Haldane, 1 October 1947. JBSHP HALDANE/5/2/4/144.

[9] Maynard Smith, J. (1997). 'Flight in birds and aeroplanes.' Vega Science Masterclass. Available at http://www.vega.org.uk/video/programme/84.

of the editors at Penguin, where they were published. From there, we will widen our view to the state of evolutionary biology around the time of publication. The Darwin-Wallace centenary in 1958 and the *Origin of Species* centenary in 1959 were two occasions for historians and biologists to reflect on Darwinian theory and its status within and as a science. We will see how the image that Maynard Smith painted fitted into this larger context and take a look at its life after the first publication while reflecting on the theoretical issues of science communication in their relation to Maynard Smith and evolutionary biology.

2.2 From engineer to biologist

2.2.1 Maynard Smith's first publication (1952)

In the years following his graduation in 1950, John Maynard Smith worked first under J.B.S. Haldane towards a PhD degree, a degree he never completed because Peter Medawar offered him a lectureship in zoology.[10] During his time as an undergraduate and as an early-career scientist Maynard Smith was interested in questions of animal locomotion. He tackled animal flight, studying mostly birds and insects, as well as locomotory adaptations in mammals, publishing by 1958 three papers on these topics among close to a dozen on his other work on fruit fly genetics. Bird flight had been of interest to him even before he started his degree.

> My other approach to biology has been through watching birds […]. Naturally, I have been interested of [*sic*] Bird Flight. Much of what I have read on this subject has been pretty fair nonsense. Even Darwin did not realise that true soaring flight is impossible in the absence of upcurrents, and modern writers do not seem to record the necessary data like wing loading, aspect ratio, and so on.[11]

The methodical engineering approach of calculating necessary properties for flight is apparent in this first description of what Maynard Smith saw as problems with the state of biological research.[12] Once a researcher himself, he found biology was not ready for work combining engineering, mathematics, and biology: he could not get published. Many

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[10] Charlesworth and Harvey 2005, 257. Medawar, 'after Haldane, has been the major influence on the way I see science' (Maynard Smith 1985, 350).
[11] Maynard Smith to Haldane, 6 October 1947. JBSHP HALDANE/5/2/4/144.
[12] It also highlights that he continued his school time habit of reading up on science subjects that interested him.

biologists – and thus reviewers for his early papers – at the time had difficulty with Maynard Smith's use of mathematics.[13] 'The importance of the nervous system in the evolution of animal flight' almost suffered the same fate as some of his other papers; the journal *Evolution* initially rejected it. The problem was less the inclusion of equations or mathematics. Instead, the rejection was justified (even more irritatingly for Maynard Smith) 'on the grounds that the author clearly didn't know enough about aerodynamics.'[14]

> Now this did slightly annoy me. If they had rejected it on the grounds that I didn't know anything about animals I wouldn't have minded so much, 'cause it was probably true. But, you know, test pilots had been trusting their lives to the fact that I knew some aerodynamics for a number of years. I felt a bit cross.[15]

The article was ultimately published by *Evolution* in 1952 after Haldane intervened.[16] Maynard Smith's first scientific publication thus connected his engineering background to his old and new love of biology, foregrounding his future focus on evolution. He looked at the flight of primitive animals and concluded that flight in these is stable, defined as follows: an animal can be said to be stable 'if, when it is disturbed from its course, the forces acting on it tend to restore it to that course […] without active muscular contractions'. This is the case for gliding animals; in flapping flight the course correction needs to be 'without any modification of that cycle of (muscular) contractions'.[17] Judging from fossil records which exhibit features necessary for stable flight – e.g. a long tail that functions as a stabiliser – and flight in gliding animals, Maynard Smith concluded that 'primitive flying animals tended to be stable' and hypothesised that this was 'presumably because in the absence of a highly evolved sensory and nervous system they would have been unable to fly if they were not, just as a pilot cannot control an unstable aeroplane.'[18] Having been an aeroplane engineer, however, he also knew that unstable planes can theoretically be controlled with the help of an automatic pilot. Instability in flight has the advantages of better manoeuvrability and a lower stalling speed (which is 'the minimum speed at which an aeroplane can fly').[19] He had encountered the practical difficulties in

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[13] Charlesworth 2004, 1107. It was no accident that Maynard Smith's first textbook for undergraduates was *Mathematical Ideas in Biology* (1968).
[14] Maynard Smith 1997.
[15] Maynard Smith 1997.
[16] Maynard Smith and Dawkins 1997, https://www.webofstories.com/play/john.maynard.smith/14.
[17] Maynard Smith 1952, 127f.
[18] Maynard Smith 1952, 128.
[19] Maynard Smith 1952, 128.

designing an unstable plane around 1942 – fighter planes obviously benefit from the advantages gained through instable flight and a functioning design was much sought after during World War II.[20] What was difficult in engineering, nature had accomplished: some birds can fly without being stable.[21] The evolution of a nervous system takes over the functions of an autopilot in planes and has enabled animals to evolve instable flight. This happened not 'in a single step'; instead, '[a]ny reduction on the degree of stability will be an advantage provided there is a parallel increase in the efficiency of control.'[22]

It is partly on this paper and on research conducted earlier with a fellow undergraduate student, M.J. Davis, that Maynard Smith's first non-specialist publication is based. Just a year after the first professional publication just discussed, 'Birds as aeroplanes' appeared in the Penguin series *New Biology*. *New Biology* was providing 'popular accounts of topics of wide general biological interest. […] *New Biology* was immensely and deservedly popular at a time when few popular science publications were available,' wrote Ruth Bellairs in her obituary of one of the two editors, Michael Abercrombie.[23] The second editor was Abercrombie's wife, M.L. Johnson; both worked at Birmingham's Department of Zoology. Penguin is not an academic publisher, yet their Pelican imprint repeatedly published non-fictional books. Johnson and Abercrombie emphasised in the first volume of *New Biology* that the series was one of 'serious science and, like all real science, it is not light reading.'[24] Their intended target audience should have at least some scientific knowledge, but neither did the editors wish to 'frighten off the ordinary reader who has no biological background whatever.' They therefore provided an overview of the articles, their difficulty, as well as some suggestions for introductory readings; they also included a glossary at the end of the volume.[25]

There was no conflict in this combination of 'serious' and 'real' science on the one hand with the appeal to the 'ordinary reader' and 'layman' on the other for Abercrombie and Johnson. Talking about serious and real science implies that (over)simplification of the content was avoided, even though that would – at least initially – limit the size of the

[20] Maynard Smith 1997.
[21] Maynard Smith 1952, 128.
[22] Maynard Smith 1952, 129.
[23] Bellairs 2000, 26.
[24] Johnson and Abercrombie 1946, 7.
[25] The glossaries were turned into the *Penguin Dictionary of Biology* (Medawar 1980, 6).

audience. The editors were aware of this, but hoped that in the future, more and more people would have the necessary basic understanding of science, and biology in particular, to follow the arguments brought forward in *New Biology.* Indeed, such an audience 'is certain to grow enormously before long', and Abercrombie and Johnson 'hope [they] shall be fortunate in stimulating some readers to acquire the background necessary to follow the more difficult articles before they have done with *New Biology.*'[26] There is an overall optimism apparent in this introduction, an optimism that a periodical like *New Biology* would, over time, create and maintain a science-literate audience. Not ten years later, the Minister of Education appointed a committee to review adult education opportunities in Britain which concluded 'in relation to the community at large, adult education students represent a social and intellectual asset the loss of which would be deplorable'.[27] The report focused mainly on universities' activities and the Workers' Educational Association, but also adult education which took place via non-specialist science as presented in books, magazines, and museums, later joined by radio and television in audio and visual formats.[28] (Natural history museums had also been growing in popularity since the late 1920s,[29] and Maynard Smith himself visited the London Natural History Museum as a child before moving to the countryside.[30])

Maynard Smith was introduced to the editors by David Lack who, after hearing Maynard Smith talk at an ornithological meeting, arranged for the publication of 'Birds as aeroplanes'. This is important for two reasons. First, for Maynard Smith this was 'a welcome success'; he was encountering difficulties publishing work in which he was applying mathematics to biology.[31] 'Birds as aeroplanes' was accompanied by a short biography to establish his status as an expert, pointing to his careers as aircraft engineer and as lecturer at UCL.

> J. MAYNARD SMITH, B.A., B.SC., Assistant Lecturer in Zoology, University College, London. He worked for six years as an aircraft engineer before becoming a

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[26] Johnson and Abercrombie 1946, 7
[27] Anonymous 1954, 865.
[28] See Chapter 2 for science in the media.
[29] Rader and Cain 2014, 113.
[30] Maynard Smith 1985, 347.
[31] Kohn 2004, 214.

> student of zoology. At present working on the genetics of the fruitfly *Drosophila subobscura,* but occasionally finds time to return to problems of animal locomotion.[32]

Penguin's Pelican imprint had started adding author biographies around the 1940s, a necessity since at the time, many of their original works were 'mostly written by lesser-known experts'[33] – as Maynard Smith was at the time. An extended biography also featured on the back of Maynard Smith's first book, *The Theory of Evolution*. The addition of biographies to author's writings has been noted by Peter Bowler, referring to the Pelican series in particular; this 'innovation' usually stressed the author's qualifications and experiences, establishing their authority on the subject[34] and it was taken over for the *New Biology* series.

The second reason for Lack's importance in the context of Maynard Smith's entry into non-specialist science writing is Lack's own experience of writing popular science books which do not fit the diffusionist model. His *Life of the Robin* was first published in 1943 and re-published in 1953 as a Pelican paperback. Lack knew whom to approach at the publishers and what they were looking for. *The Life of the Robin* was both scientifically rigorous and readily accessible by combining 'scientific description and analysis with literary and historical references to the subjects discussed';[35] his popular science was as much science as it was literature. Lack's work fits the 'science as literature,' rather than 'science and literature,' approach to popular science.[36] With his later *Theory of Evolution*, Maynard Smith placed himself in the tradition of biologists like Lack who were writing books accessible to and read by both experts and non-experts in their fields. Adding "Further Reading" suggestions to his book, Maynard Smith lists Lack alongside Charles Darwin, Theodosius Dobzhansky, J.B.S. Haldane, Julian Huxley, Ernst Mayr, George Simpson, and others.[37] "Further Reading" suggestions were not part of the article Lack helped Maynard Smith publish in 1953, but in its focus on birds their common interest is obvious.

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[32] Anonymous 1953, 127. Maynard Smith published one paper on animal locomotion, together with R.J.G. Savage, in 1956 (Some locomotory adaptations in mammals. *Journal of the Linnean Society 42*(288), 603-622). In the archive, two folders titled "Locomotion" (JMSA Add MS 86769) contain reprints on animal locomotion until 1966.
[33] Bowler 2009, 266.
[34] Bowler 2009, 266.
[35] Anderson 2013, 25.
[36] O'Connor 2007.
[37] Maynard Smith 1953, 306.

2.2.2 'Birds as aeroplanes' (1953)

'Birds as aeroplanes' both took up and went beyond Maynard Smith's first paper. It aimed at describing and explaining the 'hope to gain new insight into animal flight by using the knowledge gained in the field of engineering.'[38] Maynard Smith discussed wings, control of direction and speed, types of unpowered flight (soaring and sailing), and finally the source of power for flight. The sections on wing and control of speed and flight direction are the ones based on his previous paper, extended with a schematic drawing and brief textual explanation of the '[f]orces acting on a stable and unstable aeroplane during flight'.[39] These add to the understanding of the aerodynamics of flight, introducing the reader to the importance of the centre of gravity, lifting force and downward force and the roles they play, for instance, in allowing slow flying speeds.

The next two sections are based on different research than that which had gone into the first paper and thus first sections. They are of particular interest and importance since they indicate two aspects of Maynard Smith's writing both in his non-specialist and specialist works. Firstly, he made use of animals familiar to his readers and secondly, he did not hold back on the mathematics underpinning the biology. When he discussed flight without the flapping of wings, he at first referred to vultures and to albatrosses, pointing out the differences in their wings and structures (illustrated by schematics, showing the two birds' silhouettes in flight in a bird's-eye perspective[40]). Vultures use columns of warm air to gain lift; they soar. Albatrosses, in contrast, rely on different horizontal wind velocities over sea; they sail. Following this Maynard Smith added an example from closer to home:

> A similar, though less extreme, contrast can be seen in this country between, say, a buzzard and a herring gull; it was in fact the sight of these two birds in the air at the same time, one inland and the other out to sea, which first drew my attention to this difference in structure, and led me to speculate on the reason for it.[41]

Replacing the exotic vulture and albatross with the familiar buzzard and herring gull helps Maynard Smith evoke a much clearer image in the mind of his audience. For today's public,

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38 Maynard Smith 1953, 64.
39 Maynard Smith 1953, 68.
40 Maynard Smith 1953, 71.
41 Maynard Smith 1953, 72. This section also shows that at heart, Maynard Smith was a naturalist. He could have gone to Oxford to continue his studies under the ethologist Niko Tinbergen, like some of his fellow undergraduates, but 'felt that he would be at a disadvantage in the field because of his poor eyesight' (Kohn 2004, 214).

these different birds are probably equally familiar, but before the proliferation of nature programmes on television, it is doubtful that many readers would have been able to conjure the image of an albatross or vulture, let alone one of these birds in the wild and in flight. Knowing the power of familiar examples, Maynard Smith would stay true to this way of presentation in his *Theory of Evolution:* 'Although I have not assumed any specialized knowledge in the reader, and *when possible have drawn my examples from familiar animals and plants*, I have not omitted any subjects merely because they are difficult.'[42]

The second feature of Maynard Smith's writing is his use of mathematics. As a trained engineer with mathematical intuition, he was not afraid of approaching biological problems mathematically. We have already seen that other biologists were less at ease with equations, which had resulted in the rejection of several of Maynard Smith's early papers. His first scientific publication had therefore not included any mathematics either, but 'Birds as aeroplanes' confronted its reader with three equations. In order to explain the soaring flight of vultures, Maynard Smith introduced the reader to the concept of "sinking speed" which needs to be lower than the upcurrent of air if the bird wants to stay airborne. The sinking speed 'is a function of the "span loading", i.e. $\frac{\text{weight}}{\text{wing span}}$.' In an added footnote, Maynard Smith even invited his '[m]athematically minded readers' to 'prove this statement':

> It follows from Equations 2 and 3 […], and from the fact that the mass of air which is deflected downwards by a gliding bird in unit time is proportional to the wing span x forward speed, and *not* to the wing area. The power available to maintain flight when gliding at constant speed in still air is equal to the weight x sinking speed.[43]

For everyone else he added, '[t]hose who do not like mathematical arguments are assured that the statement fits the observed facts.'

Equations 2 and 3 come from the next section of the paper, 'The source of power for flight.' This section is based on experiments conducted by John Maynard Smith and M.J. Davies. Using hover flies (*Syrphidae*), they set out to 'determine the power developed by an insect in flight.'[44] The results of that research were never published independently: 'We tried to publish that and never could. I was equally cross about that,' remembered Maynard

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[42] Maynard Smith 1958, 12 (emphasis added).
[43] Maynard Smith 1953, 72 (emphasis in original).
[44] Maynard Smith 1953, 75.

Smith in the late 1990s.[45] Besides finding its way into the *New Biology* piece, Maynard Smith presented his and Davies' research at a meeting at the Zoological Laboratory in Cambridge. The meeting had been organised by B. Hocking of the Department of Entomology in Edmonton, Canada. In September of that year, Hocking sent Maynard Smith the reports of the meetings which summarised the experiment and results as follows:

> Working with mounted syrphid flies, the velocity of the air jet below the hovering insect was measured by a method developed independently, but similar to that described by Hollick. Metaldehyde crystals were used in place of Lycopodium spores, and were photographed by flashbulb illumination. The mass of air passing through the wings per second (m) was then calculated by using the expression W = mv, where W is the weight of the insect, and v the velocity of the air. Power was then calculated from the expression P = 1/2m.v2, and the average value determined for several species was 0.009 h.p. per lb. of flight muscle. Using Wigglesworth's figures for the rate of sugar consumption in Drosophila, the efficiency was estimated at between 1 and 2 per cent.[46]

$W = mv$ and $P = \frac{1}{2}m.v^2$ are the equations that made it into 'Birds as aeroplanes' as Equation 2 and 3,[47] the ones from which the statement about the vultures' soaring flight derives. A diagram accompanied the account of the experiment, based on a photograph taken as described with a flashbulb (see Figure 2). As Maynard Smith remarked in a 1990 letter to *Nature* concerning the 'Flight of the bumblebee', '[t]he resulting photographs were fairly awful by modern standards.'[48] The comparison with the diagram makes the interpretation of the photograph easier; it is a fascinating reminder how research can be tied in with and be dependent on technology.[49]

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45 Maynard Smith 1997. There was interest in the results, as a letter to Maynard Smith shows: Warham to Maynard Smith, 24 May 1955. JMSA Add MS 86626.
46 Hocking to Maynard Smith, 30 September 1953. JMSA Add MS 86626.
47 Maynard Smith 1953, 76.
48 Maynard Smith 1990, 719.
49 Nowadays, high-speed videography and computational modelling allow for much more detailed study of the aerodynamics of insect flight (e.g. Sane 2003).

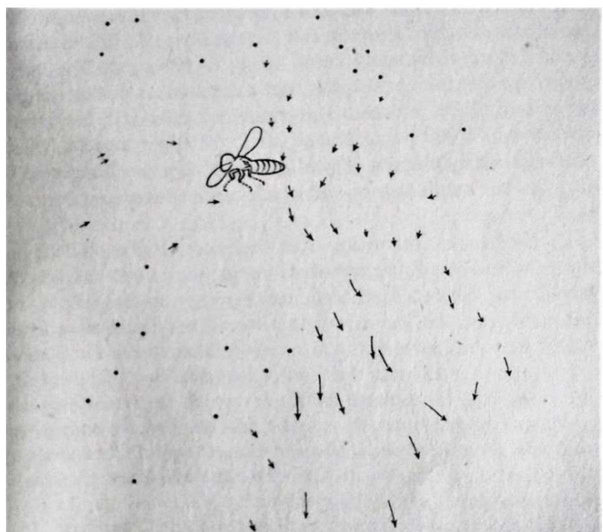

Fig. 3. Diagram of airflow round a fly held stationary. The arrows show the direction of airflow, and their length is approximately proportional to the velocity. Dots indicate stationary air.

Figure 2. Illustration (Maynard Smith 1953, 77), and the photograph it is based on (JMSA Add M 86626).

Towards the end of his paper Maynard Smith reminded the reader that amongst all the comparisons with aeroplanes, the products of human engineering and design, we must not forget that animals are adapted to their environment and functions because of natural selection and not designed for a purpose.[50] But biologists can learn from engineering – and use mathematics effectively along the way, as he proved. He would never lose the mathematical approach to biology and continue to trust in models, as he had learned in his years as an aircraft engineer.[51] Natural selection and adaptation would, in some form or other, always be at the centre for Maynard Smith's future work. His research would however draw less explicitly on his engineering background than it did during those first papers.

'Birds as aeroplanes' was a stepping stone for Maynard Smith and highlights some important elements. It allowed him to publish research he could not publish elsewhere – his work with Davis had been rejected earlier – and there seems to have been less hesitation or less strict rules about the inclusion of mathematics. But *New Biology* not only offered a platform for Maynard Smith, an early-career researcher, to get his ideas into the public domain. It also established him as an expert suited to communicating scientific ideas, placing him alongside reputable scientists publishing in the same journal and further setting up his credentials with the accompanying biographical entry. This expertise by association is repeated, more actively, through the "Further Readings" in *The Theory of Evolution*: Maynard Smith chose which works to include, linking this expertise to his.

The view that popularising scientists were damaging their career therefore does not hold in Maynard Smith's case. Bowler has already painted a more nuanced picture: the scientists who seem to have been derided for their popularising efforts – which includes Maynard Smith's mentor and fellow-publisher in *New Biology,* Haldane – were writing for the daily press. The scientific community was generally not objecting to scientists writing educational material of a more 'serious' nature. *New Biology* cannot be compared to the *Daily Worker* (another of Haldane's outlets), and '[p]rovided one kept such activity limited to a level where it still left plenty of time for research, [popularization] was welcomed rather than criticized by the majority of scientists'.[52] As Bernard Lightman has noted, despite continuities from the nineteenth century in terms of traditions which 'continue to shape the

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50 Maynard Smith 1953, 79.
51 Kohn 2004, 211.
52 Bowler 2006, 163.

way science is popularized and the way that current audiences consume it',[53] the increased professionalization of science did make a difference to popularization in terms of who wrote what and when, and how they were viewed by the scientific community. He echoes Bowler's analysis that '[e]minent scientists could retain the respect of their peers when they took on nonspecialist writing as long as they had made a substantial contribution to research at the same time'.[54] The important anomaly in the case of Maynard Smith is that in the 1950s he was not yet an eminent scientist. He had started establishing himself as a fruit fly geneticist, but the work he is best-remembered for, evolutionary game theory, was not done until the 1970s.

2.3 *The Theory of Evolution* (1958)

2.3.1 An ambitious project

After this first venture into science communication to a non-specialist audience, John Maynard Smith began a second, much more ambitious project only shortly after. On 16 February 1956, he signed a contract with the Penguin publishing house to deliver 'a literary work at present entitled: THEORIES OF EVOLUTION.'[55] His first deadline for 80,000 to 100,000 words was the 31 December of that year. The book was to be published in the Pelican imprint of Penguin. Pelicans, as the website designed for the series' relaunch in the twenty-first century explains, were 'aimed at the true lay reader' and 'combined intellectual authority with clear and accessible prose. As the first British publisher of intelligent non-fiction at a genuinely low price, Pelican became an informal university for generations of Britons.'[56] *The Spectator* covered Pelican in a 1938 piece on 'Books and the Public', explaining that it started out republishing books

> which, each in its own way, have helped make the intellectual history of this century; until now mere considerations of cost have placed them out of the reach of most people. That now they can be bought for 6d., that is for the price of a cheap cinema seat or a packet of cigarettes, is a fact of enormous importance in the struggle to overcome economic restrictions to knowledge; and it is one more indication of the

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[53] Lightman 2007, 498.
[54] Lightman 2007, 419.
[55] Memorandum of Agreement, 16 February 1956. JMSA Add MS 86759.
[56] 'The Pelican Story' 2017, https://www.pelicanbooks.com/about.

> hunger for information, for fact, for explanation, which exists unsatisfied at the present time.[57]

Later on, Pelican would publish original works too, like Maynard Smith's *Theory of Evolution*, a book project which was ambitious in two ways. First, it was to be the opening volume in a new series, the Pelican Biology Series. As such, it needed to whet the potential audience's appetite enough to buy the envisaged following volumes. Second, the editors and Maynard Smith set the bar high by wanting to cover everything – or nearly everything – relevant to the theory of evolution, which required knowledge in a variety of different fields of biology.[58]

The series was the brainchild of Michael Abercrombie and M.L. Johnson, the biologist and editor couple whom we have already met and who had introduced Maynard Smith to writing for a non-specialist audience. In 1953, the same year that they published 'Birds as aeroplanes' in their *New Biology* series, Abercrombie and Johnson had prepared a scheme for a series of books. They compared the conceived series to the Pelican History of England: the 'idea is to have, ultimately, a set of volumes covering substantially the whole range of biological sciences […] which people will buy with the feeling that they are getting a fairly systematic survey of the field.'[59] Already published books should not be duplicated in the series, and ten topics should be covered: nature of life, history of life, modern evolution theory, reproduction and life history, population and communities, parasitism, physiology of animals and plants, nervous system and behaviour, biology and human affairs, and lastly the discovery of modern biology. Concerning 'Modern Evolution Theory', the topic Maynard Smith was to write about, Abercrombie and Johnson summarised their thoughts as follows:

> There have been great advances recently, still substantially unknown to ordinary readers. It should contain something on modern systematics, and should be

[57] Anonymous 1938, also cited in Graham 2003, 60.
[58] He acknowledged as much in the preface (Maynard Smith 1958, 11).
[59] Abercrombie and Johnson, February 1953. Attached note to Memo from Glover to Lutyens, 6 May 1956. PA DM 1952/614 A/02.

> prefaced by a really serious discussion of the evidence for the occurrence of evolution.[60]

As with their *New Biology* series, Abercrombie and Johnson wanted to introduce non-specialists to a variety of important biological problems and thoughts. A book series would give them the space to explore these much more in depth, while keeping the emphasis on informative and useful writing. Highlighting the novelty of the scientific knowledge to be presented makes sense both considering their educative outlook and as a pitching strategy to the publishers and prospective authors. It is to be supposed that this, or something similar, was the starting point for discussions with Maynard Smith. He makes his first appearance in the editorial files in 1955. 'One of the prospective authors of the Pelican Biology Series,' wrote Abercrombie in August of that year, 'has now got to the state when he would like some security of tenure. This is Maynard Smith who is doing Evolution Theory'.[61] In the following letter, Abercrombie mentioned he had seen Maynard Smith's proposed outline, which he felt 'very pleased with':

> he seems to have thought his subject out afresh, and there seems to me little doubt that we shall get an excellent book from him. I know that it looks a bit formidable and perhaps a bit long; Smith[62], however, realises well enough the sort of audience he is writing for and I will keep him to it. He has merely written the headings out in rather technical language.[63]

It has to be said, however, that the headings given in the scheme almost all made it into the published book.[64] Maynard Smith used the correct terminology in both titles and text, not seeing any need to either dumb down or sensationalise his language for the benefit of the reader. On the contrary, his use of a matter-of-fact and clear style only emphasise the blurring of traditional boundaries found in the dominant view of science popularisation. Maynard Smith *was* aware of his audience, but he was also aware that this audience was multifaceted and engaged. Ultimately, *The Theory of Evolution* even bridged the categories of 'popular science book' and 'textbook', being advertised as the former and used as the latter.

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[60] Abercrombie and Johnson, February 1953. Attached note to Memo from Glover to Lutyens, 6 May 1956. PA DM 1952/614 A/02.
[61] Abercrombie to Glover, 25 August 1955. PA DM 1107/A433.
[62] Maynard Smith's last name was (and is) a source of confusion. It is always wise to check bibliographies or indexes for 'Smith, John Maynard' if nothing can be found under 'Maynard Smith, John'.
[63] Abercrombie to Glover, 19 September 1955. PA DM 1107/A433.
[64] Cf. THEORIES OF EVOLUTION by J. Maynard Smith (undated). PA DM 1107/A433.

Unsurprisingly, Maynard Smith took up this challenge. His own early science education was primarily based on reading popular science in Eton's school library: Haldane, Huxley, and Eddington, as well as Darwin, Einstein, and Marx.[65] Haldane's essay collection *Possible Worlds* particularly inspired him: 'The mixture of intellect and blasphemy was absolutely overwhelming and I've been attracted to that all the rest of my life.'[66] *Possible Worlds* collected essays which had appeared in a variety of newspapers and Haldane prefaced the collection, saying

> Many scientific workers believe that they should confine their publications to learned journals. I think, however, that the public has a right to know what is going on inside the laboratories, for some of which it pays.[67]

Haldane's essays covered a wide variety of issues, from enzymes and vitamins to cancer research, Kant and scientific thought, science and politics, eugenics, and theology. The goals and aims between Haldane's popular work and Maynard Smith's two initial works of science communication are thus different. Maynard Smith was more specifically focused on making aspects of research accessible and of presenting a coherent overview of evolutionary biology.[68] However, he shared his mentor's views on creating awareness for biological research and biological problems;[69] in later publications he commented more widely, and in interviews and debates did not shy away from commenting on his thoughts on, for instance, religion and creationism.[70]

Possible Worlds was aimed specifically at non-specialist audiences, but the other works Maynard Smith read as a student were not. He found books that oversimplified science dissatisfying, 'always [having] the feeling that difficulties were being slurred over'.[71] He wrote *The Theory of Evolution* in a style reminiscent of nineteenth-century popularisers, aiming at multiple audiences as well as twentieth-century biologists whose books could be and were

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65 Maynard Smith 1985, 347.
66 Maynard Smith 1988a, 128.
67 Haldane 1932, v.
68 There is another difference between Haldane and Maynard Smith: the latter's early-career status.
69 E.g. *The Problems of Biology* (1986). Like Haldane's, his own essay collection *Did Darwin Get It Right?* (1988), bringing together many of his essay reviews, deals with a greater variety of topics, though again more focused with evolution as a major theme.
70 E.g. Maynard Smith 1988a, Maynard Smith and Wright 2001. See also Chapter 5.
71 Maynard Smith 1958, 12.

read by both experts and non-experts, whether envisaged as having popularising potential or not.

As noted above, Maynard Smith added twelve authors to his "Further Reading" suggestions, books that had inspired him and others in their studies of evolution: Darwin, Huxley, Haldane, and Lack among them. Lack was partly inspired by Haldane's *Causes of Evolution*,[72] the work on Maynard Smith's list. Maynard Smith's suggested text by Lack was the work responsible for linking Darwin and his evolutionary theory to birds in the public eye – *Darwin's Finches* (1947). 'Just over a hundred years ago,' Lack wrote:

> Charles Darwin collected some dull-looking finches in the Galapagos Islands. They proved to be a new group of birds and, together with the giant tortoises and other Galapagos animals, they started a train of thought which culminated in the *Origin of Species*, and shook the world.[73]

This text made Lack world-famous and was a book 'by a writer today' to be 'class[ed] with the works of Darwin'.[74] This and the other books all on Maynard Smith's list 'made important and original contributions to our understanding of the causes of evolution.' And while they were for the most part, at least originally, aimed at professionals, Maynard Smith noted they could 'be read with profit by a layman'.[75] Other books on the list, Darwin's included, were consciously aimed at both the public and scientific colleagues.[76] Darwin was not the only nineteenth-century scientist using a book aimed at multiple audiences to promote a scientific, theoretical point; William Buckland's Bridgewater Treatise on geology addressed 'a range of intended audiences' and inspired 'a range of often unintended usages.' Importantly, '[w]riting the book for a wide audience gave Buckland licence to provide an overview of the subject which was of considerable importance for practitioners in his own scientific field'.[77]

Such an overview was also the aim of *The Theory of Evolution* and the Pelican Biology series. The book summarised ideas presented in the more professional literature of the "Further Readings," written in the hope that it 'will be of value to the non-specialist in

72 Lack 1973, 425.
73 Lack 1961, v.
74 Hardy 1973, 435.
75 Maynard Smith 1958, 306.
76 Lightman 2010, 7-9.
77 Topham 2009a, 17 & 18.

summarizing a set of ideas which, taken together, form perhaps the most important contribution yet made by biologists to our understanding of what the world is like and how it came to be like that'.[78] That it had potentially the same use for experts – similar to Buckland's work – became clear later in the writing process and was acknowledged by both Maynard Smith and the publisher.

2.3.2 The theory of evolution as told by John Maynard Smith

'The main purpose' of the Pelican Biology Series, of which *The Theory of Evolution* was to be the first volume, 'is to provide a systematic survey for the non-specialist of the present state of biological theory, of the background of ideas from which current research can be seen to be emerging.'[79] Maynard Smith himself had been introduced to evolution as a child – he had known about 'Darwin and so on' before coming across the work of Haldane and others in the school library. In the 1950s, after graduating from UCL and during his first years as a researcher – and thus while writing his 'Penguin' – he had been of the opinion 'that the problems of evolution had been by and large solved.' What was left for him 'was to learn about the solution.'[80]

This mindset is reflected in the change that the book's title underwent between the signing of the contract in 1956 and the publication in 1958.[81] Originally, it was called *Theories of Evolution*, published it was as *The Theory of Evolution*. Maynard Smith requested this change just several months before the publication. 'Although I agreed to write a book on "THEORIES OF EVOLUTION" I did not in fact discuss any theory of evolution other than Darwin's, so I would prefer the title "The Theory of Evolution".'[82] This one sentence captures Maynard Smith's view of evolution: there is only one. Lamarckism, the theory commonly summarised as the inheritance of acquired characters, does not go completely unmentioned, but it is worth pointing out that in 300 pages, it only appears three times. One of these is in combination with the Soviet botanist Trofim Lysenko. Lysenkoism – which reached its height in the 1940s – is briefly discussed under the subheading "Nature

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[78] Maynard Smith 1958, 11.
[79] Abercrombie 1958, 9.
[80] Maynard Smith 1988a, 129f.
[81] The first four chapters had already been drafted by 1955. Abercrombie to Glover, 19 September 1955. PA DM 1107/A433.
[82] Maynard Smith to Yettram, 11 February 1958. PA DM 1107/A433.

and Nurture" in the chapter on heredity. 'Lysenko himself believes that if an organism is reared in changed conditions, and in consequence develops along a different path, then, at least in some cases, its offspring also may tend to develop along the new path.'[83] This cautious phrasing mirrors the fact that at the time, Maynard Smith was not completely averse to Lysenkoist ideas. He had experimented with fruit flies to see if they might not show Lamarckian effects but his failure to find any was not too great a surprise.

In later years, August Weismann, a German biologist, became his 'second favourite evolutionist after Darwin'.[84] Weismann had insisted that what he called germ cells – those cells giving rise to a new organism – were unaffected by the environment; Lamarckian inheritance was thus impossible. This idea of a one-way street of influences was captured in Francis Crick's "Central Dogma", first explicitly stated in 1958 – the same year that Maynard Smith published his Penguin.

> *The Central Dogma*
>
> This states that once "information" has passed into protein *it cannot get out again*. In more detail, the transfer of information from nucleic acid to nucleic acid, or from nucleic acid to protein may be possible, but transfer from protein to protein, or from protein to nucleic acid is impossible.[85]

Like the discovery of the structure of DNA in 1953, this view is hardly touched upon in the first edition of Maynard Smith's book. The second edition, however, sees a revision of the heredity chapter and the Lamarck-Weismann argument, bringing in the work of Oswald Avery on DNA, Watson and Crick's discovery of the double-helix structure, and the Central Dogma.[86] The chapter title changed from "Heredity" to "Weismann, Lamarck, and the Central Dogma". Maynard Smith came to regard Lysenko as holding 'a manifestly false view about genetics'[87] – but he was careful to accept, point out and explain any exceptions to the rule, rare as they might be.[88] For instance, in lecture notes possibly dating from the 1990s and which discuss Weismann's book *The Evolution Theory*, we read under the heading

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[83] Maynard Smith 1958, 51.
[84] Kohn 2004, 219.
[85] Crick 1958, 153 (emphasis in original).
[86] Drake 2007, 7f. The second edition was published in 1966; Maynard Smith had suggested it in autumn 1964: 'I have been thinking I would like to do a second edition of "The Theory of Evolution", mainly to incorporate recent work in molecular biology, but also it would give me a chance to bring the work up to date in other ways.' Maynard Smith to Jacobs, 10 September 1964. PA DM 1007/A433.
[87] Maynard Smith 2001.
[88] Kohn 2004, 219.

"Weismann and MODERN BIOLOGY" that the 'Issue [is] not dead. The "Dual Inheritance System".'[89]

The allowance of exceptions and difficulties to Darwin's theory of evolution did not change the fact that the book presented one coherent view of it. The very first sentence reads, 'The main unifying idea in biology is Darwin's theory of evolution through natural selection.'[90] While the original title was inclusive, pluralistic, and referring to an undefined number of "theories", Maynard Smith changed it to a much more definitive, singular "the theory". This supports the overall perspective of the book, that 'recent advances in these various fields (of biology) […] can only be fitted together to tell a coherent story if the theory of natural selection is accepted.'[91] There might be exceptions to the rule, but the overall argument holds and is of major importance: 'natural selection as postulated by Darwin can explain the known facts of evolution.'[92]

Another, perhaps less explicit but connected reason for the change can be found in the general confusion between what scientists and what non-scientists associate with the word "theory". Studying the differences between scientific articles and their popularisations, Greg Myers points out that

> [w]hen one of these biologists calls evolution a theory, he means it is a central disciplinary concept enabling further thinking about life. When the *Times* calls it a theory, the connotation is that it is another airy idea dreamed up by scientists […].[93]

Using plural "theories" in the title of a book that was meant to depict a coherent story of a proper science would have only made matters worse or at the very least offered fuel to any sceptics of neo-Darwinism.

> By Darwinism is meant the idea that evolution is the result of natural selection. Neo-Darwinism adds to this idea a theory of heredity. In its most general form, the theory of heredity is Weismannism, that is, it is the theory that changes in the hereditary material are in some sense independent of changes in the body or "soma". In particular, the theory of heredity is Mendelian, that is, it assumes that

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[89] 'Weismann' (undated). JMSA Add MS 86837. Maynard Smith also notes, almost complainingly, that Weismann was a 'less reluctant' theoretical biologist than the 'shame-faced' Darwin: 'BUT – no algebra, only one diagram!'
[90] Maynard Smith 1958, 11.
[91] Maynard Smith 1958, 11.
[92] Maynard Smith 1958, 83.
[93] Myers 1990, 190.

> heredity is atomic, and obeys either Mendel's laws or some modification of them explicable in terms of the behaviour of chromosomes […].[94]

By using *The Theory,* singular, *of Evolution*, Maynard Smith succeeded in 'providing non-specialists with a systematic survey of the present state of biological theory'[95] and in presenting it with a strong neo-Darwinian interpretation of biological theory despite inclusive tendencies for exceptions to the rule.

Maynard Smith's strategy in providing his survey is to start with the basics – adaptation, the theory of natural selection, heredity, and variation. Having introduced the reader to these concepts and their role in evolutionary biology, he moved on to cover broader issues such as species, patterns of evolution, and the evolution of major groups. Throughout, he also discussed pros and cons of specific ideas and theories within evolutionary biology; thus chapter 16, for instance, examines Richard Goldschmidt's arguments against a neo-Darwinian view of speciation (the idea of 'hopeful monsters' with which Maynard Smith disagreed) before moving on to C.H. Waddington's notion of canalisation (which needed more research). Maynard Smith's neo-Darwinian conviction and training (courtesy of his mentor Haldane, co-founder of neo-Darwinism) are evident. He was a staunch supporter of adaptation and natural selection, and adaptation, for him, was *the* biological problem that needed solving.[96] In some form or other, he was to work on adaptation throughout his scientific career, often turning to problems that, at first sight, seemed not to be adaptive at all. ('Because it's a puzzle. You don't study things you understand; you study things that don't make sense.'[97]) Here is a strong example of popular and professional science interacting; Maynard Smith invites the public to engage with discussions which were still ongoing among evolutionary biologists and which, importantly, are not resolved even though he suggests his own interpretations of the validity of the ideas he presents.

Taken together with the "Further Reading" list, the invitation Maynard Smith extended allows a certain amount of agency for the reading audience (and again proves that we need a

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94 This definition was given by Maynard Smith at a conference on theoretical biology and first published in 1969. Cited here in Maynard Smith 1972, 82.
95 E.H. 1958, 572.
96 Maynard Smith 1995a; Kohn 2004, 225.
97 Kohn 2004, 225.

more nuanced notion of popular science in that, by communicating uncertainty, it undermines the notion of top-down dissemination of certain knowledge). They are being taken seriously rather than talked down to. From the beginning, Maynard Smith was not afraid of presenting his readers with difficult concepts, ideas, or with mathematics. As he points out in the preface, 'I have not omitted any subjects merely because they are difficult.' He was, however,

> aware that there is therefore a risk that some parts of this book will prove rather hard going. This is the most likely to be so in those sections which discuss the genetic aspects of evolution. […] I have tried to concentrate the more difficult genetic arguments into a few chapters (Chapters 5, 12, and parts of 13), which can be skipped by those with no taste for this kind of argument. But I hope that not too many readers will find this necessary.[98]

These chapters also include much of Maynard Smith's own research in genetics. He had been undertaking research in Helen Spurway's laboratory at UCL and by the end of the 1950s, he had published a dozen papers on *Drosophila* research. Fruit fly genetics had been famous since T.H. Morgan's "Fly Room" at Columbia University, and *Drosophila* species had proven to be very good for genetic research.[99] They have the advantage of being small enough to be stored in large quantities yet still large enough so that physical changes can be observed easily enough, they breed quickly and have large amounts of offspring, and the large chromosomes in their salivary glands are observable through the microscope.[100] Maynard Smith was lucky enough to be a good fly farmer – he managed to keep his flies alive.[101]

Maynard Smith worked with the European fruit fly *Drosophila subobscura*, and about half of his papers are the result of collaborations with either Sheila Maynard Smith, his wife, with Jean Clarke or with M.J. Hollingsworth. In one form or another, the works almost all deal with questions of adaptation and/or natural selection. One example is Maynard Smith and his colleagues' study of heterosis, or hybrid vigour. Vigour is defined as the presence of viability, rate of development, fertility, and longevity in an organism. 'Of these, all except rate of development are important components of fitness.' Rate of development is,

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98 Maynard Smith 1958, 12f.
99 See e.g. Sturtevant 1965/2003 on research done in the fly room.
100 Maynard Smith 1957, 85; Jennings 2011; 'Drosophila' 2016.
101 Kohn 2004, 215.

however, associated with the other three characters; 'individuals which develop rapidly tend to be fertile and long-lived.' A necessary condition for these characters to be used for the definition of vigour is that they cannot apply only to a part of the organism and that they 'must confer selective advantage in a wide range of environmental conditions.'[102] Hybrid vigour, then, describes the assumption that hybrid organisms – that is, organisms descended from genetically different parents – would have increased vigour over inbred organisms. In several papers, approaching the issue from different angles, the conclusion is that hybrid organisms do indeed seem to be more viable[103] and with a longer life expectancy[104]. Maynard Smith and Hollingsworth also found that 'slow development and infertility may result from homozygosity for different alleles or at different loci.'[105] All of these issues are of selective advantage as they increase fitness, that is, increased vigour brings with it increased numbers of offspring.

The fruit fly experiments done by Maynard Smith and his colleagues at UCL, as well as by Morgan and colleagues at Columbia University, and those of others, are covered in chapter 5 on "Artificial Selection: Some Experiments with Drosophila". Maynard Smith moves from giving the reader case studies of laboratory work – artificial selection – to showing if, and how, natural selection acts on populations in the wild:[106] while there is no direct translation of controlled laboratory experiments to nature in the wild, one can still learn from them. Firstly, *Drosophila* research has shed much light on general principles of heredity. Studies of bristle numbers in subsequent generations of fruit fly, artificially selected for either more or fewer bristles, have answered questions about the development of frequencies of individuals with different characters over time, about how closely relatives will resemble each other, and about what happens if artificial selection for one character is done to the extreme. Three conclusions could be drawn from the bristle studies:

(a) selection would at first lead to a rapid change in the population mean in either direction;

102 Clarke and Maynard Smith 1955, 172.
103 Maynard Smith and Maynard Smith 1954.
104 Clarke and Maynard Smith 1955.
105 Hollingsworth and Maynard Smith 1955. Homozygotes are offspring from genetically identical parents, where both father and mother would have the same allele, or form of a gene, such as *AA* (or *aa*). The offspring will then breed true, that is, all offspring of genetically identical parents will have the same genotype. A locus is the position of an allele or gene on the chromosome.
106 Maynard Smith 1958, 83.

(b) progress under selection would slow down, and finally stop, because there would no longer be any genetic variability for which we could select; and
(c) at this final stage, the population would be much less variable than the initial population.[107]

In other words, extreme selection leads to diminished genetic variability for selection to work on. This would also hold true for wild populations – unless there were some processes to bring about new variations to break the cycle. Thus Maynard Smith builds a bridge from the genetics-heavy chapter on selection to the chapter on "The Origins of New Variation". While there is no explicit talk of genetics as in the previous chapter, its links between natural selection and the need for new variations are unmissable if both chapters are read. Consequently, even if the reader might not have been able to follow the genetic arguments (completely) – Maynard Smith had included a six-step summary in plain text towards the end – the importance of the issues discussed becomes clear in combination with the explanation of how variations arise (and Maynard Smith did confine himself to genetic differences) and why they are important. As Brian Charlesworth has said, '[n]o one can claim to understand how evolution works without some basic understanding of classical population genetics.'[108]

Maynard Smith also brought home his main argument: that evolutionary changes are *adaptive*, not accidental.[109] Genetic differences arise by accident – say, by mutation – and are indeed often harmful. Natural selection, however, acts on these changes and thus brings about 'continuous, adaptive, and seemingly purposive evolutionary changes.'[110]

We have seen a first emphasis on natural selection – the unifying principle for the book and the theory – in Maynard Smith's discussion of genetics, but it is naturally evident from the very beginning of the book. Already in chapter 2, "The Theory of Natural Selection", the reader is asked to follow a mathematical model of a mouse population. Maynard Smith introduces us to a population of 100 dark and 100 light-coloured mice. Over the next couple of pages, owls, disease, and other natural forces diminish subsequent generations of

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107 Maynard Smith 1958, 89.
108 Charlesworth 2015, 667.
109 Maynard Smith 1958, 120. See also Drake 2007, 6.
110 Maynard Smith 1958, 120.

the original population; the survivors then breed with each other. (We therefore have a simplified model population – breeding occurs once per cycle only, so that the numbers are easier to follow). The point Maynard Smith is making is the following: the owls eat more light-coloured mice which show up on the ground more easily, while the other forces kill an equal number of mice in both populations irrespective of coat colour. Thus, the model explains the effects of natural selection on a population.[111] The example explains Haldane's notion of "intensity of selection", which gives 'a measure of how many lives are lost because not all individuals are as well adapted as are the fittest members of the population.'[112] At the same time, and not dissimilar to the laboratory experiments with *Drosophila*, it functions as a way to introduce large concepts of natural selection, with examples of natural selection working on wild selection (e.g. the peppered moth and the land snail) to follow in later chapters. In both cases, with the fruit flies and the mice, Maynard Smith first introduced his audience to a version in which parameters and variables can be controlled. Notably, this does not constitute a simplification of "real science"; it is instead a regular practice among scientists. After understanding concepts or processes based on laboratory experiments or mathematical models, it is possible to apply these practically or theoretically to populations in the wild. Similarly, Maynard Smith moved from these simplified examples to research carried out in the field, reintroduced the complications of uncontrolled variables and general complexity, to show that natural selection does work in the wild, and how.

Population of newborn mice	100 dark	100 light
Killed by owls	10	40
Survivors	90 dark	60 light
⅔ mortality due to other factors	60	40
Breeding population	30 dark	20 light
	25 breeding pairs	
Average of 8 offspring per pair		
If colour due to a single Mendelian factor	200 newborn mice in the next generation	
	116 dark	84 light

Figure 3. Illustrating Haldane's "intensity of selection" (Maynard Smith 1958, 36)

[111] Maynard Smith 1958, 34ff.
[112] Maynard Smith 1958, 36.

The population model also brings in mathematics. There is a notion that equations in popular science books are a serious problem for sales, a notion that comes from Stephen Hawking's *A Brief History of Time*. His editor is said to have told him,

> Look at it this way, Steve – every equation will halve your sales. […] when people look at a book in a shop, they just flick through to decide if they want to read it. You've got equations on practically every page. When they look at this, they'll say, 'This book's got sums in it,' and put it back on the shelf.[113]

Maynard Smith, of course, did not have equations on every page, but we saw in the previous sections on Maynard Smith's aerodynamics research that, first, he did have trouble publishing because of mathematics and that second, he was nonetheless not afraid to make use of equations. Mathematics reappears 'at the risk of irritating readers who dislike even the simplest algebra' in Maynard Smith's discussion of the Hardy-Weinberg ratio.[114] For Maynard Smith, this law was too important to ignore. (For years, his course on population genetics started with it.[115]) The formula mathematically explains why gene proportions, or frequencies of genotypes, stay stable in a population. It is a 'general rule that holds when there are different, indeed varying, proportions of alleles floating around in a population.'[116] Maynard Smith used it to throw some light on natural selection in wild populations, and in particular on the question of industrial melanism, the peppered moths in Kettlewell's research. As is the case with the model population of mice, a figure – in this case a table – is added to illustrate the mathematics and directly incorporated into the text. It was formulated, independently, by the mathematician G.H. Hardy and the physicist Wilhelm Weinberg in 1908.[117] Maynard Smith's explanation of the law is an example of his clear use of language.

> Suppose that there are two alleles, A and a, at a particular locus, and that their frequencies in a population are p and q respectively, where $p + q = 1$. If, for example, A were nine times as common in the population as a, then p would be 0.9 and q 0.1. The probability that an individual receives the allele A from his father is then p. If mating is random, there is a similar chance p that he also receives an allele A from his mother. Hence the chance of an individual receiving A from both parents is $p \times p = p^2$, which is therefore the proportion of A/A individuals in the

113 White and Gribbin 2002, 223. This view appears to have shifted given the fact that a popular science book wholly dedicated to equations exists (*It Must Be Beautiful*) with a chapter by Maynard Smith (2002).
114 Maynard Smith 1958, 125.
115 Maynard Smith 1990.
116 Depew and Weber 1995, 232.
117 Sturtevant 1965/2001, 108. See also Ruse 2006, 171f.

> population. By an exactly similar argument, the proportion of *a/a* individuals is q^2, and of *A/a* (or *a/A*) individuals is *2pq*.[118]

To Hardy, this generalised formulation of how the Mendelian scheme would affect populations of interbreeding individuals, had 'seemed so self-evident that he commented: "… I should have expected the very simple point which I wish to make to have been familiar to biologists."' But, as A.H. Sturtevant points out, '[t]hat it was not familiar is shown by the fact that it had been seriously suggested that dominant genes would automatically increase in frequency in mixed populations.'[119] Maynard Smith would have shared Hardy's feelings about the mathematical incompetence of some biologists. For him, mathematics had played a vital role before, and definitely since the 1950s, in biology, evolutionary biology in particular. 'I think that mathematics is crucial for further progress in evolutionary biology. […] Mathematics without natural history is sterile, but natural history without mathematics is muddled.'[120] This was indeed an insight that Maynard Smith had come to even before he started studying zoology at UCL. 'I read recently Huxley's "Evolution, the new [*sic*] synthesis", and there seemed to be plenty of scope for a mathematical approach to the subject of natural selection, the origin of species, and so on.'[121]

2.4 In context: two centenaries and the modern synthesis

2.4.1 The Darwin-Wallace essays (1858) and *The Origin of Species* (1859)

The date of publication for *The Theory of Evolution* did not come about by chance. 1958 marked the centenary of the Darwin-Wallace paper, the joint announcement of the ideas of Charles Darwin and Alfred Russell Wallace on evolution, and natural selection as its mechanism. Instigated by Charles Lyell and Joseph Hooker, the reading of the two essays took place at the Linnean Society in London on 1 July 1858.[122] These 'epoch-making'

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118 Maynard Smith 1958, 125.
119 Sturtevant 1965/2001, 107f; see also Depew and Weber 1995, 232f.
120 Maynard Smith 1982b.
121 Maynard Smith to Haldane, 6 October 1947. JBSHP HALDANE/5/2/4/144.
122 Huxley 1958, 4.

essays,[123] published afterwards in the Society's journal, were followed in 1859 by the publication of Darwin's *The Origin of Species by Means of Natural Selection.* Several reviewers naturally picked up on this, and the publishers were fully aware of the significance of the year too. 'It is appropriate that the first volume of Pelican Biology, coinciding with the Darwin-Wallace centenary, should be about the theory of how evolution occurs, one of the aspects of scientific knowledge that biologists can take most pride in,' wrote Michael Abercrombie in the editorial foreword.[124] *The Lancet* called it 'quite one of the best' books on evolution out there;[125] Nora Barlow, Darwin's granddaughter, praised it as a 'feat of learned compression'.[126]

Maynard Smith and his publishers were not the only ones using the two centenaries in 1958 and 1959 to their advantage. The number of books – biographies, essay collections, reprints of Darwin's works, and more – that were published during those two years is astounding. Donald Fleming, whom we have briefly met in the introduction to this chapter, classed the publications coming onto the market during the centenary, as firstly reprints and republications of original works, secondly background publications, and thirdly 'scientific estimates of Darwin from the perspective of the present.'[127] Maynard Smith's work naturally falls into the latter and is briefly mentioned as such.[128] The interesting, and perhaps striking, thing that Fleming noted is that many of the 1958-1959 publications are not quite as positive about Darwin and his theory as one might expect:

> the thing that leaps to the eye in reading the supposedly celebratory publications of a centennial year is that many of the writings display a distinct animus against Darwin or natural selection or both and that still others if taken at face value would diminish his stature.[129]

One underlying problem, Fleming complained, was a general misunderstanding of what Darwin actually achieved; books diminished his prominence in creating acceptance for evolution because they failed to understand that it was not the idea of evolution, but the idea of natural selection as a mechanism for evolution, which was so ground-breaking in

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123 Menon 1958, 233.
124 Abercrombie 1958, 9.
125 Anonymous 1958, 781.
126 Barlow 1959, 181.
127 Fleming 1959.
128 Fleming 1959, 438; see also Loewenberg 1959, 530.
129 Fleming 1959, 439.

Darwin's work. There was a sense in which the scientists – next to Maynard Smith's book, Fleming referred to the edited volume *A Century of Darwin*,[130] to a revised edition of R.A. Fisher's *The Genetical Theory of Natural Selection*, H.B.D. Kettlewell's research on peppered moths,[131] and Julian Huxley's *The Modern Synthesis* – did better justice to Darwin in placing him and his research historically than many historians. The trend is also visible in journal articles like Huxley's 'The emergence of Darwinism' or P.K. Menon's 'Darwinism through hundred years' (both 1958). As Menon said, echoing the central argument of *The Theory of Evolution*:

> To those who accepted it (Darwin's data as proofs and natural selection as causation for evolution), it provided a unifying concept in the light of which organisms ceased to be isolated entities, and came to be understood as part of the single flux of life continually changing with the changing world. Darwin gave Biology an intelligible background and made it logically comprehensible.[132]

Fleming was not the only reviewer of centennial literature to find that it was 'not entirely affirmative.'[133] Bert Loewenberg, also writing in 1959, went even further, saying that there was 'an angry stress, petulant, often carping and frequently ungenerous. A trend is already discernible, a trend which belittles Darwin, demeans his character and denigrates natural selection.'[134] While he admitted that 'natural selection is more complicated in 1959 than it was in 1859,' it 'remains natural selection. More importantly, it remains Darwin's.'[135] Like Fleming, he ultimately had to conclude that

> biologists in this instance are better historians than the professionals. They have not only succeeded in summarizing the evidence with a clarity rare among the technically expert, but they have analysed the data in the perspective of significance.[136]

Maynard Smith's volume was one of those deserving the 'centennial laurels' that Fleming and Loewenberg awarded the biologist writers. He gave a veritable overview of both seminal and recent state-of-the art research, in effect reviewing the entire field of

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130 Maynard Smith contributed the chapter on sexual selection to this 'model volume', full of essays written 'with special erudition and historical poise'. Maynard Smith's article particularly 'match[ed] these high standards' (Loewenberg 1959, 530).
131 Kettlewell's work also features in *The Theory of Evolution*.
132 Menon 1958, 233.
133 Loewenberg 1959, 526.
134 Loewenberg 1959, 526f.
135 Loewenberg 1959, 528.
136 Loewenberg 1959, 529.

evolutionary biology as far as possible. This is a feat that has stood unrivalled at least until the 1990s, when Maynard Smith wrote in the introduction to the 1993 re-issue that there still 'is no other account of evolutionary biology available which is at the same time written for a non-professional readership, and which covers the whole field'.[137]

By surveying the field as he did, Maynard Smith achieved two things. Not only did he place Darwin and his theory of natural selection scientifically and historically within "science" as a professional realm defined by theories like those in the model science physics, acting as a biologist cum historian of biology. He also managed to write a book that proved useful to both the non-specialist and the specialist. It might have been aimed, as a Pelican, at the intellectually curious British public (and soon, the American public, and after translations, non-English speaking audiences). But when the book was in the last stages before publication, Maynard Smith realised that he could make it appeal equally to professional biologists – by including a reference list.

> My original intention was to give no references, since the book is intended for laymen who have little access to scientific journals. I have given a brief list of books for further reading, and have also given the names of workers responsible for particular discoveries in the text, but without references. My reason for giving names was that it gives the reader the idea that science is something done by chaps, and not revealed from above – but the names would also make it easier for a professional biologist to trace the actual reference.[138]

Penguin agreed: 'anything that can make the book useful to the biologist proper as well as to the layman is all to the good.'[139]

This multi-layered audience initiated by Maynard Smith challenges the role of the populariser in the Fleckian and diffusionist sense. Both perspectives argue that the migration of ideas between groups defined by level of expertise requires that popular knowledge is translated, simplified, even reified, expert knowledge. The process of making knowledge more accessible includes a removal from the uncertainties of scientific research into a world of '*[c]ertainty, simplicity, vividness*'.[140] Maynard Smith however explicitly did not

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[137] Maynard Smith 1993a, 1.
[138] Maynard Smith to Glover, 21 March 1958. PA DM 1107/A433.
[139] Glover to Maynard Smith, 26 March 1958. PA DM 1107/A433.
[140] Fleck 1979, 115 (emphasis in original); see also Brorson and Andersen 2001.

omit details or difficulties while still addressing both 'true laypeople' and biologists with varying levels and areas of expertise.

Even for evolutionary biologists, the book was of value. Evolutionary biology, as *The Theory of Evolution* aptly shows, is studied in various forms and fields: genetics, ethology, physiology, palaeontology, embryology. No one could be an expert in each of these fields: '[e]ven the most specialized expert owes [...] many concepts, many comparisons, and even his general viewpoint' to popular science.[141] Maynard Smith's text bridges both disciplines and levels of expertise. In doing so, he brought a large body of knowledge into circulation. The inclusion of scientific reference lists blurs the boundaries between popular science writing and science writing aimed at professionals, like handbooks and textbooks. Indeed, not only Maynard Smith himself used *The Theory of Evolution* for teaching; other scientists and students have found it helpful; textbook writers quoted it, and several universities used it as course textbooks.[142]

Maynard Smith and the publisher's intention to make the book useful for both specialists and non-specialists was realised in the audiences and their use of *The Theory of Evolution.* The text's inclusion within the classroom meant the text reached those at the transition from non-expert to expert. This multiplicity of intended audiences mirrors the practices of nineteenth-century science writers, including Darwin himself. Evolutionary biology and other specific fields have used Darwin as an icon and role model. The aforementioned discontent of reviewers Fleming and Loewenberg of centennial era literature points to an even larger issue than simple failure to properly represent Darwin's theory scientifically and historically. Evolutionary biology as a field was still emerging as a scientific discipline. As a burgeoning discipline, evolutionary biology needed Darwin's work as their unifying theory to validate its professional status. Since Darwin's contribution, biologists had worked towards getting recognition as scientists rather than amateurs, trying to rid "evolution" of an association with values and metaphysics and planting it into the

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141 Fleck 1979, 112

142 On teaching, see Maynard Smith to MacKeith, 4 September 1973, DM 1107/A433; on finding it helpful, see Sandon to Lutyens, 3 October 1959, DM 1952/614 A.02, PA. On textbook writers, see Stevick and Colver to Siddall, 10 May 1961, and Haagen-Smit to Siddall, 6 June 1963; Young to Ferguson, 18 July 1962; and Smith to Penguin Books, 26 July 1965, DM 1107/A433, PA. On course textbooks, see Ferraguti to Maynard Smith, 18 April 1983, JMSA Add MS 86575; see also Toro and Santos 2004, 30.

realm of the objective natural sciences. As the Centennial Celebration in America, at the University of Chicago, demonstrated, for evolutionary biologists 'evolution by means of natural selection […] had become a fact'.[143]

Betty Smocovitis has studied the celebrations at Chicago in detail. She notes that at those panels organised during the festivities which directly discussed evolution, 'the supremacy of natural selection was a dominant theme […], with panelists agreeing that genetical understanding of evolutionary mechanisms was leading to major advances.'[144] The Darwin anniversary had been organised by and for evolutionary biologists; it served both as a reassessment of recent developments and a means to consolidate and reach out to a general audience. Some of the aims were thus similar to those of *The Theory of Evolution*. The difference in the medium is noticeable however. While Maynard Smith gave both a general introduction and discussion of both seminal and recent research, the panel discussions were apathetic. The presentations focused mostly on the state of the art and hardly touched on frontier research, in part because of the attempt to survey the known facts of the field, and because it was felt that the heterogeneous audiences necessitated avoiding too much technical detail.[145] It is easier to get into the difficult and technical details in a 300-page book, when the readers have the luxury to follow the arguments at their own speed. A short presentation in front of a mixed crowd is more limited in the choice of content and complexity. Still, both the book and the celebrations in Chicago were science communications with similar aims: they give an overview of core issues of evolutionary biology to an inclusive audience, discuss a variety of themes and emphasise unity and the factual nature of natural selection.

At the same time, the celebrations were 'part of an historical process of constructing disciplinary identities for evolutionary biologists and building a coherent identity for the collective community of scientists.'[146] These structures were only forming in the first half of the twentieth century. It is perhaps telling that as a student at Eton, Maynard Smith himself had been unaware that one could make a living as a biologist. That had been one of the reasons why he had decided to read engineering instead of following his passion in natural

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143 Smocovitis 1999, 279.
144 Smocovitis 1999, 298.
145 Smocovitis 1999, 299.
146 Smocovitis 1999, 321.

history.[147] It took the efforts of many scientists to create umbrella-organisations, to found journals, and to gather students to professionalise and unify evolutionary biology.[148]

2.4.2 The modern synthesis in the late 1950s

As pointed out above, evolutionary biologists at the Darwin Centennial Celebration at the University of Chicago had presented a relatively united front by the end of the 1950s. This left at least some attendees wary of a rising orthodoxy, but it implied that evolutionary biology was no longer 'a good topic for the Sunday supplements of newspapers' because it had become a professional science. The move from Darwin and Wallace's original formulations to a science worthy of departmental representation, funding, journals, students, and general recognition by other sciences had been on a bumpy road, and the journey was in fact not finished in 1959. *The Theory of Evolution* needed two revisions to keep up to date, and a lengthy introduction recounting the developments between 1975 and 1993. But by 1933 evolutionary biology had already reached the essential milestone of becoming a unified and empirical science that since then has been added to and expanded.[149]

The history of the modern synthesis started around the 1920s. After the rediscovery of Mendel's work in 1900, the geneticists (Mendelians) and selectionists (Darwinians) appeared to be at odds with each other. In the 1930s, however, a group of biologists emerged who became known as the architects of the modern synthesis, effectively combining the two approaches. The most prominent names are Maynard Smith's mentor Haldane, R.A. Fisher and the American Sewall Wright – all population geneticists.[150] They adopted 'methodologies from the physical sciences to make evolution a more positive science. In so doing they constructed a unified and autonomous science of biology. "Modernizing" evolution, they also preserved the naturalistic, Darwinian tradition that had gone into decline.'[151] They were followed by other synthetic theorists working on and with these neo-

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[147] Maynard Smith 1996 (talk at Newgenics symposium at the London School of Economics). JMSA (uncatalogued).
[148] Smocovitis 1992; Ruse 1999.
[149] Smocovitis 1992, 55.
[150] Depew and Weber (1995) add Sergei Chetverikov to that list. From the late 1930s, prominent biologists working in the synthesis period were also Ernst Mayr, Theodosius Dobzhansky, and George Gaylord Simpson, playing a 'central role in promoting cooperation and organizing evolutionary studies' (Cain 1993, 2).
[151] Smocovitis 1992, 17.

Darwinian ideas. Biologists like Theodosius Dobzhansky, Ernst Mayr, George Gaylord Simpson, or Huxley at the same time desired to professionalise evolutionary biology and to create a proper academic discipline in which they and others could work.[152] These biologists were, as Michael Ruse puts it,

> under the spell of a metavalue, in the sense of something about rather than within science. The theorists wanted to move out of the museums and into the universities and to have all of the privileges and benefits of real researchers. They wanted their science to advance to the point where objectivity is a realizable aim.[153]

Mathematics, in particular mathematical modelling, was one means to place evolutionary biology onto a more objective footing, introducing ways to measure and test natural selection; indeed, Haldane, Fisher, and Wright were looking to the physical sciences for inspiration.[154] The Hardy-Weinberg equilibrium principle – the one that Maynard Smith felt was too important to spare his readers some 'simplest algebra' – was one of those mechanisms which helped shape the body of evolutionary biology in a manner similar to that of physics. As Sheppard said,

> [t]he great advances in understanding the process of evolution, made during the last thirty years, have been a direct result of the mathematical approach to the problem adopted by R.A. Fisher, J.B.S. Haldane, Sewall Wright, and others…[155]

Maynard Smith's own involvement with and support for mathematics was an outcome of his previous training as an engineer,[156] but his mathematical intuition had been evident from his school days onward.[157] But learning from and working under and with Haldane, one of the original population geneticists, had left their mark as well. 'I think a whole generation *was* influenced by his (Haldane's) way of thinking,' Maynard Smith once said, adding, 'I've spent my life imitating Haldane.'[158]

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152 Huxley, though, was less of an active researcher and more of a synthesiser of ideas (e.g. Ruse 1999). Cain describes him as an 'ideas man' which is 'not meant as criticism; rather, I mean to highlight Huxley's role as enthusiast and visionary—more consultant and adviser than architect, engineer or builder' (Cain 2010, 360).
153 Ruse 1999, 119.
154 Smocovitis 1992, 20-22.
155 Sheppard 1954, cited in Provine 1989, 478.
156 Maynard Smith to Haldane, 6 October 1947. JBSHP HALDANE/5/2/4/144.
157 Kohn 2004, 201f.
158 Maynard Smith 1988a, 128.

Maynard Smith was thus one of the generation of evolutionary biologists who could build on the work of the architects and builders of the modern synthesis. At the same time, the rejection of his early works showed that mathematics was not yet fully integrated into biology. He would eventually publish his first textbook for undergraduates, *Mathematical Ideas in Biology*, to 'introduce biologists from a broad spectrum of the subject to the use of mathematical modelling'; the book was 'an instant success for students and teachers alike'.[159] Maynard Smith's Penguin was equally successful though with a more inclusive audience of people outside of academia. It is consequently in the tradition of evolutionary biologists like Dobzhansky, Mayr, Huxley, and Haldane, who all communicated their and their field's ideas to a wider audience of non-specialists. It is also part of the effort to promote evolutionary biology as a science. A reviewer of *The Theory of Evolution* remarked that its title is very exact; it does what it sets out to do. 'Both the author and the publisher are to be praised for a book which helps to bring the scriptures of Wallace and Darwin from the realm of tropical visions supported by the dry bones of contention into the realm of science as both Harvey and Newton understood that term.'[160] A decade later, in 1969, Maynard Smith would feel justified to say that 'only in the study of evolution is there a body of biological theory in any way comparable to the theories of physics.'[161]

By bringing the theory of evolution by natural selection into the realm of science, Maynard Smith also managed to bring his readers into the realm of evolutionary biology. *The Theory of Evolution* 'was my first introduction to John Maynard Smith and one of my first introductions to evolution,' wrote Richard Dawkins, an appreciation shared by many others.[162] It is fitting that a book which introduced so many to the theory of evolution, Maynard Smith's area of research, should have introduced us to Maynard Smith's working life. From the very beginning of his career there was an emphasis on science communication. The recent efforts in re-conceptualising popular science become pertinent considering his insistence *not* to 'popularise': there is no omitting of difficulties, no sensationalising or dumbing down either of his topic or his language. Maynard Smith relied on clear and patient language to guide the reader through both the easily graspable and the

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[159] Charlesworth and Harvey 2005, 258.
[160] MacConaill 1959, 200.
[161] Cited in Maynard Smith 1972, 82; see also Smocovitis 1992, 55.
[162] Dawkins 1993, xi; Harper 2004; Partridge 2004; Charlesworth and Harvey 2005, 258.

more difficult aspects of evolutionary biology. 'You can hear his clear, logical, patient tones on every page. Not least, there is a total absence of pretentious languaging-up. Like Darwin, Maynard Smith knows that his story is intrinsically interesting enough and important enough to need no more than clear, patient, honest exposition.'[163] The same is apparent in the book's illustrations whose simplicity had been suggested by Maynard Smith: simple line drawings were enough to get his arguments across.[164]

This strategy paid off. The few reviews that are available, ranging from one-sentence mentions to more extensive discussions, are all positive.[165] The reviewers recommended Maynard Smith's clarity,[166] the scope of the book without losing its thread,[167] and – one thing that had been very important to the author – they highlighted that Maynard Smith was not talking down to the reader.[168] (Only one reviewer pointed out minor issues with the overall presentation: 'The glossary is not a true glossary but a dictionary.'[169]) In consequence, *The Theory of Evolution* was reprinted numerous times and went through two revisions, the first in 1966, the second in 1975. In 1993, Canto reprinted the book with a new foreword by Dawkins and a long introduction by Maynard Smith, explaining the developments in the field since the last revision. Since its first print run it has been translated into at least five languages: a French translation was commissioned as early as 1962.[170] There are three Italian translations I could find, a recent Turkish translation of the Canto edition, and two Spanish translations (the review in *Arbor* from 1986 discusses the translation of the third English edition and mentions a previous translation, but does not specify whether it is of the first or second English edition). The Penguin archive also

163 Dawkins 1993, xv.
164 Glover to Maynard Smith, 23 May 1957. PA DM 1107/A433.
165 The following journals mention the book in their 'Books Received' section: *Science, New Series 128*(3328) (October 1958), 836; *Philosophy 33*(127) (October 1958), 375-378; *British Journal of Psychology 50*(1) (1 February 1959), 88; *Isis 50*(2) (June 1959), 188-190; *CrossCurrents 9*(4) (Fall 1959). It also featured as a received book in *The New York Times*, 12 October 1958, p.BR35 and *The Manchester Guardian*, 29 July 1958, p.4 mentions it in its "Recommended paperback" section.
166 Anonymous 1958, 781.
167 Erk 1961, 211.
168 Barlow 1959, 181.
169 MacConaill 1959, 200.
170 Young to Maynard Smith, 28 February 1962. JMSA Add MS 86759.

mentions that a Portuguese translation was in the works in 1962, and that is was published in Portuguese again in 1965.[171]*)*

The Canto edition both builds on and confirms the book's and its author's status. Dawkins – who knew Maynard Smith and who will return more prominently later – labels Maynard Smith as 'one of today's leading Darwinians' in his introduction[172] and points out the following:

> It is a measure both of the brilliance of the book and the endurance of the neo-Darwinian synthesis itself that the 1975 text can stand its ground without revision today. There have, of course, been exciting new developments in the field. It would be worrying if there had not, and they are discussed in his (Maynard Smith's) new Introduction. But the fundamental ideas and the great bulk of the detailed assertions of the original book remain as important and as true as ever.[173]

It remains to be said that the Pelican Biology Series and *The Theory of Evolution*, this two-part ambition, was only partly successful. While *The Theory of Evolution* 'is the best general introduction on the subject now available',[174] the series it was supposed to be the first volume of never materialised. Maynard Smith's book, as we have seen, went through several reprints and three editions. It is quoted by textbooks[175] and, as part of the Pelican family and the planned Biology Series, has been 'found so useful in the past for my own use and for students', as H. Sandon of the Department of Zoology of the University of Karthoum wrote to Penguin's Science Editor David Lutyens.[176] Within Penguin, it was suggested in 1960 to let *The Theory of Evolution* 'be among our first special reprints at a higher price[.] It is an excellent book, and if it were really pushed could become a standard school text book.'[177]

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171 Young to Maynard Smith, 22 March 1962, and Proud to Maynard Smith, 31 March 1965. PA DM 1107/A433.
172 Dawkins 1993, xiv.
173 Dawkins 1993, xv.
174 Dawkins 1993, xvi.
175 Stevick and Colver to Siddall, 10 May 1961 and Haagen-Smit to Siddall, 6 June 1963; Smith to Penguin Books Ltd., 26 July 1965. Maynard Smith also wanted to use his book as text for a course in ecology while he was teaching at Berkeley. It turned out however that the book was a bit of a 'collectors [*sic*] item this summer in California.' Maynard Smith to MacKeith, 4 September 1973. All PA DM 1107/A433.
176 Sandon to Lutyens, 3 October 1959. PA DM 1952/614 A/02.
177 Memo from Penguin Books Ltd., from WDL to PBH, 23 February 1960. PA DM 1107/A433.

Yet concerning the Biology Series, Maynard Smith proposed to the editor Bill MacKeith during the planning of his book's third edition:

> I wonder whether we might not drop the introduction by Michael Abercrombie, I don't imagine he would mind. When he wrote it, my book was to be part of a series which never materialized, consequently the introduction reads rather oddly.[178]

Why exactly the series did not happen is unclear from the archival material. Included in the editorial files is a list of twelve titles, mostly already with author suggestions, of which only two others got published (with changed titles). Following Maynard Smith's book was to be *The Course of Evolution* by F.H.T. Rhodes (in press at the time the list was compiled), and after that, *Living Mechanism: Green Plants*, to be written by G.E. Fogg and to be published in 1961.[179] Rhodes' book was ultimately published in 1962 as *The Evolution of Life*, and reprinted in the United States the following year. But in the introduction written in 1959, Rhodes did not mention *The Theory of Evolution*, nor did he refer to the Pelican Biology Series more generally. The only evidence of these origins is in Rhodes's acknowledgement that the book was written 'at the invitation of Profesor [*sic*] Michael Abercrombie', to whom he was 'most grateful for his help and interest.'[180] By the time a third edition is issued – and possibly already for the second edition – a Penguin form to be filled out with the details of the work gives "Pelican" as series title. The field for "sub-series" is crossed out.[181]

2.5 Conclusion

In this chapter we have followed John Maynard Smith in his first steps into his working life and into science communication. His first work, 'Birds as aeroplanes', bridges his move from aircraft engineering to biology and establishes his voice as a science communicator: sharing and communicating are important activities for a scientist, but Maynard Smith will not 'popularise', he will communicate. There is a three-fold reason for preferring communication over popularisation for Maynard Smith's activities. First, 'science popularisation' and 'popular science' are loaded concepts that bring with them a variety of

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178 Maynard Smith to MacKeith, 16 November 1973. PA DM 1107/A433.
179 'Pelican Biology' (undated), PA DM 1952/614 A/02. See http://www.penguinfirsteditions.com/index.php?cat=pelican500-599 for the publication details of Rhodes' and Fogg's books.
180 Rhodes 1963, 16.
181 Penguin Cover Brief, 20 January 1975. PA DM 1107/A433.

ideological and cultural baggage and ambivalences. By calling Maynard Smith a science communicator who wrote for both specialists and non-specialists instead of a science populariser, we avoid prejudging his work and activities. As we have seen he became very aware of the potential multiplicity of his audience. Consequently, a second reason for using science communication is the greater inclusiveness of the concept in terms of audiences. Thirdly, we have to look at the following chapters in this thesis. Designating Maynard Smith a science communicator allows us to look at his activities and practices throughout his career; these not only span a variety of audiences, but also a variety of media and spaces, not all of which could be readily discussed in terms of popularisation. Looking at all of these contexts as different aspects and contexts of the central activity of science communication allows an overarching argument in terms of the relation between communication and the profession and theory of evolutionary biology.

We have seen a focus on natural selection and adaptation that was mirrored by the biologists and other scientists participating in the Darwin Celebrations at Chicago University. Maynard Smith was part of a generation of scientists who could benefit from the successes of the earlier neo-Darwinists who had started the process of professionalising evolutionary biology. He surveyed the field and emphasised the known facts as well as the ongoing research. But he was also part of a select few biologists who could, and would, 'do the sums' and he would rather annoy readers with algebra and equations than exclude what he considered to be a vital part of studying evolutionary biology. Considering that not even the 'specialists', the evolutionary biologists themselves, easily took to mathematical argumentation as was evident in the early rejections, the inclusion of such argumentation in non-specialist science is a clear sign of Maynard Smith's understanding of evolutionary biology.

This brings us to another way in which Maynard Smith's early work bridges different spheres. Next to connecting his previous to his new career, and to blurring the lines between specialist and non-specialist audiences, it falls both into and outside of the categories of popular, textbook, and journal science and their roles. *The Theory of Evolution*, and also 'Birds as aeroplanes', are not easily categorised as popular science in the usual sense, since there is no attempt, even an active avoidance, of simplification and fact-making. The Pelican book in particular does not claim that everything is explained or that the need for discussion is exhausted. 'The best science writing,' Maynard Smith once said, 'ought to reflect controversy and uncertainty'.[182] And in spite of being marketed to a non-scientific audience, the book came to be used by scientists as well – as, or as part of, textbooks and teaching material, for instance. But because of the inclusion of open questions – for instance, the discussion of Goldschmidt's and Waddington's research – and recent research such as Maynard Smith's own work on *Drosophila*, *The Theory of Evolution* is also not a clear example for textbook science.

The Theory of Evolution reflects Maynard Smith's multifaceted nature as a science communicator and the interconnectedness between his professional and popular work and publications. As we have seen, the text ties in with two types of professionalisation: not only Maynard Smith's own professional legacy, but also that of Darwin's lasting impact. This latter feat happened through Maynard Smith's contribution to the growing literature on Darwin and his theory of evolution by natural selection published during the centenary years of 1958 and 1959. Maynard Smith's mission was to prove the theory of natural selection as true and central to our understanding of evolution and biology, presenting a distinct neo-Darwinian perspective. Another, more subtle contribution: he pushed his life-long conviction that mathematics plays a vital part in this understanding, which in Maynard Smith's work – popular and professional – are clearly integrated. As the *Observer* noted upon the book's republication by Canto editions:

> 'Just a theory', was President Ronald Reagan's description of Darwinist evolution. Yes, but what a theory, one which has been robustly and repeatedly confirmed, using data and techniques that Darwin could not have imagined. This book – first published in 1958 but substantially revised with a long new introduction – is the best written introduction to the subject: well written, trenchant, an intellectual adventure story.[183]

The next chapters show how Maynard Smith came to continuously add to our understanding of evolutionary theory, with more mathematical and genetical arguments and studies. But first, how does John Maynard Smith the biologist as science communicator translate to the spoken word? In the next chapter, we will look at a widening of his

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182 Berwick 1996.
183 Anonymous 1993.

communication activities, a widening both in media (from articles and books to radio and television) as well as in topic (from strictly scientific issues to science and society relations). Again, he was imitating his mentor Haldane to whom it was 'vitally important that the scientific point of view should be applied, so far as possible, to politics and religion.'[184]

[184] Haldane 1932, v.

3 Bringing science home: a social responsibility?

3.1 Introduction

'All very very best with your t.v. work.. it is fine', wrote the editor of *Breakthru*, an international poetry magazine, to Maynard Smith after his 1967 *What is Life?* episode on DNA and evolution.[1] By then, the biologist was a veteran broadcaster. A decade earlier, *The Theory of Evolution* had established him as a scientist who could not only do science but communicate it successfully at various levels. (Melvyn Bragg still introduced him as the author of *The Theory of Evolution* in a 1999 episode of *In Our Time*.[2]) Even before then, Maynard Smith had crossed the line from written communication to spoken communication on radio and television, and he proved to be a powerful broadcaster and eloquent champion for evolution and science. The new media brought in new audiences to communicate to and with, new styles and forms of how to communicate, and new topics and themes to communicate on. It also brought challenges peculiar to its own, on which Maynard Smith reflected from his point of view as a scientist engaged in broadcasting.

Maynard Smith amassed roughly one hundred broadcasts in over forty years.[3] He was particularly active in the 1960s, and again in the 1990s, appearing mostly on radio (Figure 4). As someone who listed 'talking' as one of his two recreations of choice for his *Who's Who* entry (the other one was gardening),[4] broadcasting almost came naturally. 'It was more remarkable than it sounded,' one commentator observed after a Maynard Smith broadcast, 'since Maynard Smith did it without a script, recording it in two ten-minute bursts: afterwards the producer was torn between pride at his speaker's virtuosity and annoyance at the fact that no one would *realise* it was off the cuff.[5]

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1 Geering to Maynard Smith, 5 December 1967. JMSA Add MS 86765.
2 Bragg 1999.
3 From the listings in the BBC Genome project (http://genome.ch.bbc.co.uk), the digitisation of the *Radio Times* listings from 1923 to 2009, it is sometimes not clear to me whether a broadcast is a repeat or not. Thus the number of broadcasts may be inflated. At the same time, it is equally possible I have missed broadcasts; anything not from the BBC proved harder to find.
4 'Maynard Smith, Prof. John' 2007.
5 Ferris 1964, 23 (emphasis in original).

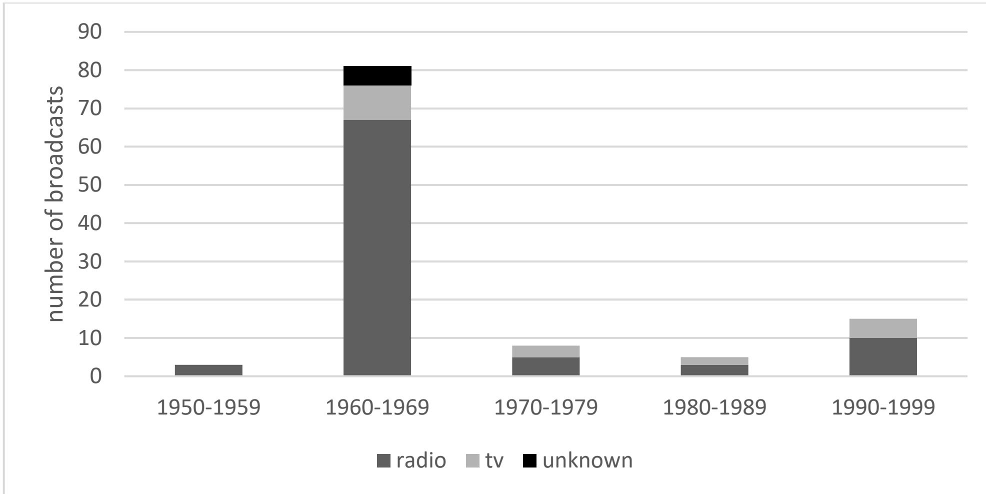

Figure 4. John Maynard Smith's broadcasts, 1950-1999.

The previous chapter focused on Maynard Smith's written non-specialist communication. But the increasing attention to more recent decades in the scholarship on written science communication necessitates increased study of non-print media: the radio, television, and the internet. As Jane Gregory and Steve Miller noted, '[a]lthough scientists and science writers achieved commercial success and popular acclaim with books and articles, their readerships were tiny compared to the audiences for science broadcasts.'[6] There are several general histories of broadcasting in Britain,[7] although historical approaches to media studies in general are lacking.[8] Scientific broadcasting specifically is still a largely unstudied area in radio and television studies as well as histories, but as a number of recent in-depth studies shows, it is not an understudied area. Arne Schirrmacher has worked on science broadcasting in the Weimar Republic,[9] Marcel LaFollette has published on the American context,[10] and Jean-Baptiste Gouyon has discussed the relation between science and film-making.[11] Tim Boon and Allan Jones focus on scientific broadcasting in Great Britain, writing about scientific documentaries in film and television, *Horizon,* and more broadly about the BBC's science broadcasting from the beginnings of the BBC, usually going up to the late 1960s.[12] Scientific radio broadcasts of the early twentieth

[6] Gregory and Miller 1998, 41.
[7] E.g. Paulu 1981, Crisell 2002, Briggs 1961-1995, Curran and Seaton 2010.
[8] Pickering 2014.
[9] Schirrmacher 2010.
[10] LaFollette 2008, 2012.
[11] Gouyon 2016.
[12] Boon 2008, 2013, 2014, 2015, 2017; Jones 2010, 2011, 2013, 2014, 2017.

century, on the other hand, have 'received little attention, despite helping to shape British understanding of science', as Neil Morley notes in his study of the biologist H. Munro Fox FRS (1889-1967) and his popular science.[13] For the mid-twentieth century we can look at Jared Keller's recent dissertation "A Scientific Impresario" (2017), which admirably addresses science on BBC radio between 1945 and 1970 by tracing the career of the producer Archibald (Archie) Clow.[14]

The following account of John Maynard Smith's broadcasting activities will do three things. First, it continues the efforts to look at mid-twentieth century popular science, focusing on the 1960s and 1970s. But second, it will shift the focus from the BBC and its science programmers to a scientist's point of view, following the example of Morley and Paul Merchant, who has recently published on scientists broadcasting and writing about science and religion in the 1980s, drawing on oral histories.[15] It thus elucidates how scientists as broadcasters both conformed to developments internal to the BBC and critically reflected on their relationship with the media. Finally, the focus on one scientist's broadcasting activities allows me to look at both radio and, to a lesser degree, television. Four case studies will thus reveal that Maynard Smith acknowledged and accepted increasing mediation through the BBC and its producers because radio and television were important outlets for his conviction to communicate science to non-specialists. Nonetheless, he stayed publicly and privately critical of both format and content decisions and reflected on the science-media relationship.

Maynard Smith's involvement with *Horizon* gives us a first direct clue that he not only overcame the supposed doubts of scientists towards popularisation and the media, but that he did so very successfully. He had been chosen as a scientist to be profiled in the *Horizon* pilot of 1963, and Gerald Leach, involved in the planning of the programme, had made it clear that

> the emphasis here should be on the individual man and the way his own personality, imagination and background affects the choice of his work and his own personal contributions to it. Life and work must be united.[16]

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[13] Morley 2019.
[14] Keller 2017.
[15] Merchant 2018.
[16] Cited in Boon 2015, 97.

This pilot never aired, but footage can briefly be seen in the seventh episode of the 1995 series *Seven Wonders of the World*, in which Maynard Smith discusses his personal seven wonders, including the flight of the albatross – a nice throwback to his 'Birds as aeroplanes' paper! Maynard Smith then appeared in the second *Horizon* episode on "Pesticides and Posterity" (1964), in "Genes in Action/Scientists and War" (1966), and as presenter of "The First Ten Years" (1974). He worked as scientific advisor on "The Lysenko Affair" (1974)[17] and narrated "The Selfish Gene" (1976) – in a 'wonderfully warm and engaging manner' and as suggested by Richard Dawkins, who did not want to do so himself.[18] This engagement did not go unnoticed at the University of Sussex, Maynard Smith's academic home since 1965. In the laudatory speech given on the occasion of Sussex awarding Maynard Smith a doctorate in science, *honoris causa*, on 12 July 1988, we hear that:

> He excels as a communicator, being that rare phenomenon – a scientist who can make science comprehensible to a wider audience. And it is this skill that has made his face so familiar to audiences of the BBC's "Horizon" programme, his credibility as a media man no doubt being enhanced by his uncanny likeness to every child's vision of the ideal professor.[19]

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[17] Jones to Maynard Smith, 31 December 1974. JMSA Add MS 86765.
[18] Dawkins 2013, 281. See Chapter 4 on the *Selfish Gene* episode.
[19] Presentation address on the occasion of the conferment of the degree of Doctor of Science, *honoris causa*, of the University of Sussex, 12 July 1988. JMSA Add MS 86760. Richard Dawkins has similarly remarked that he was very much intrigued by the picture Penguin used on the back of the first edition of *The Theory of Evolution*: 'The wild, nutty-professor hair, aslant like the pipe in the cheerfully smiling mouth: even the obviously intelligent eyes seemed somehow askew as they laughed their way through thick, round glasses (this was before John Lennon made them fashionable) badly in need of a clean. […] I kept peeping at the back cover as I read, then returned to the text with a smile and renewed confidence that this was a man whose views I wanted to hear' (Dawkins 1993, xi).

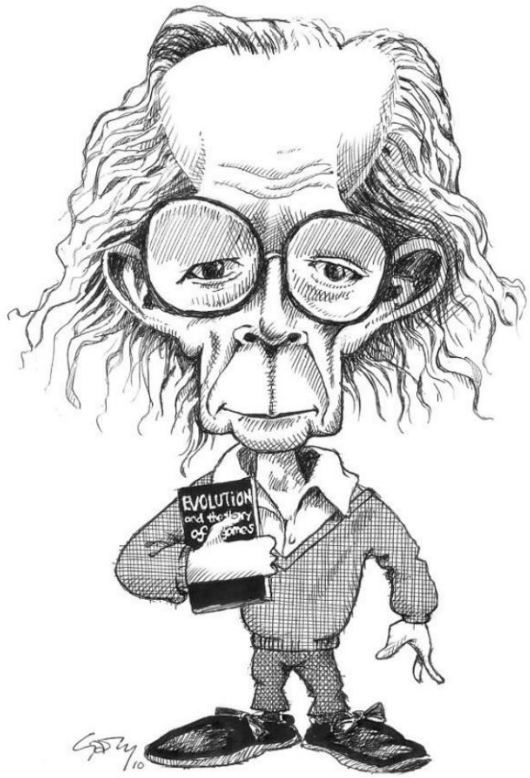

Figure 5. Caricature capturing Maynard Smith's 'wild, nutty-professor hair'. © Gary Brown, 2010.

But looks and personality alone do not make good science broadcasting. 'Putting a scientist before a microphone did not by itself constitute science broadcasting,' programmers increasingly argued. 'The broadcasting professional had to frame the broadcast through advice, encouragement, advocacy of particular styles of presentation, and other editorial input.'[20] With different producers, science broadcasting took different forms. Mary Adams, for instance, who worked as an adult education officer for the BBC from 1930 onwards, produced a number of "science and society" broadcasts. She considered herself as more than a facilitator for scientists to speak.[21] So while science broadcasting originally consisted mostly in giving scientists a platform to write talks and lecture on straight science, with little to no interference from programmers and producers, this policy shifted towards increasing mediation through the BBC.[22]

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[20] Jones 2010, 108.
[21] Jones 2011.
[22] Keller 2017.

In consequence, the professions of broadcaster and scientists did not always work together easily, struggling with questions of boundaries between the professions, expertise, authority, and control.[23] During his broadcasting career, John Maynard Smith came across these issues as well. In correspondence and talks he noted that he sometimes struggled with not having as much control over the final product as he liked or with the lack of visibility of the scientist as a person in broadcasts.[24] Scientists and scientific institutions have repeatedly criticised the BBC's handling of science broadcasting and tried to convince it to create a single department concerned with science, preferably with scientists having a greater say in the planning of projects.[25] The BBC had no producer responsible for science throughout the corporation, no science department, and no scientific board or advisor, until 1964.[26] Science was, however, more prominent on the BBC than scientists often thought, and it has been so from the corporation's earliest days.[27] Producers in individual departments dealt with science according to their department's type of presentation, so that 'among radio departments there were Talks, Features, Schools, Overseas Broadcasts and News, and among television departments there were Television Talks and Outside Broadcasts.'[28] From these, 'science programmes emerged from competition between […] Documentaries, Talks and Outside Broadcast (OB).'[29]

How does science broadcasting fit into the BBC more broadly? Written in the corporation's charter were the aims to 'inform, educate and entertain.'[30] The order was important, particularly to the company's first Director-General, John Reith. He had high ideas for what

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[23] Jones 2010, see also Jones 2014, Keller 2017.
[24] E.g. Maynard Smith to Jones, 6 January 1975. JMSA Add MS 86765; Beardsley 1983; Maynard Smith 1983a.
[25] Jones 2010.
[26] Jones 2010, 69. Indicative of this structure – that science had no subject-specific or special place within the BBC – are two tables given by Colin Seymore-Ure in his overview of *The British Press and Broadcasting since 1945*. They outline the changes in contents covered by the BBC and ITV between 1956 and 1994. "Science" does not appear as a separate category. The tables' categories are in fact based on both types of programme (like those already pointed out, e.g. "Documentaries", but also "News") and types of content (e.g. "Religion", "Sport"). Similar to the way science is handled by the BBC, this representation hides science behind formats covering not various topics (Seymour-Ure 2001, 156f).
[27] Jones 2010, 102 and 249.
[28] Jones 2014, 703f.
[29] Boon 2015, 89.
[30] Seymour-Ure 2001, 64.

radio could and should do; as one commentator put it, Reith used 'the brute force of monopoly to stamp Christian morality on the British people.'[31] Therefore anything produced by the BBC was to 'be "elevating as well as entertaining". An ethos of self-conscious paternalism pervaded the organization.'[32] This paternalistic view of the public was something the BBC had in common with many elite scientific organisations.[33] It expressed itself in the idea that the audience should not just be given what it thinks it wants, it should be given what it needs – and it often does not know what it needs. Under Reith, the BBC therefore followed an ideal of mixed programming; the audience should not become complacent or only listen to a narrow set of programmes. Horizons needed to be widened and 'characters' needed to be trained.[34]

World War II proved to be a turning point for the BBC. In the spirit of boosting public morale, the audience was given more of what it wanted; lighter entertainment replaced the more serious talks and classical music.[35] This was reflected in the changing landscape of available radio channels and their intended audiences. In 1946, the BBC had three radio channels: the Third Programme, the Home Service, and the Light Programme. It envisaged the distribution of listeners as 6%, 20%, and 74% – figures which Curran and Seaton have called 'wholly unrealistic' and 'based more on a hunch than on statistics'.[36] In reality, they write, the Third Programme was always more in 1-2% range.[37] The BBC's second Director-General, Sir William Haley – whose brainchild the Third Programme was – emphasised in 1948 that the BBC 'rests on the conception of the community as a broadly based cultural pyramid, slowly aspiring upwards.'[38] Thus the Third Programme was to be reminiscent of the Reithian mixed programming, to be judged as a whole and with the view that it was the programme everyone should be striving for. Maynard Smith's broadcasts fall onto this pyramid of programmes and audience conceptions as follows: he never appeared on the Light Programme (or BBC Radio 2, as it was after 1967). The majority of his programmes

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31 Taylor cited in Curran and Seaton 2010, 104.
32 Jones 2014, 702f.
33 Jones 2013, 446.
34 Seymour-Ure 2001, 64; Curran and Seaton 2010, 143. This applied not only to adult audiences; children's broadcasting too was aimed at 'produc[ing] children as exemplary citizens' (Oswell 1998, 375).
35 E.g. Curran and Seaton 2010, 149.
36 Curran and Seaton 2010, 150.
37 Curran and Seaton 2010, 151.
38 Cited in Curran and Seaton 2010, 150.

aired on the Home Service (later BBC Radio 4), followed by the Third Programme and Network Three (BBC Radio 3).

3.2 Explaining science: *Who knows?*

In 1954, Maynard Smith was still working at UCL's zoology department with Haldane and Spurway. Peter Medawar had offered him as job as a lecturer, and it was Medawar whom Archibald Clow, producer of scientific broadcasts at the BBC, went to visit that year. He might remember, Clow wrote to Maynard Smith, that during that visit they had talked about his research in genetics. 'I am now looking for some new topics for Science Survey and would be very pleased if you would come over and have coffee or tea with me some time and explore the possibilities in this subject with me.'[39] Maynard Smith would go on to write a script for and deliver a talk on "Mules, Maize and Mongrels", thus entering the world of science broadcasting one year after publishing his first popular science article. The contact with Clow proved to be a fruitful one: in 1959 – after two more appearances and with already ongoing preparations for a three-part school broadcast on 'Looking alike' – Clow asked Maynard Smith to appear on his panel show *Who Knows?*[40] The programme had been on air since 1956; designed for a general audience, it 'developed into one of the highest-rated series on BBC radio'.[41] The *Radio Times* advertised it as follows:

> Sam Pollock puts listeners' questions to a panel of scientists in the first of a new series of programmes. […] What has been in the papers recently? Russian biologists sacked: cosmic rays interrupt radio again: a new flat TV tube: jet planes approach the heat barrier: the path of the Earth's first artificial satellite.
>
> More information about such events, and what scientists themselves think about them, will be heard in the answers given to questions about science, technology, and so on, sent in by listeners.[42]

The first panel consisted of Robert Boyd, Harry Collier (industrial biologist), Peter Sykes (chemist), and G.P. Wells (zoologist); Wells was to take over chairmanship in 1958 until the programme ended in 1967. The year before, *Who knows?* had moved from the Light

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[39] Clow to Maynard Smith, 15 September 1954. BBC WAC RCONT1, John Maynard Smith Contributor File I.
[40] Clow to Maynard Smith, 1 December 1959. BBC WAC RCONT1, John Maynard Smith Contributor File I.
[41] Keller 2017, 198.
[42] 'Who knows?' (27 April 1957), *Radio Times 1694*, p.25.

Programme to the Home Service, where it was to stay. The concept and format stayed the same throughout the eleven years of the programme's running time. Maynard Smith himself first appeared in an episode broadcast on 8 January 1960[43] and last in July 1967[44]. In that period, and including repeats, listeners could have heard Maynard Smith answering their questions thirty-nine times. He thus gathered a substantial amount of experience in speaking freely and into a microphone, but without moving away too much from the roles he was already used to: the teacher and lecturer.

The question of didacticism is central to much of science broadcasting, and science popularisation and communication in general. Could, and should, you achieve a translation of the lecture hall onto the airwaves? As pointed out above, producers mostly thought there was more to science broadcasting than just that. While scientists were the experts on the content, producers were the experts on the medium and its processes. So while scientists may have preferred the format of lectures and talks,[45] producers were more aware of the possibilities and limits of television and radio as spaces for science communication. Thus, as Keller notes, towards the end of the 1960s the BBC began to shift from the original straight talk format, in which scientists would write and present their own programmes, to increasing mediation through the producer. The interview format is one example of the scientists' increasingly being contributors rather than creators. This shift reflected, first, the establishment of the BBC and second, a growing critical awareness of science in the British public.[46] (*Who Knows?* was still very much an informative programme; in fact, Clow found that listeners 'placed a much higher premium on information' rather than entertainment.[47] The programmed last aired in 1967.[48]) As Aubrey Singer, head of the Features and Science Programmes department since 1963,[49] said in a 1966 lecture, '[b]roadcasting not only affects but is affected by the climate of opinion.'[50] Audiences therefore needed to be taken into account. Even more important was the fact that producers,

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[43] *Radio Times 1886* (1 January 1960), p.50.
[44] *Radio Times 2278* (6 July 1967), p.38.
[45] Boon and Gouyon 2014, 473.
[46] Keller 2017, 257.
[47] Keller 2017, 194.
[48] Keller 2017, 35.
[49] Boon 2008, 226.
[50] Singer 1966, 743.

> because they are working continuously in the field, are creative and conscientious journalists who can anticipate and fairly reflect what is of sufficient importance to make good television and who are aware of reactions to past programs.[51]

They were thus better placed at suggesting topics than scientists. Equally important, 'the televising of science is a process of *television*, subject to the principles of programme structure, and the demands of dramatic form.'[52] After all, science often does not lend itself to depiction on television – much of it happens inside scientists' heads or involves particles too small or objects too far away to capture on film (at least until more recently).[53]

A difference between radio and television is, of course, the added visual element of the latter. Radio can use sound that is related to the topics discussed, interweaving effects with the spoken word 'to bring an added level of awareness to the recipient.'[54] But it also relies on the intimacy of carrying voices into the listener's living room: 'people like hearing other people tell stories.'[55] Maynard Smith's hobby of 'talking' fared him well, his natural ability to explain and entertain in the spoken word was suited to radio broadcasting. In fact, at least in the early stages of science on television, when technological means of depicting science were in their infancy, radio may have been *more* powerful: there were no jarring visuals to distract from the voice. As Arthur Calder-Marshall noted in *The Listener* in 1964:

> If I knew more about science, "Information" by John Maynard Smith (Third, March 9), the first of a series of six talks on current scientific concepts, might have provoked me to criticism. But I found its exposition far clearer in its explanation of molecular biology than those elaborate television mock-ups of the structure of DNA looking like hat and coat stands in 'contemporary' furniture stores. This was exposition to the unenlightened on the highest level.[56]

3.3 Reflecting on science

3.3.1 'Biological Backlash' (1967)

In particular on radio, in interview form, Maynard Smith talked about wider implications of science and scientific research, and the role of the scientist in society. This is a direct result

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[51] Singer 1966, 744.
[52] Singer 1966, 744.
[53] Gregory and Miller 1998, 122.
[54] Keck 2010, 733.
[55] Keck 2010, 731.
[56] Calder-Marshall 1964, 496.

of changes within the BBC, related to developments in the British society's attitude towards science. 'The days when you and I marvelled at miracles of science […] are over. We've grown up now – and we are frightened. The honeymoon of science is over,' said scriptwriter Gerry Davis in the late 1960s.[57] This increasingly critical view of science was reflected in the BBC's move towards mediation of science.[58] Rather than allowing scientists to write and develop their own programmes, like Maynard Smith was still able to do in the 1950s and 1960s,[59] interviews and panel discussions became the standard format. Scientists were relegated from the role of creator to the role of contributor. Content too shifted from straight science talks to issues around science, its implications for society, and similar.

Maynard Smith was part of this trend, although initially sceptical of it. As he told Mick Rhodes, a producer of science talks at the BBC:

> Many scientific discoveries do have effects on human beings and these can sometimes be quite interesting to discuss, but discussions about the effects on human beings of advances in biology (for example, artificial insemination) have about as much to do with science as discussions about royalties do with English literature.[60]

In the same letter, Maynard Smith emphasised that '[t]he interesting things about science are the ideas' rather than 'chaps' (Rhodes had asked Maynard Smith about suggestions for a series of science talks, stating that '[a]ny subject that includes people is intrinsically of greater interest than one which leaves us out'[61]). However, Maynard Smith agreed that a 'series on what recent advances in biology are likely to mean for human society in the future could be interesting.' He enclosed an article from the magazine *Daedalus* to give Rhodes an idea of what he was thinking of – 'but this is not really science'.[62]

Although the *Daedalus* article is not actually enclosed to the letter in the archive, we can be fairly sure he was referring to his 'Eugenics and utopia', published in spring of that same

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57 Cited in Gregory and Miller 1998, 44.
58 Keller 2017.
59 'Mules, Maize and Mongrels' (1954), the 'Looking Alike' three-part series (1960), 'Jigsaws and Penny-Whistles' (1963), 'Information' (1964), 'DNA and Evolution' (1967), and the outlier, 'Cheese' (1997) – which discussed bacteria. 'Scientific knowledge and the way to find it' and 'The scientific interpretation of evidence', two of his three talks for the 1965 'Christianity and the Natural Sciences' series (see Chapter 5), were concerned with scientific methods (cf. JMSA Add MS 86606).
60 Maynard Smith to Rhodes, 2 November 1965. JMSA Add MS 86765.
61 Rhodes to Maynard Smith, 27 October 1965. JMSA Add MS 86765.
62 Maynard Smith to Rhodes, 2 November 1965. JMSA Add MS 86765.

year, 1965. *Daedalus, Journal of the American Academy of Arts and Sciences* was founded in 1955 to combat the increased specialisation and isolation of scholars and intellectuals into disciplines that often failed to communicate with each other. It was not intended to be a means of popularisation, but the editor Walter Muir Whitehill (a historian and medievalist) hoped 'that its contents will prove of interest to fellows of all classes in the Academy.'[63] 'Eugenics and utopia' fits that aim in discussing the feasibility and desirability of three types of eugenics (selective, transformative, and biological engineering), briefly bringing in Olaf Stapledon's science fiction work, especially *Last and First Men* (1930) which inspired Maynard Smith to go into genetics and evolutionary biology.[64] Maynard Smith took biological actualities and possibilities but, as he told Rhodes, he did not go into detail of the science or scientific ideas behind these; the science is discussed only insofar as it is necessary to understand the larger arguments around what applied eugenics might mean in the short and long term for human society, whether or not it would be 'worth bothering' and what biologists should do about it.[65]

The article does therefore discuss people and the implications of science – Rhodes' preferred focus – and has enough weight on the science and scientific methods behind the ideas for Maynard Smith as well. Rhodes then developed the four-part series 'Biological Backlash', correspondence on which presents the next exchange between the two. Science journalist Gerald Leach – who had been instrumental in the establishment of *Horizon* – interviewed ten leading biologists on technology and science and their implications. Maynard Smith was one of them.[66] A year previously, on the BBC2 programme *People to Watch*, Maynard Smith had already been interviewed by Robert McKenzie and Erskine Childers, talking about the control of birth and death.[67] In 1969, he was going to talk about 'The conscience of the scientist' – and the *Horizon* episode "Pesticides and Posterity" from

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[63] Whitehill 1955, 5.
[64] Maynard Smith and Weiner 2000, 78.
[65] 'I think the answer to this question is that we should not recommend that anything be done except the simple and limited measures suggested above. The reason for this is that I believe recommendations of positive eugenic measures can at the present only distract attention from the more urgent and important questions. The most urgent message which biologists have to convey to the public is that if something is not done to arrest the present increase in world population, then that increase will be arrested by war, disease, and starvation. Eugenics can wait, birth control cannot' (Maynard Smith 1965a, 503).
[66] The other interviewees were W.H. Thorpe, Alex Comfort, Joseph Hutchinson, John Kendrew, Palmer Newbould, J.W.S. Pringle, C.H. Waddington, J.N. Morris, and Donald Broadbent.
[67] Maynard Smith, McKenzie and Childers 1966.

1964 had addressed questions similar to the ones in 'Biological Backlash' (and the follow-up broadcast of 'A geneticist's view', 1967) and 'The conscience of the scientist': 'the scientific and moral aspects' as well as environmental and long-term consequences of research into and the use of chemicals.[68]

Thus Maynard Smith did link research to the question of possible consequences and discussed these in programmes and in essays based on these programmes. Importantly, these concerns did not start with his career in broadcasting; he had already spoken on wider implications of science in 1955. At a conference on the effects of radioactivity, he spoke as a geneticist, warning that '[t]he effects […] of what we are doing to-day will not become apparent for some 100 years, and it will be about 5,000 years before half the deaths for which we are responsible will have occurred.'[69] Science does not exist in a vacuum, and neither should scientists, according to Maynard Smith. '[S]cientists like being in their laboratories and they don't like talking on the radio or involving themselves in politics or getting worried about their conscience,' he complained in 1969, and thus 'anything which enables a scientist to go back to his laboratory with a clear conscience and get on with it will be comforting.'[70] To avoid engaging with the public and with politics cannot be a valid way of behaving for scientists, according to Maynard Smith.

The mentioned series 'Biological Backlash' covered four topics: "Impact on Environment", "Impact on Man", "Avoiding Action", and "Dreams and Goals", each 'quite simply, an investigative report – the likes of which would not be out of place on a twenty-first century radio network.'[71] They were first broadcast on 7 March 1967 (7.30pm), 15 March (8.15pm), 22 March (8.20pm) and 30 March (7.30pm) respectively.[72] 'Biological Backlash' is one of the early examples of increasingly mediated scientists (all interviews were pre-recorded, then edited by Leach) and of the producer overruling the scientist in what is interesting and in how to present it, and it validated Rhodes' argument for humans and scientific consequences over Maynard Smith's preference for ideas. Audience research reports – which were based on questionnaires sent out to a panel of viewers – show that the

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68 'Horizon: Pesticides and Prosperity [sic].' *Radio Times 2116* (28 May 1964), p.13.
69 Cited in 'Doctors discuss dangers of high radiation' 1955, *The Irish Times* (6 June), p.3.
70 Maynard Smith 1969a, 178.
71 Keller 2017, 238.
72 Rhodes to Maynard Smith, 3 March 1967. JMSA Add MS 86765.

average ratings for each episode were 70, 67, 66 and 73 respectively. All of these were above the average for programmes on the Third Programme of the previous year, which had been 62.[73] This average, or Reaction or Appreciation Index, is 'the mark out of a ten given by each panellist, averaged out to a percentage'.[74] Commentators praised the speakers for speaking lucidly and expertly, without using jargon or being patronising, but mostly the programme for its subject matter.[75]

The subject matter and style of 'Biological Backlash' exemplified the BBC's shifting concerns in science broadcasting as well as Rhodes' approach to it:

> The point of many of Rhodes' programmes was not to simply blame science for the problems of the 1960s […]. In fact, many of Rhodes' programmes that were critical of science nevertheless also looked to science and scientists for answers.[76]

Hired by Rhodes, Leach chose extracts from his interviews which he then linked and framed with short interludes, either transitioning from one sub-theme to the next or from one speaker to another. He thus created a narrative and set the tone, summarised views and drew conclusions; he is the mediator between the scientists and the audience. 'Leach was quite literally taking over the communication of science from scientists.'[77] While Leach was in control of the framing, he still relied on his subjects' expertise. In terms of content, each scientist talked about the theme from this professional point of view, as zoologists, physicians, ecologists or psychologists. But there were also comments on larger, social issues – and these were often instigated by Leach. Thus in the second half of episode 3, "Avoiding action", Leach moved to the relationship between science and government, and the role of the former in the latter.

> If society won't call for biological advice sufficiently, isn't it up to biologists, and other scientists, and technologists to force advice on us? [...] To act as a front line early warning system and solution-finding system for progress I put this challenge to several biologists and got, on the whole, rather pessimistic answers.[78]

73 Audience Research Report, Biological Backlash, 4. Dreams and Goals. 14 April 1967. BBC WAC R9/6/183, LR/67/418.
74 Lawrie 2018, 239f.
75 Audience Research Report, Biological Backlash, 4. Dreams and Goals. 14 April 1967. BBC WAC R9/6/183, LR/67/418. See also Keller 2017, 238ff.
76 Keller 2017, 236.
77 Keller 2017, 239.
78 Leach 1967, "Avoiding Action", p.7. JMSA Add MS 86765.

The three biologists whose extracts were chosen to comment were Maynard Smith, Thorpe, a zoologist and ethologist, and Kendrew, a biochemist and crystallographer. The latter two in particular talked about a lack of science-government dialogue. Kendrew, 1962 Nobel Laureate and a member of the Council for Scientific Policy, did not have much hope in scientists branching out from their specialisms to talk about something else because for most scientists this would equal 'selling their souls.'[79] And while in America scientists seemed involved in advising policymakers through committee work, in Britain

> one's always up against the difficulty, with any kind of scientific advisory operation which is mounted, of finding the people to it: people who think it's worth doing; people who have any kind of experience or interest in it; you find yourself always going round the same little gang.[80]

Thorpe commented that American-style Technological Assessment Boards were desirable, if they worked. Organisations like the Royal Society already advised the government, and biologists were more fairly presented now than before. But at the same time, looking at the number of committees, out of over sixty less than a dozen dealt with biological issues. If humans were to 'survive in any kind of dignified way' this imbalance needed to be addressed.[81]

Maynard Smith who, in terms of science, was asked by Leach to discuss antibiotics and radiation as well as chemicals in foodstuffs and environmental biology, also moved beyond his specific scientific topics. At one point, Leach asked 'if it wasn't a prime duty for all scientists to spell out as clearly as possible the implications of their work.'[82] Maynard Smith agreed, but pointed out that for most scientists, this was not at the forefront of their minds when doing science: 'Perhaps I could digress [...] and simply talk for a moment about what scientists do think about their duties.' These duties are different to the ones other, older, professions have. Whereas the Hippocratic Oath, for example, is in place to protect the patient, scientists' ethics 'are concerned to defend ourselves as scientists. You know, you don't tell lies, you don't pinch other people's ideas, you don't publish results which are not

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[79] Kendrew 1967, "Avoiding Action", p.8. JMSA Add MS 86765.
[80] Kendrew 1967, "Avoiding Action", p.11. JMSA Add MS 86765.
[81] Thorpe and Leach 1967, "Avoiding Action", p.12f. JMSA Add MS 86765.
[82] Leach 1967, "Avoiding Action", p.8. JMSA Add MS 86765.

reliable.' But, Maynard Smith continued, '[t]here is no comparable set of ethical principles in science concerned with our effects upon the general public.'[83]

Moreover, scientists focused on immediate research problems rather than consequences because they could not be sure to solve the set problems: 'It is, in a sense an excuse, and not a very strong excuse – the only excuse I have for not really spending an awful lot of time, other than a kind of science fictional kind of imagining, wondering about what would happen if one found a cure for ageing – my real excuse for this is that I don't really expect to find a cure for ageing.'[84] (Over the past few decades, the field of ethical technology assessment (ETA) has made use of scenarios – Maynard Smith's 'science fictional kind of imagining' – exactly in order to determine, as much as possible, any possible hard and soft outcomes of newly developed science and technology so as to avoid (negative) unintended consequences.[85]) Leach then asked if scientists ought to consider their topic of research more carefully, or to choose something 'which is of social value'. Here Maynard Smith was less willing to agree, although he conceded that 'at least we might have an ethic about not deliberately choosing research which is likely to be lethal.' More important for Maynard Smith was that science ought to be an open and international business – when that is given, science is at its best.[86]

Thus, Maynard Smith talked both about ideas and people with Leach. While the details or methods of science are less prominent, the question about responsibility and codes of conduct in and for science and scientists are clearly something Maynard Smith thought about and considered important. How much becomes clear in yet another broadcast: 'The conscience of the scientist' (1969).

3.3.2 'Scientific Hippies': the BSSRS (1969)

'The conscience of the scientist' was broadcast on 7 July 1969 and does two things: in terms of format, it is an example of the original mode of presenting science on the radio – a

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83 Maynard Smith 1967, "Avoiding Action", p.8f. JMSA Add MS 86765.
84 Maynard Smith 1967, "Avoiding Action", p.9. JMSA Add MS 86765.
85 E.g. Boenink, M., Swierstra, T. and Stemerding, D. (2010). Anticipating the interaction between technology and morality: A scenario study of experimenting with humans in bionanotechnology. *Studies in Ethics, Law, and Technology 4*, 1-38. Hard outcomes or impacts refer to anything quantifiable, whereas soft impacts are less easy to determine: 'the way technology influences, for example, the distribution of social roles and responsibilities, moral norms and values, or identities.'
86 Anonymous 1967, 606.

straight talk, pre-recorded on 20 May 1969.[87] There is no questioning by an interviewer, no mediation by the BBC. In terms of content, however, it reflects the more critical, reflective attitude towards science. It does so from *within* science, giving Maynard Smith's perspective which was originally aimed at fellow scientists. At the same time, a comparison of the script to that of 'A geneticist's view', which gives the 1967 interview between Maynard Smith and Leach in full, shows that many points of the 1969 talk are extensions, even intensifications, of points made then. Maynard Smith picked up on things he and Leach had discussed in terms of the consequences of science, intended and unintended, and whether scientists had a responsibility towards society with regards to these consequences and their work more generally.

For Maynard Smith, science is fundamentally driven by curiosity and the sense of satisfaction one gets from solving a problem. But doing science for science's sake had become difficult to argue in the light of developments during and after World War II: because of often unintended or unforeseeable consequences, a view was emerging that scientists should perhaps 'be rather more responsible about what they do'.[88] While he had been hedging in the interview with Leach, Maynard Smith now asserted that scientists do in fact have a special responsibility towards the public, they do need a code of conduct, and they do need to be publicly and politically active – whether they like it or not. The answer to the problem of indirect and unintended consequences cannot be to stop doing science, however, as there is no telling whether or not these will be harmful or beneficial to mankind. It also cannot be to shift responsibility to the government or society: 'No other profession would accept this argument.'[89]

A scientist's responsibility lies in accepting first, 'that the consequences of scientific research are not individual but public' and second, that they 'give rise to political problems, and that these political problems are unlikely to be solved unless scientists play their part in solving them'.[90] In other words, knowledge means responsibility, and scientists needed to

[87] Maynard Smith, 'The Conscience of the Scientist', script. BBC WAC TLN 21 TC 1612. Cf. Maynard Smith 1969a for the *Listener* version. The talk was so successful that it was repeated (John to Maynard Smith, 22 July 1969. BBC WAC RCONT12, John Maynard Smith Contributor File III).
[88] Maynard Smith 1969a, 178.
[89] Maynard Smith 1969a, 179.
[90] Maynard Smith 1969a, 180.

acknowledge this, share their knowledge (for instance on advisory boards, like Maynard Smith had done in the 1950s), and generally leave their labs to engage with society.[91] At the same time science must not be secret;[92] it is international and collaborative – a point Maynard Smith had already made when talking to Leach two years previously. All the while, scientists talking on the social responsibility of science or on social and moral responsibilities in general are in danger of appearing "holier than thou". 'I hope,' Maynard Smith closed 'The conscience of the scientist', that 'I haven't given the impression that I'm snow white on this issue myself':

> My own work, if it were successful, might have results more disastrous than atomic bombs. I work at the moment on the causes of aging, and clearly, if we were to discover the causes and it turned out to be possible to prevent the process of aging, so that, as Bernard Shaw imagined in *Back to Methuselah*, human beings could live for 300 years, this might have quite disastrous social consequences. And it's not really an excuse to say that I don't really expect to find such a cure. My excuse—and it's only interesting because my excuse is the same as any other scientist would give for research of a fundamental kind—is, first, that I want to find an answer, that I think the answer is in itself worth having; and second, that an answer would bring with it great benefits, as well as great risks; and finally that it is the business of society, and not merely my business, to ensure that scientific discoveries are used wisely.[93]

How come Maynard Smith gave a pre-recorded talk on this topic, rather than discussing it in an interview or on a panel, like he had some of the issues with Leach? "The conscience of the scientist" grew out of a talk he had already delivered elsewhere: at the inaugural meeting of the British Society for Social Responsibility in Science, BSSRS for short (and 'Bisrus' to some of their friends[94]).[95] The society's formation was a reaction to the shifting attitudes towards science, the same that informed the BBC's increasingly reflective attitude towards science: 'In 1969 growing awareness that science not only provided benefits but

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91 Maynard Smith 1969a, 180.
92 Maynard Smith qualified this by pointing out that in some cases secrecy is at least understandable, if not desirable, namely when research is conducted in or by industry.
93 Maynard Smith 1969a, 180. His work on ageing, particularly an excerpt from a documentary showing this work, was used in a portrait of the late New Wave singer-songwriter Poly Styrene. Styrene is seen watching Maynard Smith on television and his discussion of egg transplants and biological engineering; she wonders if this kind of research should be done on humans and comments: 'In the wrong hands, and used the wrong way, I mean, it's terrible. I mean, I find that quite frightening' (Clisby 1979).
94 Bell 2017, 149.
95 Maynard Smith to Contracts Department, Talks, 26 June 1969. BBC WAC RCONT12, John Maynard Smith Contributor File III.

also created severe problems led to the formation of the Brit. Soc. Soc. Resp.'[96] The meeting took place on 19 April 1969 at the Royal Society 'to the congratulations of most witnesses (Nature excepted)'.[97] Earlier in 1969, Maynard Smith had been one of many scientists whom Nobel Laureate Maurice Wilkins approached in a circular letter. Wilkins was looking for support in founding an organisation 'to examine the moral + social issues involved in scientific research + education'.[98] Among the scientists contacted were J.D. Bernal, Sir Lawrence Bragg, Francis Crick, Sir Julian Huxley, Sir Peter Medawar and Max Perutz as well as 'Others, not FRS'.[99] (Maynard Smith was elected to the Royal Society in 1977: 'well deserved and long overdue', according to E.O. Wilson, a sentiment echoed in other congratulations sent to Maynard Smith.[100]) As of 2 April 1969, Wilkins and his five co-authors (C.F. Powell, M. Pollock, R.L. Smith, D.H. Butt and S. Rose[101]) had received 78 letters of support, Maynard Smith's among them.[102] Maynard Smith's talk shows why: his views aligned clearly with the aims of the BSSRS: 'to keep an eye on what goes on in the backrooms of science'[103]; 'sponsored secret research[] should not become as rife in Britain as in the United States'[104]; 'the idea of knowledge for its own sake as justification for doing scientific research must be examined very critically'[105]. Internally, however, there was a sense of disappointments with the speeches as a whole, given a 'lack of concrete activity' which was blamed on 'not enough briefing'.[106] Maynard Smith's later, actual, involvement seems to have been limited too. Although he tentatively agreed to be a full-time member of the

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96 Undated notes [1969?]. MWP KPP178/11/1/4.
97 Rosenhead 1972, 134. Also see Anonymous 1969a, 1190.
98 Baldwin to Wilkins, 19 February (undated). MWP KPP178/11/1/2.
99 FRSs to whom Wilkins's et al letter sent 19-21 February 1969; Others, not FRS to whom letter has been sent. MWP KPP178/11/1/2.
100 Wilson to Maynard Smith, 5 April 1977. Marion Lamb wrote: 'I've just seen the latest list of Fellows and I'm glad to see that the Royal Society has at long last decided to improve its standards. Congratulations – they really should have elected you years ago!' (27 March 1977). Richard Lewontin wrote (31 March): 'You know, I am sure, how I detest self-perpetuating honorable societies whose members occasionally deign to admit someone to their ranks. One of the chief reasons for this attitude on my part is that it takes them so bloody long to recognize real merit. Needless to say, I am delighted that the British branch of the self-elected elite has finally done itself the <u>real</u> honor of admitting you to its numbers.' Maynard Smith echoed Lewontin's ambiguity in a letter (to Rothman, 5 September): 'To be honest, I have mixed feelings about the whole thing. I don't really like these exclusive societies, but if you can't beat them, join them.' All JMSA Add MS 86766.
101 Anonymous 1969a, 1190.
102 Letters of support to Wilkins et al letter. MWP KPP178/11/1/2.
103 Wilkinson, 'Scientists draw up code of ethics for Brave New World'. MWP KPP178/11/1/2.
104 Anonymous 1969b, 320.
105 Wilkins to Wedgwood Benn, 19 June 1969. MWP KPP178/11/1/2.
106 Minutes of SSRS Committee, 23 April 1969. MWP KPP178/11/1/4.

society's Science Advisory Board, he makes no appearance on the list of attendees for the first meeting.[107]

Ritchie Calder, science correspondent with the *Daily Herald*,[108] dubbed the scientists involved in the founding of the BSSRS "scientific hippies", but not negatively. Rather, he was glad 'the initiative had been taken by the younger scientists.'[109] In addition, the BSSRS promised to be a British equivalent to the Pugwash movement,[110] although the society felt 'that P. was not very active, had little appeal, and little cash.'[111] But the long-term effects and radicalism of the BSSRS, which folded in the early 1990s, are sometimes debated as well. In fact, in its early years, the society was 'reasonably establishment' with members 'following in a long tradition of socialist scientists'.[112] Scientists like the crystallographer J.D. Bernal (whom Maynard Smith knew, even if not well[113]) had been attracted to socialism; indeed, Bernal became the personification of "red science" whose ideas were 'initially very influential in wartime and post-war Britain'.[114] According to Bernal, research 'was to be carried on for the "benefit of humanity as a whole",' which required a reorganisation of the 'structure, funding and management of science in the capitalist economies'.[115] Jacob Bronowski, a mathematician and historian, even argued for the 'moral superiority of science', insisting that 'science and scientists were the standard-bearers of truth'.[116]

Britain's history of left-leaning scientists, politically active in the 1930s, continued in the BSSRS. The new generation had the blessing of the older one, some of whom wrote in support to Wilkins and the other founders.[117] American visitors to the UK in the 1970s

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[107] Committee Meeting, 25 June 1969, and "To all members of the Science Advisory Board", 6 January 1970. MWP KPP178/11/1/4.
[108] Muddiman 2003, 393.
[109] Calder 1969, 617.
[110] Pugwash Conferences on Science and World Affairs emerged in the 1950s, drawing on Bertrand Russell and Albert Einstein's manifesto on the nuclear threat. In 1995, the Nobel Peace Prize was awarded to Pugwash and its co-founder, Sir Joseph Rotblat. ('About Pugwash' [n.d])
[111] They still '[d]ecided to maintain good relations and seek invitations to P. seminars', however. Minutes of SSRS Committee Meeting, 7 May (undated). MWP KPP178/11/1/4.
[112] Bell 2017, 152. Among the original letters of support were also several Nobel Laureates, a majority of FRS, a Lord and a DBE as well as OBEs.
[113] In Freeman 1997.
[114] Muddiman 2003, 388.
[115] Muddiman 2003, 391 (citing Bernal 1939).
[116] Desmarais 2012, 574.
[117] E.g. J.D. Bernal, Joseph and Dorothy Needham, Lancelot Hogben, and Sir Julian Huxley, who had been active in the Social Relations of Science movement and/or were part of what Gary Werskey has

voiced their wonder at this situation, some positively, others critically. Joe Hanlon described the BSSRS as 'part of the establishment, effectively, it's the left edge of the establishment. That was very weird. It was absolutely wonderful.'[118] Richard C. Lewontin, while he agreed with the sentiment, felt that it made BSSRS ineffective:

> I have never been anywhere where Marxism is so respectable as Britain. Half of the people in the University of Sussex over the age of 40 are former members of the CP [Communist Party]. The Student Union representing every student on the Campus is 100% Marxist as far as I can tell from its meetings. Yet the left is in bad shape because it is so respectable. I have the feeling that it is 100% "radical chic." There is virtually no attempt to do real agitation if it involves the slightest bit of unpleasantness. The most they will do is make a polite demonstration in front of the US Embassy, and I do mean polite.[119]

Lewontin was a biologist who stayed at Sussex's School of Biological Sciences. The school's dean, since its foundation in 1965, was none other than John Maynard Smith.

Public engagement and 'public understanding of science' as such started after World War II, and the British left felt that 'society was to decide the direction, means and outputs of science'. At the same time, however, this perspective was still 'tinged with elitism, in that it put scientists as the source of information and opinion about science, and envisioned them gaining positions of power through the public affirmation they sought to generate through public communication'.[120] Maynard Smith and the BSSRS's views thus predate some of the points on the 'public understanding of science' movement addressed in the Royal Society's 1985 report which too 'asked for more science in the mass media and urged scientists to improve their communications skills and to consider public communication as a duty'.[121]

Maynard Smith's political engagement is not a surprise. Studying at Cambridge in the late 1930s, he had joined the Communist Party in 1939, feeling they were the only ones fighting fascism, and spent more time with political activities than studies. However, he had some

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termed the 'Visible College'. See Filner 1977 and Werskey 1978. Cf. Letters of support to Wilkins et al letter (as at 2 April 1969). MWP KPP178/11/1/2.

118 Cited in Bell 2017, 166.

119 Cited in Bell 2017, 165f.

120 Gregory and Lock 2008, 1253.

121 Gregory and Lock 2008, 1254.

'deviationist views' – like considering Stalin to be a dictator, or wanting to enlist – so he was sent onto a 'training course on Communist policy, Marxist philosophy and Soviet history in the vacation.'[122] His active political engagement continued after he left university and until after the war. Already as an engineer he felt that work took up too much time for politics, and when he chose to change careers and go into science in the mid to late 1940s, he really felt he could not do both: 'it may seem a funny way of putting this, but I couldn't serve two masters. I could devote myself to politics or I could devote myself to science.'[123] At this point, the decision had nothing to do with intellectual incompatibilities and was simply a question of time and effort.

Even though Maynard Smith 'abandoned' politics and later Communism, he stayed left-leaning and had been imbued with an awareness of philosophical and political influences on one's science. His activities in relation to the bomb tests of the 1950s were also a sign of continued, though now science-related political activity. He remembered this episode talking to Leach.

> I was thinking of the days immediately after the war, when one was attempting to persuade people that atom bomb tests were likely to cause mutations; and this was obstinately denied by governments and by people who wanted to test bombs in those days. Now it's sort of automatically accepted, but it took a fair bit of work.[124]

Leach asked what this work had been: 'sitting in railway compartments and travelling up and down the country to go to odd meetings, you know, at which one was making really almost political speeches.'[125] Maynard Smith felt he was battling a persistent black-and-white picture: either radiation was viewed as harmless or as demonic. He considered his role as a geneticist with knowledge about mutations to be educating the public about the grey areas. Speeches were one thing, committees another, less direct way to do so. Although not on the committee set up by the Medical Research Council, he still participated by 'occasionally [doing] sums for the people who were'.[126]

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122 Maynard Smith (undated), 'Reminiscences of a Cambridge Communist'. JMSA Add MS 86817: 'The course did have one excellent result – I met my future wife there: we are still together.'
123 Maynard Smith and Erickson 2004. JMSA (uncatalogued).
124 'A geneticist's view', script (1967). BBC WAC TLN21/T K0 41 D.
125 'A geneticist's view', script (1967). BBC WAC TLN21/T K0 41 D.
126 'A geneticist's view', script (1967). BBC WAC TLN21/T K0 41 D.

3.4 Defending science

'It may be that I'm paranoid,' Maynard Smith reflected in 1983, 'but I am left with the impression that the press of this country, sometimes supported by television, are giving a false picture of the present state of evolutionary biology.'[127] He did his own bit to rectify this situation, giving us the third theme that emerges from Maynard Smith's science broadcasts: defending science, and specifically the theory of evolution and Darwinian natural selection, against challenges from both inside and outside of science. Two of these – creationism and punctuated equilibria theory – will be discussed in detail in Chapter 5, which is why I will keep this section short.

In terms of the science-religion relationship, Maynard Smith discussed the differences between them in a series of school broadcasts in 1965 (with the transcripts filed as 'God broadcasts' in his archive).[128] A year later, he discussed the work of the French Jesuit palaeontologist Teilhard de Chardin (1966)[129] and in early 1980, he joined an *Everyman* episode entitled 'Genesis fights back' (1981)[130].

Again in the 1980s, the programme *The World About Us* produced an episode called 'The trouble with evolution...' (1980), in which Maynard Smith, Stephen J. Gould, and Edward Steele examined puzzles to the theory of evolution. At the same time, the film also 'ask[ed] if there is a serious alternative to Darwinism'. Gould, that same year, had asked whether a 'new and general theory of evolution [was] emerging'[131] and had published both on punctuated equilibria theory[132] and anti-adaptationism, challenging the neo-Darwinian orthodoxy. Steele, an Australian immunologist, was spending 1980/81 in the United Kingdom 'arguing vociferously that he ha[d] firm experimental evidence for a Lamarckian mode of inheritance'.[133] (His visit had been arranged by Medawar in response to these claims; he suggested the experiments needed to be repeated.[134]) Maynard Smith did not agree with either of these challenges. Lamarckism was again part of a 1995 Radio 4

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[127] Maynard Smith 1983a, 25.
[128] JMSA Add MS 86606.
[129] *Radio Times 2207* (1966, 24 February), p.42.
[130] *Radio Times 3028* (1981, 19 November), p.39.
[131] Gould 1980.
[132] Punctuated equilibria theory is also discussed by Gould in 'Genesis fights back', cf. transcript in JMSA Add MS 86616.
[133] Lewin 1981, 316.
[134] Maynard Smith 1983a, 24; Lewin 1981.

programme for which Maynard Smith was interviewed.[135] Although less directly defending science *against* anything, the programme 'Quantum Leaps: Lifelines' (1998) played into this theme as well: 'Professors Steve Jones, Richard Dawkins and John Maynard-Smith [*sic*] tell the story of the intellectual journey that firmly established Darwin's place in scientific orthodoxy.'[136]

This is only a brief snapshot of the programmes with which Maynard Smith defended either science in general or Darwin's theory of natural selection in particular. These broadcasts are an extension of his other themes in that they often related to things outside science (religion) and include explanations of the issues at stake. They are also extensions of the trends identified by Keller: rather than being uncritically pro-science, or the current orthodoxy in science, they examine challenges to the scientific orthodoxy and discuss outside views. One of these broadcasts leads us into the next part of this chapter, reflecting on the (re)presentation of science on the media: in Maynard Smith's archive, the transcript of 'Genesis fights back' is kept in the same folder as the draft for his 1983 presidential address to the Zoological Section of the Association for the Advancement of Science, entitled 'Science and the media'. These reflections are from Maynard Smith's point of view, as a scientist broadcasting on the BBC, offset against the points of view of BBC producers and programmers.

3.5 Reflecting on (re)presentation

Maynard Smith developed a critical view of the science-media relationship. On the one hand, he acknowledged that good science journalism could be a boon to scientists who did not have the time or the skills to speak about their work to non-specialists. On the other hand, he was troubled by mediation through the media, with misrepresentation being his main worry and accusation.

3.5.1 Science journalism

Science journalism as a profession emerged and became institutionalised in Britain in the interwar period.[137] It plays an important part in science communication and as a mediator

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[135] *Radio Times 3711* (1995, 2 March), p.109.
[136] *Radio Times 3877* (1998, 28 May), p.104.
[137] Hughes 2008, 11.

between science, scientists, and the public. Maynard Smith acknowledged that most of the time 'one has to choose between describing science, and doing it.'[138] He saw the emergence of science journalism as a profession as 'inevitable', for two reasons: first, 'science has become too important to be left to scientists' and second, while a 'working scientist can write a newspaper article, an essay or a book in his spare time, [...] he cannot make a television programme that way.'[139] At the time of speaking, in 1983, Maynard Smith had ample experience of the demands scientific broadcasting had on one in terms of time and work. He was aware of the constraints that the new media put on the ease and level of access a scientist had to them. What is more, scientific specialisation often led to isolation in terms of knowledge of science as a whole, which is why Maynard Smith had 'long been resigned to the fact that a competent science journalist is likely to be better-informed than a university professor about almost every aspect of science except the narrow field in which the professor works.'[140]

The problem with science journalism, as Maynard Smith saw it, was not *that* it reported on science (instead of scientists) but *how* it reported on science. There were three worries: excessive focus on controversies, the social consequences of science replacing science itself, and the depersonalisation of science.[141] Maynard Smith's understanding of what science broadcasting should do is in conflict with that of professional broadcasters, who put narrative, news value, the broadcasting medium and the audience first.[142] The manners in which science and the media operate and address their audiences are very different, in part because their audiences are very different. Maynard Smith was aware that a scientist talking on the media and to the public, rather than to other scientists, needed to adapt their way of talking.[143] 'Scientists on the whole are reluctant to stop hedging and qualifying and to come right out with it.'[144] But they need to learn to communicate and speak on television,

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138 Maynard Smith 1993b, 1.
139 Maynard Smith 1983a, 22f.
140 Maynard Smith 1970, 590.
141 Maynard Smith 1983a, 25f.
142 E.g. Jones 2010, Keller 2017.
143 Maynard Smith 1983a, 29.
144 Maynard Smith 1969a, 180.

'because I think that at their best they can convey scientific ideas better than anyone else, because they understand them better, and care about them more.'[145]

Although not suggesting that radio may be a good entry level, Maynard Smith was generally more positive about and comfortable with science on the radio than on television. For many it was easier to talk into a microphone than a camera, and 'radio producers have been more willing to look for scientists who will do so.'[146] It has to be said that radio producers had more time and experience in establishing formats and programmes than television producers, although once they did, television took over in popularity.[147] What is more, 'the big challenge for television producers and scientists alike has been to reconcile the inherent unruliness of science with the laws of visualization enforced by a medium primarily valued for its ability to entertain a large audience with moving images.'[148] Radio relies on sound alone and in that sense is a "blind" medium.[149] It may also be that the standard format of broadcast lectures or talks suited scientists better than being interviewed for television documentaries or being shown at work. Maynard Smith himself certainly started out on the radio and throughout his broadcasting career often appeared as a speaker or lecturer.

But as we know from 'Biological Backlash', he was also interviewed for programmes. Science journalists, or interviewers more generally, are mediators, increasingly used by the BBC since the 1960s. In 1983, Maynard Smith suggested that one should insist on live interviews:

> In fact, it doesn't much matter *what* you say when interviewed for a television programme,[150] unless you have the strength of mind to insist on being interviewed live. The producer usually films about fifteen minutes, and uses one. So, to offer some advice I have never had the sense to follow, if you are interviewed, and there is one particular point you want to make, then make that point, and no other. Otherwise, you'll find that the one thing you really wanted to say has been left out.[151]

145 Maynard Smith 1983a, 28.
146 Maynard Smith 1983a, 29.
147 Keller 2017, 181.
148 Van Dijck 2006, 7.
149 Crissell 2002, 3.
150 This equally applies to radio, of course.
151 Maynard Smith 1983a, 28.

He echoed general worries about misrepresentation that scientists were having ever since the BBC increased mediation of them and their content. 'The most bitterly argued controversies in which scientists have found themselves in recent months have been over the editing of film,' noted scientist turned producer R.W. Reid in 1969: scientists were afraid of misrepresentation by the media.[152]

But Maynard Smith's broadcasting career also shows that negative experiences do not have to be the case. 'Biological Backlash' exemplifies good science journalism and – for Maynard Smith – acceptable mediation: a good interviewer who could establish rapport with their interviewees and a good relationship between producer and scientist can prevent (or at least ameliorate) misgivings in scientists about mediation. Further correspondence concerning 'Biological Backlash' shows that after the interview, Rhodes wrote to Maynard Smith once more. He had been fascinated by the conversation between Leach and him and it would be a shame not to use all the material. Rhodes asked if Maynard Smith would agree to his interview being a broadcast in itself.[153] Maynard Smith did agree – but asked to see a full transcript first. 'I am sure I said a number of extremely stupid things to Leach on the assumption that he would remove the most stupid of them'.[154] Maynard Smith relied on Leach, trusting him to mediate without misrepresenting what had been said. After reading the transcript, Maynard Smith remarked that he was 'horrified to see what I said under the influence of drink but I suppose it is only fair to let it stand.' He extended the trust from Leach to Rhodes, requesting one sub-clause to be cut but leaving the rest to his digression.[155]

3.5.2 The trouble with documentaries

From the mid-1960s, Maynard Smith began doing more television work. He started with two *Horizon* episodes, "Pesticides and Posterity" (1964) and "Genes in Action/Scientists and War" (1966), in addition to the series' unaired pilot of 1963. These were followed by three more episodes in the 1970s. Those three were all significant, for either the BBC, Maynard Smith himself, or – in hindsight – the course of evolutionary biology at large:

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[152] Reid 1969, 457.
[153] Rhodes to Maynard Smith, 3 February 1967. JMSA Add MS 86765.
[154] Maynard Smith to Rhodes, 6 February 1967. JMSA Add MS 86765.
[155] Maynard Smith to Rhodes, 22 September 1967. JMSA Add MS 86765.

First, the BBC chose Maynard Smith to narrate the programme's anniversary episode "The First Ten Years" (1974). Second, he advised on "The Lysenko Affair" (1974), a topic close to his heart as it had caused his final break with the Communist Party (although he did not leave the party until the invasion of Hungary in 1956). Third, Richard Dawkins suggested John Maynard Smith should narrate the *Horizon* episode based on his book *The Selfish Gene* (both 1976).

'The idea for *Horizon* arose in the context of a review of scientific programming', Tim Boon tells us in his history of the programme's establishment,[156] and coincided with the BBC starting its new channel, BBC2.[157] BBC2 was imagined in contrast to BBC1, from which it should differ, offering something new. 'BBC 2 must appeal to a broad majority of the audience, but we must make the nature of this appeal new, different, and exciting. BBC 2 must capture the national imagination, and if it doesn't, the majority of viewers won't bother to convert their sets or to put up new UHF aerials.'[158] There was to be a focus on "culture" (with the danger of elitism never far away): literature, art, and music, but the programmes also included the sciences and social sciences.[159] *Horizon*, the BBC2 programme on science, therefore set out 'to present science as *a culture* – as a field of human achievement and endeavour as lively, varied and rewarding as any other'.[160] Science should be presented the same way as other human activities,[161] and *Horizon* be a programme on "ideas", 'communicat[ing] to people in other fields; arts fields for instance.'[162] The level of content was to be 'at or a little above the Scientific American level'[163] – something Maynard Smith would have been familiar with, as he frequently wrote book reviews and articles for the comparable popular-science magazine *New Scientist.*

The pilot, produced in 1963 and based on the arts magazine *Monitor,* featured a short film profiling John Maynard Smith.[164] Then still at UCL, he was shown working on fruit flies, his main research focus at the time (before moving on to more theoretical work after

156 Boon 2015, 90.
157 Boon 2017.
158 Peacock 1963, cited in Boon 2017, 327f.
159 Boon 2017, 327f.
160 Leach 1964, cited in Boon 2017, 330 (emphasis in original).
161 Boon 2015, 103.
162 Short 1964, cited in Boon 2015, 102.
163 Singer 1959, cited in Boon 2015, 97.
164 Boon 2015, 100.

becoming dean at Sussex's School of Biological Sciences in 1965). The pilot itself was not received well by the programme director, and it never aired. But Maynard Smith had made enough of an impression as someone at ease on television to be called back for the second *Horizon* episode that did air. "Pesticides and Posterity" (1964) asked, 'Is the widespread use of highly persistent pesticides raising a new kind of ecological problem for our own and future generations to solve? Do we yet know enough to assess the risks we are taking?'[165] In this episode, Maynard Smith moved from being the passive subject of a profile, focusing more on him as a scientist in his social environment, to the active role of speaker. Together with Lord Rothschild FRS (director of research at a chemical company) and Robert Boote (Nature Conservancy) he discussed short films on pesticides.[166] We find Maynard Smith in a role that he occupied throughout much of his broadcasting career: the scientific expert speaking on science and its consequences beyond science – in this case the environment. Essentially being a panellist in a studio, we are also reminded of his earlier – and at this point in fact still on-going – involvement with *Who knows?* In later instances, both on TV and radio, Maynard Smith would frequently be an interviewee, speaker or lecturer, all of which are active roles with him in control.

In spite of some negative press on this episode – Watt, reviewing it for the L.A. based magazine *Variety,* called it 'generally uninspired with a minority appeal', adding it was 'thorough enough, but production was routine, and for a life-and-death subject, showed lack of imagination'[167] – *Horizon* itself kept going and had screened over 1,100 editions by its fifty-year anniversary in 2014.[168] Maynard Smith returned to discuss "Genes in Action" in 1966, in which he and Dr John Curdon of the University of Oxford again deal with the implications of scientific research, this time in genetics.[169] One could consider Maynard Smith's first two *Horizon* episodes as complementary to his episode "The Biologist" for the series *Discovery and Design,* in which he discussed 'the aims and methods of a research biologist'.[170] As pointed out above, however, the three episodes in which Maynard Smith was involved in the 1970s are particularly significant. They are so not only for the reasons

[165] *Radio Times 2116* (28 May 1964), p.13.
[166] Boon 2015, 108f and Boon 2017, 335.
[167] Watt 1964.
[168] Boon 2015, 87.
[169] *Radio Times 2225* (30 June 1966), p.15.
[170] *Radio Times 2288* (14 September 1967), p.26.

already given – being the anniversary episode, treating a personal turning point for Maynard Smith, and becoming an influential episode for the history of evolutionary biology – but also because they highlight some of the issues that Maynard Smith had with science broadcasting.

Figure 6. "The Lysenko Affair", screengrab of titles.

Particularly pressing was the problem of control over content and presentation for Maynard Smith in documentaries. In the mid-1970s he had acted as adviser on the Horizon episode "The Lysenko Affair".[171] Trofim Lysenko was a Soviet biologist active in the 1940s who rejected Mendelism and favoured Michurinism, a form of Lamarckism, in his agricultural practice. Maynard Smith cited Lysenko's definition of heredity in his *Theory of Evolution*: 'Heredity is the property of an organism to require certain conditions for its life and development, and to respond in definite ways to various conditions.'[172] Lysenko, Maynard Smith added, 'believes that if an organism is reared in changed conditions, and in consequence develops along a different path, then, at least in some cases, its offspring also may tend to develop along the new path.'[173] Geneticists, however, had shown that this is an impossibility; although conditions can influence an individual's phenotype, its offspring is not affected unless subject to the same conditions – the changes are not hereditary: 'if two flies which have developed dumpy wings as a result of a heat shock during their pupal life

171 Jones to Maynard Smith, 31 December 1974. JMSA Add MS 86765. Maynard Smith is not mentioned in the credits which do explain the episode was based on the books *The Rise and Fall of TD Lysenko* by Zhores A. Medvedev and *The Lysenko Affair* by David Joravsky.
172 Lysenko cited in Maynard Smith 1958, 51.
173 Maynard Smith 1958, 51.

are crossed, their offspring develop normal wings, unless they too are exposed to a heat shock.'[174]

Writing in the same year as Francis Crick's coinage of the "central dogma" in writing, this explanation of why information transfer only works one way was not yet cited by Maynard Smith. In fact, ten years earlier, at the peak of the Lysenko affair,

> [t]he idea of the inheritance of acquired characters did not seem to me obviously false: indeed, I was prejudiced in its favour. There is something deeply undialectical about a gene that influences development, but is itself unaffected. I therefore do not think that those Marxist philosophers who supported Lysenko were merely jumping on a bandwagon, although doubtless some were. If they sincerely believed that Marxism was a good guide to scientific practice – and I certainly thought that in 1948 – then they were right to support Lysenko.[175]

Lysenko, who since 1939 was president of the Lenin Academy of Agricultural Sciences,[176] was putting his ideas into practice in agriculture. He suggested that he could increase crop yields by changing the environment; the plants would follow suit and adapt – an idea that is based on Michurinism (Michurin is cited in the BBC *Horizon* episode as saying, "change the surroundings and the plants will change"). For Maynard Smith, a member of the Communist Party since 1939, Lysenko was 'the crack in the dyke' – while he had dismissed gulags as capitalist propaganda, he could not dismiss the official Party endorsement of a science which he knew to be false.[177]

> [T]he thing that ultimately undermined my... my faith, if you like, and in a sense it was like being a member of a religious movement I think, if I'm honest, really it was the Lysenko Affair. And people have sometimes said to me, "For goodness sake, why swallow the Gulags and start getting fussed about a few geneticists being put in prison and some errors in science?" The difference was, that what I knew about the Lysenko business was said by the Russians themselves, it wasn't something I could dismiss as capitalist propaganda, it was something that the Russians were publishing. I can remember to this day reading the 1948 book about the proceedings of the Lenin Academy of Agricultural Sciences or something, and being absolutely horrified.[178]

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174 Maynard Smith 1958, 51.
175 Maynard Smith 1992, 49.
176 Jones 1979, 26.
177 Maynard Smith 1992, 49; see also 'Reminiscences of a Cambridge Communist', JMSA Add MS 86817.
178 Maynard Smith and Dawkins 1997, https://www.webofstories.com/play/john.maynard.smith/17.

"The Lysenko Affair", first broadcast on 30 December 1974, opens with a re-enactment of Lysenko's speech given at exactly that 1948 meeting which horrified Maynard Smith. Close-ups of Lysenko (played by Terrence Hardiman) are intercut with scenes depicting the ripping up and burning of books on genetics and the destruction of laboratories by uniformed men. As the speech ends, we see the assembled academicians rising and applauding Lysenko, while the narrator explains that, 'In 1948, with these words, the study of the science of genetics officially ceased in Soviet Russia.' For the next hour, re-enactments, or dramatisations, are mixed with historical footage of Soviet farmers toiling in the fields with primitive ploughs, Stalin, World War II, and Soviet industrialisation and collectivisation. The script interweaves the dialogue during the dramatisations with the narrator's voice-over explanations. The episode shows the lead-up to the 1948 meeting, chronicling Lysenko's beginnings and career, his interactions with Nikolay Ivanovich Vavilov (a Soviet geneticist who defended Mendelism against Lysenko and died in a Soviet prison camp in 1943), as well as the larger issues of Russia's problems with feeding its large population, Nazi Germany invading Russia and Nazi scientists leading to an association of genetics with eugenics and fascism. It then comes full circle by dramatising in more detail the 1948 meeting, closing with Lysenko's speech and more footage of soldiers destroying labs and burning books. The closing words are spoken over a pile of burning books in a dark barn or stable and a closing door, shutting out the light: 'Lysenko's biology became the official dogma. Tragically, it lasted until 1965. But the consequences for the agricultural sciences are still apparent today.'

Figure 7. "The Lysenko Affair", screengrab of closing image.

Historical documentaries have their origins in Britain. Classically, a narrator would dominate, and archival footage be used as illustration. In the 1970s, these forms of (re)presenting history on television were 'replaced largely by more entertaining forms' like inclusion of oral history interviews (which we do not have in "The Lysenko Affair") or fictionalisations of events (which we do have).[179] The hybrid of factual and fictionalised presentation chosen by this *Horizon* episode's writer John Wiles and producer Peter Jones tells an effective story based on history. But the format raises several questions with regard to the perception of history told in this manner and in how far "fact" can be differentiated from "fiction". These are exactly the issues that John Maynard Smith raised after watching "The Lysenko Affair". He wrote to the producer:

> I think you got the spirit of the thing about right. However, I am not very happy about dramatized reconstructions about issues as controversial as this one. The audience have a right to know which remarks were actually made and which have been invented. My impression was that you had kept less close to the available written sources than you might have done.[180]

Since his impression may be wrong, however, Maynard Smith wondered if he could be sent the programme's script to check it against the source material. In particular, he was thinking about the 1948 meeting – since transcripts existed for this meeting, there was no excuse for not using them.[181] Jones' reply is reminiscent of Singer's principles of science broadcasting: 'priority must be given to the medium rather than to scientific pedantry.'[182] Jones too established effectiveness and engagement value of a programme over literal accuracy. He agreed that dramatisation of the past is 'a particularly difficult question' that 'certainly worrie[d him] and many others who have made this sort of programme'. There were guidelines but general, informal discussion within the BBC had been inconclusive. Jones trusted in the audiences' ability to realise that parts were dramatised and thus to an extent fictionalised: 'after all, no record can exist of many of the private conversations portrayed in the film.' He ensured Maynard Smith, however, that even those scenes were based on research in an attempt to be as authentic, if not accurate, as possible. Importantly, and certainly for Maynard Smith – who was put at ease by Jones' letter – was the following

[179] Ebbrecht 2007, 36.
[180] Maynard Smith to Jones, 6 January 1975. JMSA Add MS 86765.
[181] Maynard Smith to Jones, 10 February 1975. JMSA Add MS 86765.
[182] Singer 1966, 744.

point. The hybrid of modes of presentation was in fact particularly effective for science documentaries.

> The alternative at the moment is to use a conventional documentary form, possibly communicating at a lower level and not succeed in getting to grips with the "activity" of science" [*sic*]. (This in fact is one of the things that I would suggest is an advantage of this format; namely that we are actually dealing with the activity of science in addition to the concepts and ideas.)
>
> I do not know whether you will agree with this but most conventional science documentaries can deal quite well with an idea or a concept sometimes very well, but it can only rarely communicate what doing science is like in a particular political or historical climate.[183]

As noted above, science is not always straightforward to translate from the lab or office. Science documentaries employing dramatisation can be said to both illustrate and construct science[184] (the same goes for historical documentaries, and in the case of "The Lysenko Affair" we are dealing with both science and history). While documentaries aim at presenting reality, they are 'a Janus-face genre, at the same time evidence and artifice'.[185] Maynard Smith's complaint about blurring the lines between fact and fiction in re-enactments echoes that directed at producers when they first started using these new ways of visualisation. The BBC continued to use dramatisations in their documentaries however, and increased the use of re-enactments and staged scenes after 1980, greatly 'expand[ing] the creative possibilities of producers and directors'. At the same time, re-enactments 'were almost invariably paired off with the authoritative expository mode, often voiced through a reminiscing scientist. As a result, the fiction effect was made subordinate to the reality effect.'[186]

Maynard Smith saw potential dangers in the voice-over as a method of presentation as well. He feared that it rendered scientists in science features invisible as people. In 1983 he spoke at the annual meeting of the British Association for the Advancement of Science on "Science and the Media". This is the same talk in which he spoke favourably of good science journalism as discussed earlier. In the latter part of the talk, however, Maynard Smith highlighted that science journalism and science broadcasting do not always get it

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183 Jones to Maynard Smith, 28 January 1975. JMSA Add MS 86765.
184 Van Dijck 2006, 14.
185 Corner 1996 referenced in Gouyon 2016, 18.
186 Van Dijck 2006, 10.

right. It was this part which *Nature* reported on as well, in a short note called 'Scientists to be seen and heard':

> Editors should give more prominence to scientists as people in their science features [...]. Scientists, for their part, should make a greater effort to be understood by the public, even at the cost of abandoning some of the qualifications they might ordinarily make to cover themselves.[187]

The latter relates to a point Maynard Smith had made already in 1969: 'Scientists on the whole are reluctant to stop hedging and qualifying and to come right out with it.'[188] Even though he made a point of saying that this should not deter them from learning how to speak, and then speak, on the media, these fears may have been and may still be exacerbated by the authority that invisible voice-overs convey. José van Dijck talks of the "expositor mode" which 'in its most prototypical form consists of a voice (or voice-over) explaining what a scientific idea, paradigm, or discovery entails.' If the voice is that of a scientist – even better, of the scientist whose research is presented – this adds additional authority, credibility, and institutional legitimacy to the claims made.[189] Such authority, credibility and legitimacy do not necessarily help audiences to take in qualifications the scientist may include about their research. As Scott and White have noted, the voice-over presents the viewer with 'an authoritative commentary by an omniscient narrator, combining the "objective" discourse of scientific knowledge (facts and figures) with touches of anthropomorphism'.[190] Personalising research and identifying it with the people doing it, as Maynard Smith preferred, comes thus with the danger of over-stating these people's certainty about the object or results of their research as well.

3.6 Conclusion

As Morley notes, we must not forget scientists' non-specialist communications as being of less value than their specialist outputs.[191] Some scientists, like Munro Fox, 'successfully juggled the two activities', rather than letting one take over the other, as happened, for instance, with Sir Julian Huxley or Sir John Arthur Thompson, whose research output

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[187] Beardsley 1983, 6.
[188] Maynard Smith 1969, 180.
[189] Van Dijck 2006, 8.
[190] Scott and White 2003, 321 cited in van Dijck 2006, 13.
[191] Morley 2019, 89.

diminished as their non-specialist work increased.[192] John Maynard Smith was equally exceptional in maintaining both a highly successful research career and being a public intellectual who regularly appeared on radio and television. Yet he was also unusual – when Paul Merchant interviewed scientists on their public engagement, he found that '[t]he desire to communicate beyond science seems to have been more strongly connected to their own experience than to a concern for the experience of others. [...] there is very little talk of duty or interest in public understanding in these interviews.'[193] In Maynard Smith, we have seen the opposite: a focus on explaining science and it being a scientist's social responsibilities. He returned to radio and television time and again, becoming more and more 'every child's vision of the ideal professor' as his hair grew whiter, wilder and longer, wearing 'spectacles [...] so dirty as to be practically opaque'.[194] His broadcasts fulfilled a number of roles, which often overlapped and reinforced each other: explaining science, reflecting on science, and defending science. All of these also had elements of advertising science: Maynard Smith projected his enthusiasm for science and his feeling of its importance for society.

While it is impossible to limit the different types of broadcasts to specific time periods, a general trend is visible. This trend aligns with the analyses of recent work on scientific broadcasting in the UK, namely that the BBC – and Maynard Smith almost exclusively appeared on the BBC – moved away from expositional programmes to programmes that mediated science and scientists in both content and format. *Horizon*, the BBC's flagship science documentary programme, is only one example of the BBC moving from a predominantly celebratory depiction of science to 'a more critical turn that would be confirmed throughout the decade' just about the same time that the BSSRS was founded. 'It was thus falling in line with the critical approach to science and technology observed in other mass media for the period'.[195] Maynard Smith himself changed from being the creator of his own content in the very first broadcasts to being primarily (though not exclusively) a contributor from the late 1960s onwards. In terms of content, his work changed from straightforward exposition of scientific ideas to discussion of science and society relationships to defending science against creationism and neo-Darwinism against

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192 Morley 2019, 98.
193 Merchant 2018, 377.
194 Nanjundah 2005, 77.
195 Boon and Gouyon 2014, 477.

punctuated equilibria and Lamarckism. While initially critical of focusing more on science's social implications than science's ideas, he came to discuss both. In fact, he carried some of these ideas over into his support for the British Society for Social Responsibility in Science, which tried to address the same shifts in attitudes towards science from within science that the BBC was meeting in its shift to more science-critical programming.

At the same time that Maynard Smith reflected on the science and society relationship he also reflected on the science and media relationship, staying critical both publicly and privately. Given his conviction that scientists needed to speak about their work, it is not surprising that he submitted to the BBC's mediation – it was an important platform for speaking to non-specialists – but he could not shake off his preference for accuracy over authenticity in science broadcasting. As Reid, the scientist turned producer, said in 1969, the founding year of the British Society for Social Responsibility in Science:

> Television wants science, but science needs television. It needs television because television can provide the stimulation for the duologue which is so badly needed between those inside and those outside science. It is clear that the rate of scientific and technological advance is becoming so great that society is in danger of no longer being able to cope at the same rate with the harmful effects which accrue along with the benefits. It is a duty of science to communicate its progress in a way society can understand, and so that society can respond and join in the acts that need to be performed to accommodate the progress.[196]

Regarding the related 'public understanding of science' movement, this did not fully take off until a 1985 report by the Royal Society, which addressed policy issues in regard to the public's (lack of) scientific knowledge and understanding. Like Maynard Smith had in his 1969 'The conscience of the scientist' article, '[t]he report asked for more science in the mass media and urged scientists to improve their communications skills and to consider public communication as a duty'.[197]

The following chapters will move away from the focus on communicating science to non-specialists and yet it will never completely disappear. Chapter 4, for instance, will return us

[196] Reid 1969, 458.
[197] Gregory and Lock 2008, 1254.

to *Horizon* and Chapter 5 brings back the topic of defending science, which has only been touched upon above.

PART 2: PROFESSIONAL SCIENCE

The previous chapter talked about Maynard Smith and his early interest and strong presence in communicating science to non-specialists, even before he was a well-known scientist himself. His communications in written and spoken form are linked by a strong emphasis on the fact and facts of evolution by natural selection, by an attempt to reach diverse audiences on a spectrum from non-expert to expert, and an increasing reflection on the state and implications of his science, evolutionary biology, and science in general.

The end of Part 1 left Maynard Smith in the early 1970s, although his broadcasting and popular publishing continued well into the 1990s. The "birdwatcher's version" of his and Eörs Szathmáry's *Major Transitions of Evolution* (1995) was published in 1999 as *The Origin of Life*. Maynard Smith discussed the book's claims with Melvyn Bragg and Colin Tudge on BBC Radio 4's *In Our Time* in April 1999. Now, moving from the popular into the professional world – although the two were never quite that distinct for Maynard Smith – we first have to briefly turn back on ourselves and look at the 1960s again, and from there continue to the late 1970s and the mid-1980s. This shift from "popular" to "professional" science reflects a shift in Maynard Smith's working life. The 1970s in particular are the time when he produced some of his best-known work, evolutionary game theory. He was awarded with being elected Fellow of the Royal Society in 1977.

Historiographically, we are staying in the history of evolutionary biology as our overarching theme and in terms of biological issues, group selection is the uniting focus. I am then bringing in issues from the world of scientific priority and intellectual property, as well as the question of the origin and development of scientific ideas. Both chapters have Maynard Smith reviewing a manuscript sent into a scientific journal as their starting point but with diametrically opposed outcomes: conflict and collaboration. In Chapter 3, the issues of priority and property are therefore closely linked to the issue of scientific controversy (explored in more detail in Part 3). Specifically, it addresses the relationship between John Maynard Smith and William Hamilton around the idea of "kin selection". Chapter 4, on the other hand, discusses the development of evolutionary game theory and evolutionarily stable strategies based on work of and collaboration with George Price.

4 Conflict over kin and kindness

Within science, reputation rests largely upon discoveries and theories which are often named after their discoverer or the person who first developed them. In priority disputes claims are therefore made 'to have done something innovative before others did it' and the 'the ownership (of intellectual property) asserted is of an individual's right to public credit for an innovation.'[1] Given the nature of science, with its formal and informal networks of communication and circulation of ideas, and the fact that it draws on shared and available knowledge and techniques, priority disputes are rather common. Studying points of contestation like these brings out dynamics of science that are usually hidden, like gender and hierarchical biases, politics and ideologies.[2] Intellectual property can thus function as a tool 'prompting the questions that might save us from accepting too simple a version of what happened and why.'[3] Still, 'intellectual property has stubbornly remained, within the history of science, a specialized interest and a peripheral topic.'[4]

This oversight becomes even more pertinent when connected to science communication. 'The scientific community,' said Jerome B. Wiesner, science advisor to John F. Kennedy, in 1962, 'constitutes an extremely complex social system which is very little understood, least of all by the scientists themselves.'[5] This social system is, according to Ludwik Fleck, highly influential for recognition and understanding in science; he wrote of the social causes and conditions of knowing: any realisation is the result of the particular social and scientific circles a scientist is part of (*Denkkollektive* in Fleck's terminology).[6] It is also, in large part, mediated through scientific literature. Fleck devoted several parts of his monograph to different types of literature. "Journal science" is defined by its preliminary and personal nature: reports and articles mostly do not present final facts nor overarching systems that everyone can and will agree to. Travel of ideas back and forth through the *Denkkollektive* and other types of literature (handbooks, popular books) will, over time, transform these into accepted knowledge.[7] (The sentiment is, in some sense, echoed by

1 MacLeod and Radick 2013, 190; see also Pinch 2015, 281.
2 Pinch 2015, 282.
3 MacLeod and Radick 2013, 199.
4 MacLeod and Radick 2013, 189.
5 Cited in Ravetz 1996, 243.
6 Fleck 1935/2017, 53ff.
7 Fleck 1935/2017, 156f.

Jerome Ravetz, when he wrote 'scientific inquiry is a human activity, in the short run imperfect and fallible, and in the long run conditioned by social influences acting in an extended time.'[8]) But Fleck misses out on the some larger issues around how journal science functions: not only in the sense of what its function is, but how it itself functions. On the first point, we need to bring back in intellectual property and priority, on the second, and relatedly, the system of peer review and refereeing.

Some of the issues were brought to light in public controversies around fraud and plagiarism in the 1980s. As Marcel LaFollette writes, 'cases began to surface at Harvard, at Yale, at state universities, and in several different fields.'[9] This led to discussions within science and politics about ethics and funding. She categorises different violations of 'legal, social, and moral norms'.[10] One, which has received 'relatively little attention from scientists or publishers', is misconduct by referees of article manuscripts submitted for publication in journals.[11] Scientific articles and research reports are unusual in terms of intellectual property in that the 'property comes into existence only by being made available for use by others; and a research report hoarded in secret is almost certain to depreciate in value.'[12] A case study will illustrate this and other issues around journal sciences: the kin selection controversy between John Maynard Smith and William Hamilton. Part of the story that follows has been told in Oren Harman's biography of George Price and Ullica Segerstråle's Hamilton biography as well as her book on sociobiology.[13] Those discussions address the Hamilton matter primarily in the context of the relationship between the three scientists and the issues around group selection. They also touch that most sensitive of issues, scientific priority and giving due credit for one's ideas and inspirations. I will develop these points, bringing them together and focusing specifically on the types of (mis)communication that form the backbone of the controversy.

Figure 8 summarises the timeline of the events in order to help the reader follow the case. First, I recount the story of the 1964 papers and their publication in the context of peer reviewing and scientific publications. After that I offer a citation analysis to take a

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8 Ravetz 1996, 243.
9 LaFollette 1992, 1.
10 LaFollette 1992, 32 and chapter 2.
11 LaFollette 1992, 54f.
12 Ravetz 1996, 245.
13 Harman 2010, Segerstråle 2013, 2000.

closer look at the amount of attention the papers and concepts at the heart of the conflict have received. The next part sees the conflict shift from problematising peer review to different conceptualisations of scientific priority.

year	**event**
1955	Haldane publishes 'Population genetics' in *New Biology*
1962	Vero Wynne-Edwards, *Animal Dispersion in Relation to Social Behaviour*
summer 1963	Hamilton submits draft introducing inclusive fitness to *JTB* and in August, goes to Brazil for field studies
autumn 1963	Hamilton publishes 'The evolution of altruistic behavior' in *The American Naturalist*
1963	2 reviewers return draft, *JTB* sends it to Maynard Smith – Maynard Smith at some point discusses it with Lack and others in Oxford
February 1964	Hamilton, still in Brazil, finishes revisions
14 March 1964	Maynard Smith publishes 'Group selection and kin selection' in *Nature*
July 1964	Hamilton publishes 'The genetical evolution of social behaviour' in two parts in the *JTB*
ca. August 1964	Hamilton returns from Brazil
19 October 1972	Price alerts Maynard Smith to Hamilton's feelings
24 October 1972	Maynard Smith's reply
28 August 1975	Maynard Smith reviews Wilson's *Sociobiology* in the *New Scientist*, including anecdote on Haldane and the genetics of altruism
1 July 1976	Hamilton writes letter to the *New Scientist*, doubting the Haldane anecdote
22 July 1976	Maurice Dow writes to the *New Scientist* in support of Maynard Smith
29 July 1976	Maynard Smith replies to Hamilton in the *New Scientist*
19 October 1977	Hamilton writes directly to Maynard Smith
27 October 1977	Maynard Smith replies
23 October 1980	Hamilton apologises to Maynard Smith for doubting the Haldane anecdote

Figure 8. Chronology of the Hamilton-Maynard Smith conflict.

4.1 1960-1964: refereeing inclusive fitness, publishing kin selection

William D. Hamilton has been described as 'a good candidate for the title of most distinguished Darwinian since Darwin'.[14] He was an eager naturalist during his childhood years, collecting and botanising in Kent, and then read genetics at the University of Cambridge. He became intrigued by the ideas of Ronald A. Fisher, whom we have briefly encountered previously as one of the three founding fathers of the modern synthesis – the others being J.B.S. Haldane and the American Sewall Wright. When Hamilton studied at Cambridge, Fisher was still around but not teaching anymore; he had retired in 1957.[15] But Hamilton was influenced by his book *The Genetical Theory of Natural Selection* and by neo-Darwinism, although he noted that others were not so much: 'all my supervisors and lecturers so far are strongly anti-mathematical biology'.[16] He therefore had to discover Fisher and his work for himself.[17] In the late 1950s, Hamilton decided to study the genetics of altruism for his PhD. He had difficulties getting funding though. The combination of the words "genetics" and "altruism" seemed to put off a lot of people, who were possibly suspecting eugenicist ideas. Lionel Penrose at the Galton Laboratory at University College London was one of them.[18] Ultimately, however, Hamilton secured a scholarship at the London School of Economics, and once he outgrew his supervisors there, he became co-supervised by Cedric Smith, thus making his way into the Galton Laboratory after all.[19]

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[14] Dawkins 2000.
[15] Segerstråle 2013, 55.
[16] Segerstråle 2013, 51.
[17] Hamilton 1996, 21.
[18] Segerstråle 2000, 59; Segerstråle 2013, 75-77; Hamilton 1996, 14.
[19] Segerstråle 2013.

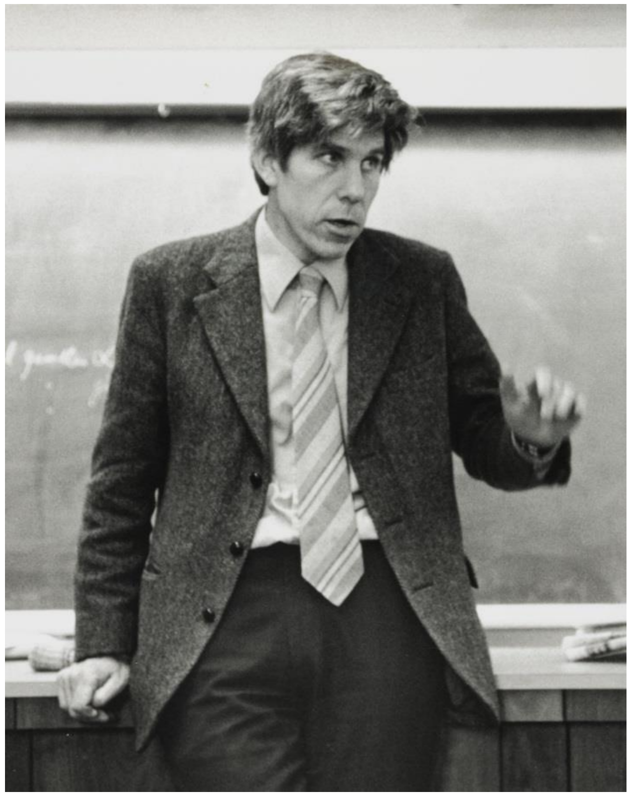

Figure 9. William D. Hamilton. Harvard, 1978. © Sarah Blaffer Hrdy.

In later years Hamilton recalled feeling unappreciated and unsupported as a graduate student. He was mostly working from home or, occasionally, would go and sit on a bench at Waterloo station to work while having people around. He does not seem to have spent much time at the Galton Laboratory, where he did not have a desk. Sheila Maynard Smith, John Maynard Smith's wife who was working there at the same time, did not recall seeing him around.[20] Hamilton, however, remembered that at some point he was introduced to John Maynard Smith, who was still teaching at UCL in the early 1960s. Cedric Smith had introduced the two and, as Hamilton pointed out in a letter sent to Maynard Smith in 1977, told him 'with his usual unambiguous clarity […] that I was working on "altruism"'.[21] Unfortunately, Maynard Smith could not recall that meeting or the young man and his project. One reason may have been Hamilton's awkward personality,[22] another that Maynard Smith did not have much respect for Hamilton's supervisor.[23]

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[20] Segerstråle 2013, 64f.
[21] Hamilton to Maynard Smith, 19 October 1977. JMSA Add MS 86764.
[22] Segerstråle 2000, 62.
[23] Maynard Smith to Hamilton, 27 October 1977. JMSA Add MS 86764.

> I mean, I think Cedric Smith was and is a good statistician but I don't think he understood what biology was all about. If Bill was then anything like he is now, and he probably was more so, he was a deeply inarticulate young man. And I can just imagine myself being introduced to this inarticulate kid by an academic I didn't greatly respect, and not realising I was being introduced to a genius, how the hell do you know?[24]

Why were they discussing this failed meeting from the 1960s in the late 1970s? A priority conflict, simmering away on Hamilton's part since 1964, had finally made it out into the open in 1976. The conflict was about Hamilton's ground-breaking 1964 paper (in two parts) on 'The genetic evolution of social behaviour' and Maynard Smith's 1964 letter to *Nature*, 'Group selection and kin selection'. The former had been published in July, the latter in March – and both were discussing a way in which individualist selection could explain altruistic behaviours.

Hamilton's 1964 paper had grown out of his PhD work. By 1962, Hamilton had been working on the altruism problem for roughly three years but he still had not published anything. '[W]ith my hope of receiving my PhD at the time seeming to founder […], I urgently needed something to represent the fruits of the 3 years I had spent doing research.'[25] He sent a short paper to *Nature* in which he summarised his main points and findings. It was almost immediately rejected as 'too specific' for the journal. So Hamilton resubmitted his paper, this time to the *American Naturalist*, where it was accepted and published in 1963. Entitled 'The evolution of altruistic behaviour', it tackled the problem that

> the classical mathematical theory of natural selection […] cannot account for any case where an animal behaves in such a way as to promote the advantages of other members of the species not its direct descendants at the expense of its own.[26]

Hamilton briefly summarised what Fisher, Wright, and Haldane had thought on the subject and referenced a paper Haldane had published in *New Biology* in 1955.[27] At the same time,

[24] Maynard Smith and Dawkins 1997, https://www.webofstories.com/play/john.maynard.smith/36.
[25] Hamilton 1996, 3.
[26] Hamilton 1963, 354.
[27] Hamilton 1963, 354f.

after many revisions already wanted by his supervisor Cedric Smith, he submitted a long version with the full details of his "inclusive fitness" idea to the *Journal of Theoretical Biology*.

Inclusive fitness,[28] as formulated by Hamilton, is made up of two parts: direct and indirect fitness. Fitness is usually taken to be the number of your offspring that survive to adulthood. In the context of inclusive fitness, this is direct fitness: your own reproductive success. The important conceptual realisation, however, lies in indirect fitness. Hamilton understood that organisms will also attempt to maximise the reproductive success of their relatives. That is, certain types of behaviour – like altruism – evolved because they guarantee that copies of your own genes are passed on to the next generation through your relatives. The closer you are related, the higher the degree of altruism as, for instance, you share half of your genes with your siblings and parents, a quarter with your grandparents, and an eighth with full cousins.

After submission of his long paper outlining inclusive fitness, Hamilton took on a different adventure. One reason was that by then, he was 'utterly tired of it',[29] another that his supervisors suggested a PhD needed more than theory and mathematics. Therefore Hamilton left Britain in August 1963 to do field studies on social insects in Brazil; he stayed for a year.[30] While in Brazil and collecting and observing insects, he also needed to revise his paper. The editor had informed him of the reviewer's wishes. This reviewer turned out to be John Maynard Smith,[31] a fact that Hamilton at no point mentioned in his autobiographical reminiscences *Narrow Roads of Gene Land*. In fact, Maynard Smith does not appear at all in the chapter on the 1964 papers, despite – or perhaps precisely because of – the priority conflict about to ensue.[32] This omission in 1996, thirty years after the episode described, shows the long-lasting impacts it had. Although it took a while, Hamilton made the requested changes and sent off the revision in February 1964.[33] When he returned from Brazil, he found that his paper had been published by the *Journal for Theoretical Biology (JTB)* in July 1964. But he also found that Maynard Smith – his referee – had published a letter in

[28] 'inclusive fitness' 2016.
[29] Hamilton 1996, 29.
[30] Segerstråle 2013, 86.
[31] Segerstråle 2013, 103.
[32] Cf. Hamilton 1996, chapter 2.
[33] Segerstråle 2013, 103.

Nature in March 1964, which contained an idea, "kin selection", which was close to Hamilton's "inclusive fitness".

As suggested by the letter's title, 'Group selection and kin selection', Maynard Smith understood these two ideas as opposed. The paper points to the fragility of group selection, highlighting kin selection as an alternative explanation for certain kinds of behaviour in animals. Before the 1960s, group selection was the main explanation for altruistic behaviour: animals would behave in a manner detrimental to their own survival and reproduction chances "for the good of the species". A common example of behaviour that was explained in such group-selectionist terms are warning calls – drawing the predator's attention to yourself, thus putting yourself at risk while warning the whole group. Another example is that an individual forgo reproduction but support others, such as worker bees do in a colony. Kin selection explains such altruistic behaviours differently.[34] Altruism did not evolve because it is good for the species or group, but because it is good for the individual animal. The idea is 'the evolution of characteristics which favour the survival of close relatives of the affected individual'.[35] Relatives share your genes, so if they survive they will pass on those genes they share with you to their offspring. '[A]ltruists benefit their relatives who tend to share the same genotype as themselves.'[36]

Group selection was hugely popular among some biologists and the levels of selection question is still 'one of the most fundamental in evolutionary biology'.[37] Since their student days, neither Hamilton nor Maynard Smith had liked group selection.[38] Others, for instance Haldane and Lack, were not agreeing with it either. As neo-Darwinists they could not see how natural selection could work on a group or species level. But in 1962, the year before Hamilton's draft for the *JTB*, the ethologist Vero Wynne-Edwards had published a book called *Animal Dispersion in Relation to Social Behaviour,* an explicitly group-selectionist account of animal behaviour. When he first came across it, Maynard Smith did not read it himself but gave a copy to Haldane. Haldane had temporarily returned from India, where he had emigrated to in 1957, and was being treated for cancer in University College Hospital.[39] He

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34 Anonymous 1976.
35 Maynard Smith 1964, 1145.
36 Charlesworth 2017, 776.
37 Okasha 2008, 138.
38 Hamilton 1996, 21; Maynard Smith and Erickson 2004, JMSA (uncatalogued).
39 Kohn 2004, 227.

mocked the group-selectionist assumptions made in the book, in particular that animals have 'group adaptations to regulate population sizes':[40]

> there are these blackcock, you see, and the males are all strutting around, and every so often a female comes along and one of them mates with her. And they've got this stick and every time they mate with a female, they cut a little notch in it. And when they've cut twelve notches, if another female comes along, they say, "Now ladies, enough is enough!"[41]

So when, in 1963, the *Journal of Theoretical Biology* sent Maynard Smith Hamilton's paper to review, he had become 'acutely aware of the need to promote an individual-selectionist approach to evolutionary change',[42] which Hamilton's paper suggested. Then Lack called from Oxford, inviting Maynard Smith to discuss the book and the group selection issue. (Wynne-Edwards' arguments on the development of the rate of reproduction in a species were in direct contradiction to Lack's.[43]) At the meeting with Lack, Niko Tinbergen, and Arthur Cain, Maynard Smith brought up the ideas he had come across in Hamilton's manuscripts. They came up with the term "kin selection" to distinguish them from group selection, the term which Maynard Smith then used in letter to *Nature*.[44]

Hamilton's paper Maynard Smith recommended for publication, after struggling through it for the reviewing process. The two previous reviewers had in fact failed to grasp the mathematics used by Hamilton, so the editor had sent it on to Maynard Smith who also recalled that

> it was deeply obscure. It is a hard paper to read […]. It was made more obscure by the trivial fact that his (Hamilton's) notation was one of indices which were either open circles or closed circles, but on his typewriter, all circles were closed, it was a messy typewriter. […] I can remember wading through this and saying, I understand why the other referees didn't understand it, I'm not understanding this. Fortunately, I went on just long enough before giving up, and came, about halfway through the paper, to this discussion of social insects.[45]

Maynard Smith agreed with the editor that the paper contained a great idea, and his reaction mirrored that of Thomas Huxley on encountering Darwin's work: 'Of course, why didn't I

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[40] Ruse 2009, 472.
[41] Kohn 2004, 227.
[42] Ruse 2009, 472.
[43] Borrello 2005, 45.
[44] Segerstråle 2000, 63.
[45] Maynard Smith and Dawkins 1997, https://www.webofstories.com/play/john.maynard.smith/36.

think of that!'[46] But to help readers understand and appreciate the ideas, he suggested that the paper be split into two. 'The first part would be a derivation of the concept of inclusive fitness. The second part would show how inclusive fitness played out in practice in some concrete cases and give examples from nature.'[47]

The two 1964 publications, with Maynard Smith, the referee of Hamilton's paper, publishing a letter and introducing a different term for an idea Hamilton had developed before Hamilton's paper was out, suggest a priority dispute that was not obvious to Maynard Smith. It took George Price, an American polymath with whom he was collaborating, to point it out to him in 1972. Hamilton, according to Price,

> thinks that you wronged him on the matter of "kin selection". His account of the matter is that you refereed his 1964 paper for the Journal of Theoretical Biology, and required a major revision (changing it from one paper to two) that caused a nine-month delay in publication, and meanwhile you sent Nature a letter with the term "kin selection" that has received much of the credit for the idea.[48]

For Hamilton, this was a matter of intellectual property if not outright plagiarism. 'The genetical evolution of social behaviour' was his report on three years' worth of research, and 'this property is […] real and important to those who possess it. As a certification of the scientist's accomplishment, it can bring immediate rewards. And as an implicit guarantee of the quality of his future work, it brings in interest for some time after its production.'[49] He was an early-career researcher who needed to build up a portfolio of publications for the future, and who demanded recognition for his efforts and original insights. The refereeing system of scientific publishing should have guaranteed the establishment of the ideas as Hamilton's. In fact, the term "peer review" was not coined until the early 1970s and the system of refereeing that has come to define scholarly publishing is equally a product of the mid- to late twentieth century.[50] The function of the scientific journal itself has shifted over time, from publishing 'interesting or intriguing phenomena […] worthy of future

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[46] Harman 2010, 167; Segerstråle 2000, 54.
[47] Segerstråle 2013, 103.
[48] Price to Maynard Smith, 19 October 1972. JMSA Add MS 86764.
[49] Ravetz 1996, 245.
[50] Moxham and Fyfe 2018; Baldwin 2018.

consideration' to establishing credibility of and priority for research.[51] Journals still are a means to advance science by publishing new ideas but at the same time exert quality control over them:

> In principle, the materials become public with the minimum of delay, are guaranteed to be of at least a minimum standard of quality, and can be put to use without the time-consuming process of obtaining permission, or negotiating for rights with the owner. All that is required for the protection of the personal property embodied in them is that a result which is used in another paper be cited there.[52]

To ensure that quality control, the system of peer review has been introduced. Melinda Baldwin also links it to general trends toward standardisation (as well as to lighten editorial workloads).[53] Peer reviewing then came to be 'cast as the only acceptable method of evaluating scientific quality' over public debates in the 1970s.[54] Although these processes developed after the Maynard Smith-Hamilton episode, the general idea and related expectations were already in place.

Baldwin mentions the current crisis of peer reviewing, referring to discussions over whether it does in fact guarantee scientific quality. What it ignores is another inherent problem in refereeing – not linked specifically to peer review. Maynard Smith once remarked, 'I seem to have this fate of getting ideas from other people's manuscripts when I referee them, but I suppose it's unavoidable.'[55] In a way it probably is; once read – and possibly read quite intensely, in order to make sure of viability, quality etc. – how could an idea not continue a life of its own in the reviewer's mind? Jeremy Ravetz, in his *Scientific Knowledge and its Social Problems,* gives two examples of scientists who repeatedly got into priority disputes because they developed other people's ideas after coming across them informally or in the reviewing process. Jean-Baptiste Biot, a French nineteenth-century physicist, had a habit in which he learned 'of a discovery informally from a colleague or friend, and then with his experimental skill and the superior material resources at his disposal to exploit the discovery and report on his own series of experiments, before his informant had the opportunity to develop the work.'[56] Even more 'notorious' was another

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51 Moxham and Fyfe 2018, 873.
52 Ravetz 1996, 246f.
53 Baldwin 2018.
54 Baldwin 2018, 558; cf. LaFollette 1992.
55 Maynard Smith and Dawkins 1997, https://www.webofstories.com/play/john.maynard.smith/42.
56 Ravetz 1996, 256.

Frenchman, the mathematician Augustin-Louis Cauchy (another nineteenth-century example). Drawing on Hans Freudenthal's account in the *Dictionary of Scientific Biography*, Ravetz tells us that

> [o]n receiving a paper for refereeing, he (Cauchy) could not resist the temptation to recast the proof, improving the result, developing and generalizing it in all sorts of ways, and finally publishing it in a journal to which he had rapid access. When the paper which had originally stimulated him finally appeared in print, it would seem singularly crude and pointless in comparison to the results already published by the master.[57]

Freudenthal added in the original account that

> This looks like extremely unfair behavior, and in any other case it would be—but not with Cauchy. Cauchy did not master mathematics; he was mastered by it. If he hit on an idea—and this happened often—he could not wait a moment to publish it.[58]

Cauchy even founded his own journal to publish more quickly and on whichever subject had taken his interest at any given time. At the same time however, Freudenthal wrote, Cauchy was careful to report on papers sent for review honestly and properly, and he was 'the most careful in quoting others.'[59]

Parallels with Maynard Smith are not that hard to draw. He was aware of the merit of Hamilton's work and advised the *Journal of Theoretical Biology* to publish it. Although he may not have grasped its full potential immediately or really dug into the details of the mathematics, he did see a way in which it could and, from his point of view, should be developed, and that was in specific opposition to Wynne-Edwardsian group selection.[60] So after discussion of these issues with colleagues at Oxford, he formulated a model of his own under the name "kin selection" – influenced by what he had read in Hamilton and because he was actively trying to distinguish Hamilton from Wynne-Edwards.[61] In fact, Maynard Smith's self-perception was 'as someone who at an early point was drawing attention to Hamilton's contribution', knowing 'that Hamilton's big *Journal of Theoretical*

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57 Ravetz 1996, 256.
58 Freudenthal 1981, 134.
59 Freudenthal 1981, 134.
60 Kohn 2004, 228.
61 Kohn 2004, 229; Segerstråle 2000, 63.

Biology paper was forthcoming and would clarify any details further.'[62] Hamilton's priority and right to "inclusive fitness" in terms of intellectual property is in fact guaranteed by this paper when we include the backstage processes of journal publication: 'A result belongs to the man who first publishes it, or whose paper first reaches the editor of a recognized journal.'[63] And yet the episode can be construed as referee misconduct, as Hamilton did. This is an aspect of the refereeing system that does not receive much attention from either scientists or publishers. LaFollette suggests it may be because 'it remains hidden behind a veil of ambiguity.'[64] Like Hamilton, who had been out of the country when the respective 1964 papers were published, the author may only become aware of the similarities some time after publication. In the Hamilton case, perception was another problem. Although Maynard Smith later agreed that he should have cited Hamilton's papers as (in press), at the time he felt that citing the previous 1963 paper was sufficient to show he was building on Hamilton's ideas. He was reframing them specifically for the group selection debate which was what occupied him.

At the same time, Maynard Smith possessed a mathematically-intuitive mind that was quick to grasp an idea's potential. Cambridge zoologist Tim Clutton-Brock has pointed out that it was not unusual for Maynard Smith to come across an idea in a seminar or other, more or less formal settings, and to start thinking about it mathematically, developing an argument into a mathematical model.[65] Academia is full of instances of such communication in which a project or problem may be only partially formulated and without the protection of a publication to reinforce a scientist's intellectual property rights. 'If scientists were working in a social vacuum, this frequently lengthy period during which a project is not property, would not be too significant. But scientists generally need to communicate informally through the interpersonal channel about their work; and every such communication puts one's property at risk.'[66] And Maynard Smith has claimed – according to Hamilton – that 'in science the main thing is to advance human understanding as fast as possible, in comparison to which end scientists individual reputations are very

[62] Segerstråle 2000, 63.
[63] Ravetz 1996, 253; see also LaFollette 1992.
[64] LaFollette 1992, 54f.
[65] Personal communication, 11 May 2018.
[66] Ravetz 1996, 254.

secondary.'[67] Up to a point, Hamilton wrote, he agreed with that ideal but pointed out that the second part was in practice often difficult to hold up. He suggested that Maynard Smith, too, probably did – and maybe even should – bother more about priority and recognition of individuals than he let on.

The Hamilton case seems to have made Maynard Smith more cautious about referencing when he was using other's ideas that may not have been published yet. Thus he wrote to Alan Grafen in 1987:

> You may remember that when we were talking last time I was in Oxford you produced what I thought was an extremely ingenious explanation of why there are long-term but very slow trends in evolution. You have probably forgotten this. However, I would like to use the idea in something I am planning to write. Why don't you write a one page paper for the JTB? Or if you prefer, I will simply give you a "personal communication" acknowledgement.
>
> But I do think it would be better if you actually published it.[68]

4.2 1964-1975 and beyond: inclusive fitness *versus* kin selection

The conflict between Hamilton and Maynard Smith seems to have, if not resolved, at least been put aside after Price mentioned it in 1972. There was certainly no communication from Hamilton to Maynard Smith. The wider scientific community, of course, was not quiet on the ideas presented in Hamilton's paper in the *JTB* and Maynard Smith's letter to *Nature*. Doing both a short-term and long-term bibliometric analysis – specifically, for this case, analysis of frequency of and trends in use of these two publications and the terms "inclusive fitness" and "kin selection" – highlights some interesting points with regards to perceived and real reception as well as a difference between use of the terms as opposed to the mathematics behind inclusive fitness and kin selection. At the same time, the sum total of citations alone does not, of course, reveal anything about the kind or depth of engagement with the source. Yet Michael Ruse's citation analysis of two types of works by Stephen Jay Gould (more on him in Chapter 5) showed that 'random sampling suggests that the

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[67] Hamilton to Maynard Smith, 19 October 1977. JMSA Add MS 86764.
[68] Maynard Smith to Grafen, 13 April 1987. JMSA Add MS 86576.

perfunctory tends more to the popular publications and utilization to the professional publications.'[69]

With regards to Hamilton's work, I am not the first to look at the number of citations for the 1964 paper. He himself did so in a commentary for *Current Contents*, remarking that 'the rise in citation of the combination, after a slow start, eventually became dramatic', to the point at which it was *JTB*'s 'most cited paper ever.'[70] In an endnote in the second edition of his *Selfish Gene*, first published in 1989, Richard Dawkins used bibliometrics to illuminate the work's life in the professional world as a 'prime example of […] dormancy followed by rampant propagation.'[71] By using the *Science Citation Index* (same as Ruse did for analysing Gould and others), Dawkins picked up on the same trend as Hamilton: there were very few citations after publication and until the mid-1970s, after which followed an exponential growth. He identified 1973/74 as the starting point for the upsurge in citations and thus interest in Hamilton's ideas (he uses kin selection, not inclusive fitness). Nowadays, the *Science Citation Index* is available online, and counting of citations need not be done by hand anymore. The results differ however, depending on whether one uses for example the databases at Web of Science or SCOPUS. Not only do they cover a different set of journals, SCOPUS, unfortunately, currently only holds cited references back to 1970. These can be supplemented by looking at Web of Science.

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[69] Ruse 1999, 148.
[70] Hamilton 1996, 21.
[71] Dawkins 1989, 325-329.

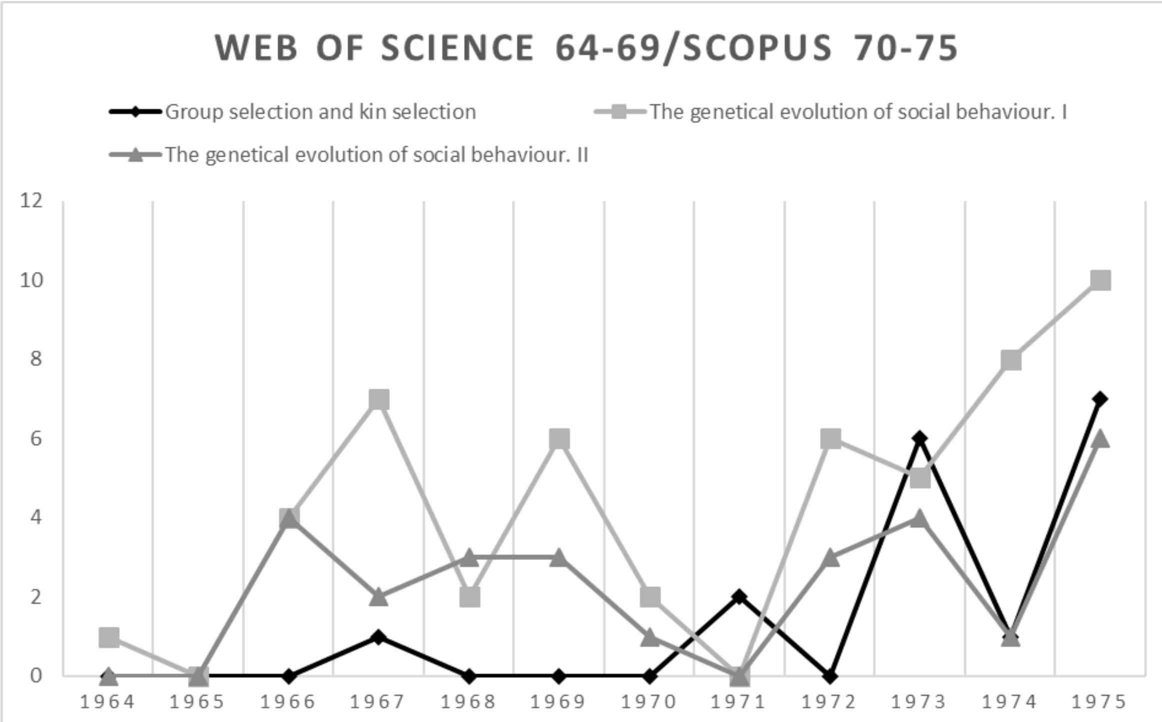

Figure 10. Citations 1964-1975.

The first thing we have to note is the difference in citation for the two parts of Hamilton's paper. Ullica Segerstråle, when commenting on Maynard Smith's claim that by suggesting splitting the paper he had wanted to help readers understand Hamilton – and thus help Hamilton, – has noted that 'Maynard Smith's recommendations probably did help to highlight the significant point of Hamilton's paper':

> One indicator is a much-thumbed copy of *Group Selection* (Williams, 1971), borrowed from a huge American research university. There Hamilton's paper is republished (with corrections) in its two parts. Part II has been dutifully marked and underlined by students. Part I remains in pristine condition.[72]

Curiously, in citations the reverse is true: SCOPUS (Web of Science) lists a total of 7912 (8336) citations for Part I and only 1984 (1656) for Part II. As Michael Ruse has pointed out, citation numbers do not necessarily reflect engagement. But it seems telling that while the natural history examples discussed in Part II are, for many, necessary to understand the mathematics of Part I, in the end it is naturally the mathematics that the scientists use and therefore reference. Long-term analysis confirms that the first part of Hamilton's paper is still one of biology's most-cited works. After 1980, Hamilton's work, even just the second

[72] Segerstråle 2000, 69.

part which has fewer citations, was also always more in circulation than Maynard Smith's (except for a spike in 1984, cf. Figure 11). These figures show that biologists were clearly using Hamilton's inclusive fitness more than Maynard Smith's kin selection. As Robert Trivers said, when asked by Maynard Smith about the episode with Hamilton: 'We all know of his unique value to our field'. He added, 'and what's more, he (Hamilton) knows we know.'[73] But the discussions from the 1970s right until 1980 and possibly beyond – this brief exchange with Trivers was in 1979 – show that Hamilton still felt resentful.

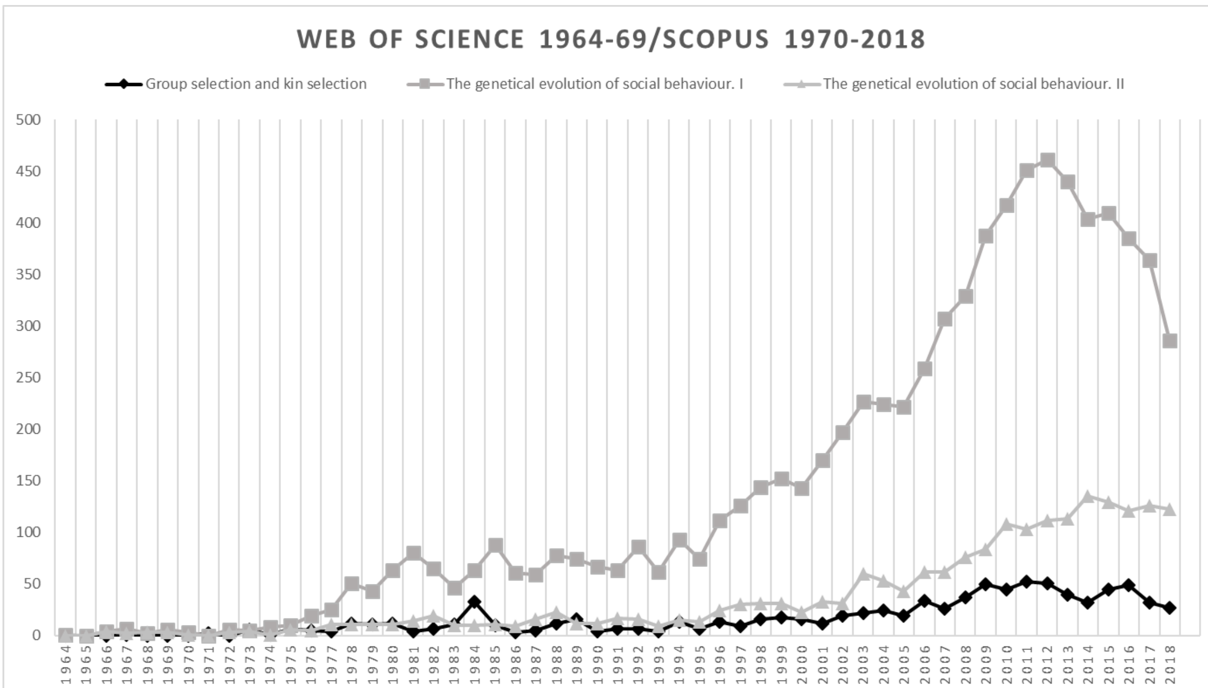

Figure 11. Citations 1964-2018.

It is of course possible that Hamilton was less concerned with the use of his mathematics and more with the (use of the) term "kin selection" itself. We have seen that Dawkins, for example, uses only kin selection rather than inclusive fitness in his endnote which analyses the bibliometrics of Hamilton's papers. Using Google Scholar and Google Ngram Viewer, we can take a look at the use of the two terms. Searching for "kin selection" between 1964 and 2018 on Google Scholar returns ca. 28,800 results, "inclusive fitness" lies below that at 26,500 results.[74] Changing the search parameters to look for the search term

73 Trivers to Maynard Smith, 30 April 1979. JMSA Add MS 86764.
74 Search conducted 11 December 2018.

only in the title, as opposed to anywhere in the text, returns 305 results for "inclusive fitness" and 590 for "kin selection" (Figure 12).

Google scholar	Anywhere in text	In title
"kin selection"	28,800	590
"inclusive fitness"	26,500	305

Figure 12. Google scholar citations for "kin selection" and "inclusive fitness".

Google Ngram Viewer uses text-mining techniques to search the corpus of Google Books for a set phrase or phrases, creating a graph to show trends and frequency in usage.[75] Tracing "kin selection" and "inclusive fitness", it first becomes obvious that until 1975, the year before Hamilton publicly voiced his misgivings about Maynard Smith or at least the origin of genetic altruism, kin selection was used more often than inclusive fitness (except for a spike in 1971; cf. Figure 13). This is more evident when changing the settings to "smooth" out the results into averages to make the graph more legible (Figure 14). (A smoothing factor of 3 means that averages for a period of three rather than one year is used to produce the graph.) Considering the longer term, kin selection and inclusive fitness both have their moments of being used more often than the other (Figure 15) but on average, inclusive fitness takes the lead over kin selection (Figure 16).

[75] Google Books represents 4% of all publications which, as pointed out in the University of London's postgraduate online research training (PORT) on text-mining, 'are not necessarily representative of publications in any given year'; at the same time, Google Books is the largest collection available. See https://port.sas.ac.uk/mod/book/view.php?id=554&chapterid=328 (retrieved 11 December 2018).

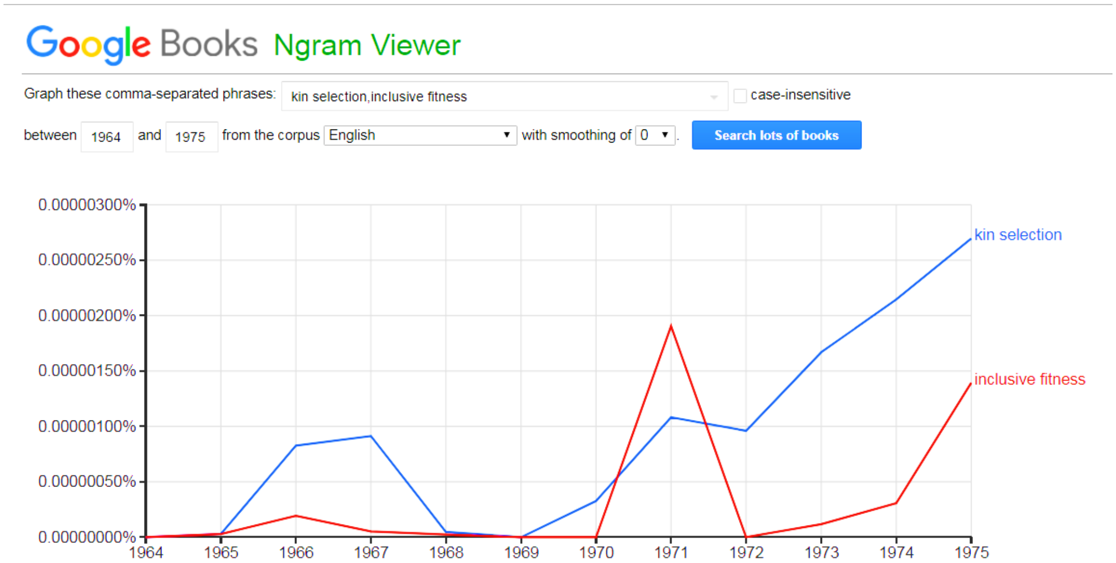

Figure 13. *Google Books Ngram Viewer 1964-1975. Smoothing of 0.*

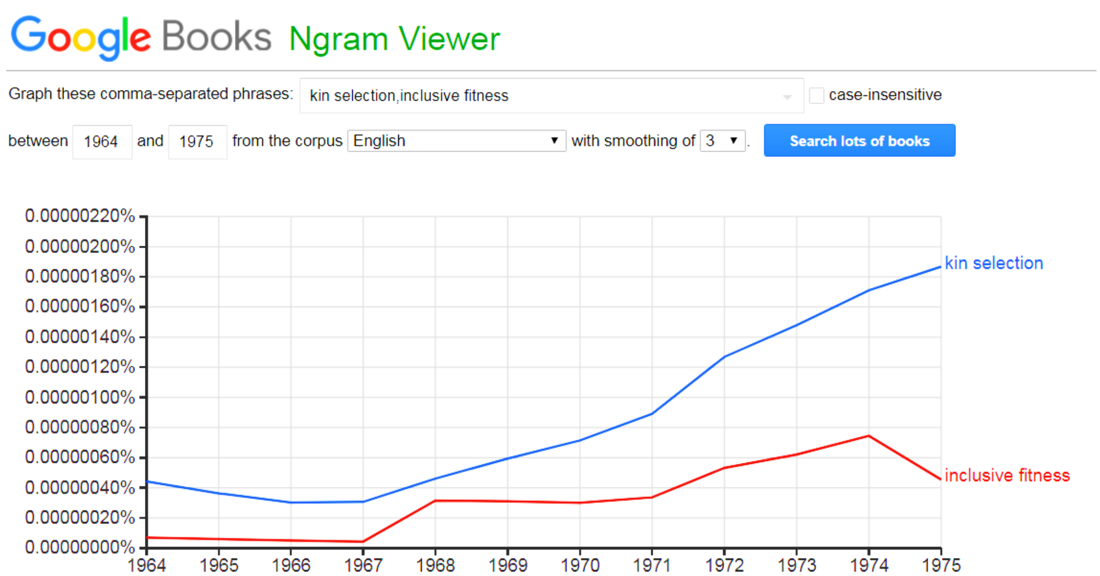

Figure 14. *Google Books Ngram Viewer 1964-1975. Smoothing of 3.*

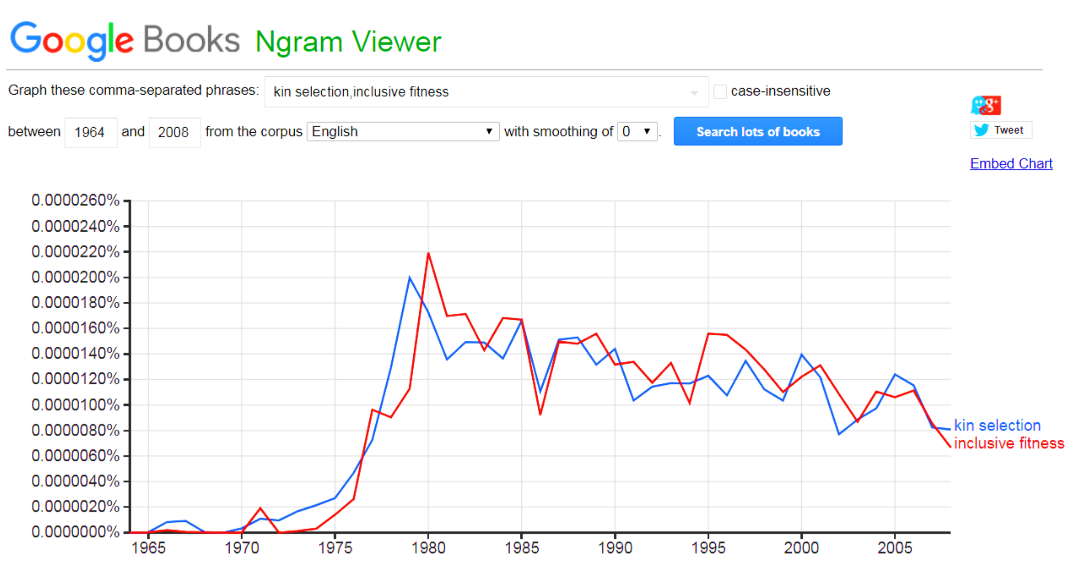

Figure 15. Google Books Ngram Viewer 1964-2008. Smoothing of 0.

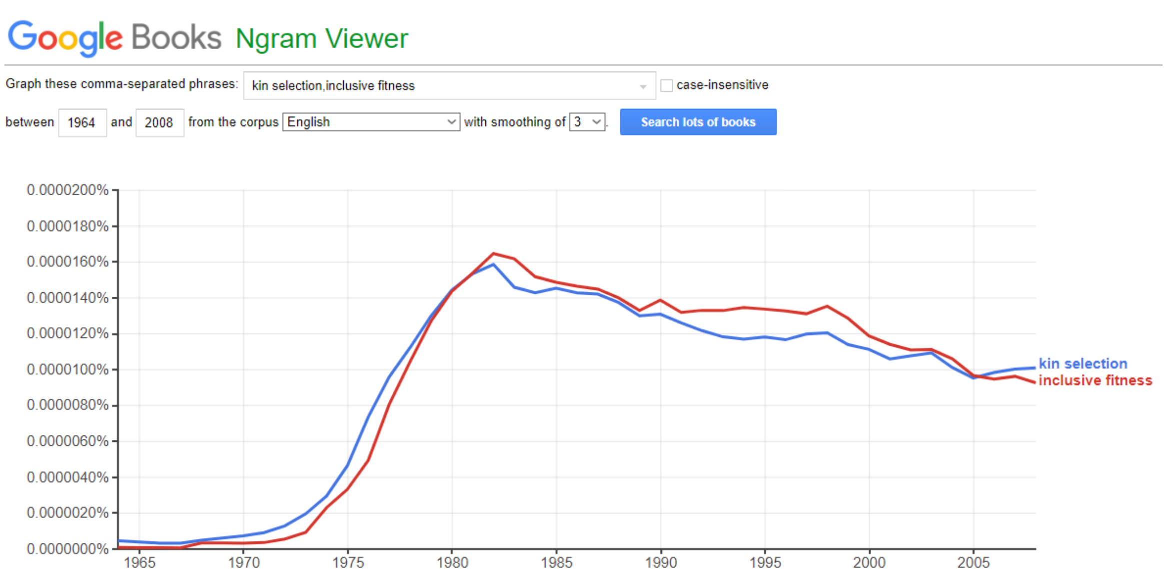

Figure 16. Google Books Ngram Viewer 1964-2008. Smoothing of 3.

This second set of analysis, focusing on the actual terms rather than citations of the papers, provides a noteworthy supplement. Bibliometrics showed that Hamilton is cited many times more often than Maynard Smith – even in the 1970s when Hamilton felt underappreciated. In terms of terminology, however, kin selection caught on more than inclusive fitness, at least initially before anyone (including Maynard Smith) was aware of the Hamilton-Maynard Smith conflict. After the 1980s and Maynard Smith's attempts at pushing Hamilton's priority, kin selection takes a slight step back in frequency of use. It is used about twice as often as inclusive fitness in article titles, however, which suggests that it still provides a good summary of the idea.

In the first part of this chapter we have looked at the story behind the two works published in 1964 and pointed out that, on the part of Hamilton, a priority dispute was developing because he felt a senior researcher had not given him the credit he deserved. The bibliometric analysis in this part looked at both the short term (in particular up to 1975 when Hamilton's views were about to become known – see following section) and the long term (until the present). It makes it clear that while Hamilton's ideas indeed took some time to gather momentum, only to then surge in popularity, as also analysed by Dawkins – so did Maynard Smith's. In fact, both of Hamilton's papers are mostly ahead of Maynard Smith's letter in terms of citations. After a rather tumultuous-looking citation history in the first decade – the small numbers and short time period do not allow for much of a trend to emerge – all three papers follow along similar trajectories. The obvious difference is the large gap between Part I of Hamilton's paper and Part II as well as Maynard Smith's *Nature* letter. The opposite trend is only visible when looking at the use of terms rather than citations of papers and thus, presumably, use of mathematics: in that case Maynard Smith's kin selection was originally more popular than Hamilton's inclusive fitness. That was not, however, a trend that continued beyond the 1980s, except for use in article titles. It is possible that Hamilton's feeling of having been slighted by Maynard Smith stemmed at least in part from the popularity of the term kin selection – it summed up his idea, it was and is used by scientists to describe his idea, but it was *not his term*. Kin selection is so pervasive Hamilton used it himself in his 1996 reminiscences of the origin of the 1964 papers.[76]

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[76] Hamilton 1996, 26.

4.3 1975-1977: jumping into rivers with Haldane

It is unclear whether the above-mentioned silence between 1964 and 1975 was because Hamilton felt intimidated by Maynard Smith's rank or thought he had missed the opportunity to speak out because he only learned of the similarities in the other paper several months after publication. Segerstråle has pointed out that even after attaining his PhD, Hamilton's 'scientific standing was by no means clear.'[77] (He had only published two papers and no real teaching experience.) Price, for his part, had preferred if Maynard Smith did not bring it up with Hamilton as Hamilton had talked to Price about this in confidence.[78] Maynard Smith's reaction to learning about the issue from Price had been to conclude:

> I don't think Bill Hamilton feels too badly about things now. I certainly won't discuss the matter with anyone. But I will try to set the record straight, without making too much of an issue of it, because Bill certainly deserves any credit that is going. I leave it to you whether to say anything to Bill or not.[79]

But Maynard Smith was too optimistic and did not realise – or understand – how deeply Hamilton felt about the matter. It finally erupted out in the open in 1976 (after Price, who might have had a chance at mediating between the two, had passed away).

A year previously, in 1975, Harvard biologist Edward O. Wilson had published his book *Sociobiology. The New Synthesis*, which was to cause a controversy in its own right.[80] Maynard Smith wrote a review for the magazine *New Scientist* in August of that year, mentioning Haldane and Hamilton in relation to altruism and kin selection. On the face of it, this had nothing to do with the dormant conflict between Hamilton and Maynard Smith. But a year after the publication of the review, the magazine received a letter by Hamilton which read: 'Sir,'

> Having been abroad for almost a year I have only recently noticed Maynard Smith's review of *Sociobiology* […]. I was astonished and rather dismayed by an historical anecdote in it which I had not heard before.[81]

[77] Segerstråle 2013, 112.
[78] Price to Maynard Smith, 19 October 1972. JMSA Add MS 86764.
[79] Maynard Smith to Price, 24 October 1972. JMSA Add MS 86764.
[80] E.g. Segerstråle 2000.
[81] Hamilton 1976a, 40.

In an unlucky turn of events, Hamilton had again been out of the loop of publications because of a field trip to Brazil, and again, it was something written by Maynard Smith that caught his eye. Only this time he did not keep his feelings to himself – it may be that he felt secure enough in his scientific standing at the time to call out Maynard Smith, or it may be that, having nursed the grudge for over ten years, he felt unable to stay quiet again.

The review itself, 'Survival through suicide', pointed out that altruism is a central problem for evolutionary biology that had been recognised since Darwin's days: how do you explain 'acts which increase the probability of survival of the social group at the expense of risk to the individual'?[82] The answer is neo-Darwinian and gene-centric, which means that even though Darwin had the correct hunch that family selection played a role, it was not until his theory had been combined with a knowledge of genetics that the answer was graspable. According to Maynard Smith, one of neo-Darwinism's founding fathers, Haldane, had grasped the basics of the answer to the problem of altruism in the 1950s: 'I first heard the idea in the now-demolished Orange Tree off the Euston Road,' he wrote in the review, 'J. B. S. Haldane who had been calculating on the back of an envelope for some minutes, announced that he was prepared to lay down his life for eight cousins or two brothers.'[83] From these starts – not the solution, only the essence of one – it took a few more years until Hamilton generalised it: 'The decisive step was taken in Hamilton's papers in 1963, in which he introduced the concept of "inclusive fitness", and applied it to the evolution of the social insects.'[84] This properly started the study of altruism in genetic terms and Wilson's book, Maynard Smith concluded that section of the review, was significant because it was the first trying to use such explanations across the board, 'from slime moulds to man'.[85]

Within that story, as presented by Maynard Smith, Hamilton is given credit for the formalisation of an idea, while he is being placed into a line of thought extending from Darwin via Haldane. He is pivotal in that he turned an idea into a useful research tool. But Hamilton had two issues with Maynard Smith's version of events. First, it suggested that Haldane, doodling in a pub, had come up first with the essence an idea on which Hamilton

[82] Maynard Smith 1975a, 496.
[83] Maynard Smith 1975a, 496.
[84] Maynard Smith 1975a, 496.
[85] Maynard Smith 1975a, 496.

had worked for years, struggling on his own as a postgraduate student at the Galton Laboratory and the London School of Economics. Second, as he said, it was an anecdote 'which I had not heard before', and he wondered why no one had told him of Haldane's idea back when he was working on the genetics of altruism. Maynard Smith had obviously known about it but when they had been introduced in the early 1960s – when Maynard Smith had still been working at UCL – he had not mentioned it. (Maynard Smith, of course, did not remember that meeting as mentioned above.) Nor had any of the other former colleagues of Haldane, who had been working at UCL until his emigration to India in 1957. As Hamilton wrote to the *New Scientist*,

> Haldane's former colleagues were wholly uninterested in my proposed research on "altruism". […] During most of my time at UC attitudes to my project ranged from indifferent to hostile and this only began to change about the beginning of 1963 when my main model was already worked out and written up.[86]

He wondered if it were not actually his own words – which Maynard Smith had come across refereeing his manuscript – that had now become associated with Haldane. Maynard Smith denied the allegation in his reply published in the *New Scientist* on 29 July 1976. He did not feel that the words are too similar to Hamilton's phrasing and that there are enough similarities to Haldane's 1955 article. He did feel, however, that there is 'no doubt that the credit for the idea should go to Hamilton': 'What matters in science is not merely to understand an idea, but to see its relevance and to work out its consequences.'[87] When thinking about the conflict, also in terms of the Maynard Smith-Price collaboration and evolutionary game theory to be discussed in the next chapter, this last sentence is of major importance. It relates to what is referred to as the "attributional model" of discovery which 'draws attention to the social processes by which scientific discoveries are recognized and "attributed." This approach seems to make better sense of the fact that what counts as a discovery can vary over time'[88] – better sense than the "point model" of discovery which assumes one can unambiguously pinpoint a discovery to a specific person, place and date. Attribution also hints at another fact, which will become important in the kin selection dispute: is more importance attributed to originality or relevance and utility of an idea? In

[86] Hamilton 1976a, 40.
[87] Maynard Smith 1976a, 247.
[88] Pinch 2015, 281. The attributional model was first developed by Augustine Brannigan (1981).

other words, does having an idea qualify as a scientific discovery or are there other criteria that need to be fulfilled?

For Ludwik Fleck, the point model describes a popular myth of how science works – he did not use the concept specifically, but summarised it quite succinctly: 'The discovering subject is characterised as a type of conqueror like Julius Cesar who wins his battles in veni-vidi-vici mode. One wants to know something, one does one's observations or experiments – and instantly one knows.'[89] The history of science is more complicated than that and no scientist works in a social vacuum; Fleck preferred to think of it as a conversation with many speakers talking across and over, at and with each other. In the end, however, through this 'lively interaction', they will find a central, shared idea.[90] Similarly, Ravetz problematised the concept of a "result" 'as an atomic unit with no history of its own':

> a problem, especially a deep and new one, has a complex and usually long phase of gestation. The initial insight may flicker in and out of plausibility, as the developing argument for it encounters evidence which confirms or disconfirms it. The problem itself may change in mid-course, or it may lie dormant for a while, awaiting conclusive evidence.[91]

These observations talk about the development of scientific ideas as more complex and situated within a social environment, thus complicating the idea that one can easily figure out who discovered something and when. Maynard Smith's point about working out relevance and consequence rather than "just" understanding something deals more with the actual content of scientific discoveries – at what point is it worth to award recognition to a scientist, and what kind of recognition. But that view too emphasises that ideas develop – there are stages of understanding and levels of utility depending on how developed an idea is.

What is problematic in the Hamilton-Haldane case is the combination of priority and publicity or popularity. Apart from the fact that Hamilton felt his own contribution was minimised and perhaps even marginalised – Haldane, as founding father of neo-Darwinism with a larger-than-life personality, could easily overshadow him he feared. The Haldane quip is a very neat summary of Hamilton's work on genetic altruism and easily quotable. It

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89 Fleck 1935/2017, 111.
90 Fleck 1935/2017, 23.
91 Ravetz 1996, 253.

almost made it into the 1976 *Horizon* episode based on Richard Dawkins' *The Selfish Gene*. The book – as we shall see in the following chapter – was based in large part on the work of Hamilton, Maynard Smith, Robert Trivers, and George Williams. Dawkins had not felt up to presenting the programme himself so had suggested Maynard Smith as both an experienced broadcaster and an expert in the area himself. In preparation for the programme, *Horizon* staff were inquiring with biologists about the ideas in the books, Hamilton among them. In July 1976, Hamilton then received a letter thanking him for making 'perfectly clear the situation regarding your publication vis-à-vis John Maynard Smith. I appreciate enormously being put so fully in the "picture".' The letter writer, presumably producer Peter Jones, continued,

> We have actually taken out the reference to the Orange Tree Pub from the film and I feel sure that we can place your work on altruism in its proper perspective.
>
> I haven't seen John Maynard-Smith since we met but will be seeing him at the end of next week to do our final recordings and I feel confident that we can steer our way through the development of the theory in a fair way. Richard Dawkins has recently seen the film and has also helped me to appreciate the history of these particular ideas.[92]

The story, and mostly the line about jumping into the river, did make it into various other contexts, however, from non-specialist to specialist writings. In 1993, in a semi-popular introduction to the use of games in biology, Karl Sigmund wrote on the importance of thought experiments. He illustrated his point with the example of Haldane, who 'computes for how many nephews he would be prepared to lay down his life'.[93] The Haldane anecdote also quite literally became textbook. In the third edition of Neil A. Campbell's *Biology*, published the same year as Sigmund's book, we read:

> British geneticist J. B. S. Haldane anticipated the concepts of inclusive fitness and kin selection by jokingly saying that he would lay down his life for two brothers or eight cousins.[94]

Philosophers of science are equally susceptible to the quip. Jonathan Birch not only recounted the story ('As legend has it'…[95]) but titled his introduction "Jumping into the

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[92] Jones(?) to Hamilton, 8 July 1976. BBC WAC T63/109/1.
[93] Sigmund 1993, 4.
[94] Campbell 1993, 1184. Thanks to Greg Radick for pointing out this passage.
[95] Birch 2017a, 1. Birch wrote his thesis on kin selection from a philosophical point of view (2013) and continues to publish in that area (e.g. 2014, 2015 (with Okasha), 2017b, 2018, 2019).

River…". But he is much more critical, referring to Hamilton's disputing Maynard Smith's story. (His book is a philosophical discussion of Hamilton's and Price's ideas of social evolution.)

In more discussions aimed at non-specialist audiences the quip makes appearances too. In 2002, Infonation's documentary series *The Edge* profiled Bill Hamilton in an episode called "Secrets of the Clouds". Evolutionary psychologist George Fieldman is shown saying that 'Hamilton's Rule was neatly described by J.B.S. Haldane, who said that he would lay down his life for two brothers or eight cousins."[96] More recently, the story made a reappearance in Lee Alan Dugatkin's 2006 book *The Altruism Equation:*

> it was another of Haldane's off-the-cuff remarks that would mark the start of the modern mathematical theory of kinship and altruism—something that was sorely needed, as no such theory existed in Haldane's day. Haldane was keen on telling people that he would jump into a river and risk his life to save two brothers, but not one; and that he would do the same to save eight cousins, but not seven. Using himself as an example, the point Haldane was trying to make was that the more closely related two individuals are, the greater the probability that one will sacrifice for the other. That is, if we know something about the genetics of blood kinship, we can make predictions about the amount of altruism that will occur. In retrospect, it seems obvious that if kinship matters in selecting for altruism, then the degree of kinship should matter as well. But that was far from obvious in Haldane's era—indeed, he appears one of the first to have even thought about the question this way.[97]

Was Haldane indeed one of the first? Haldane in fact not only told this story in a pub, as recalled by Maynard Smith in his *Sociobiology* review, but also discussed altruism in one of his *New Biology* articles – the same Penguin series in which Maynard Smith's first popular article appeared. In 1955, Haldane wrote

> What is more interesting, it is only in such small populations that natural selection would favour the spread of genes making for certain kinds of altruistic behaviour. Let us suppose that you carry a rare gene which affects your behaviour so that you jump into a river and save a child, but you have one chance in ten of being drowned, while I do not possess the gene, and stand on the bank and watch the child drown.

[96] 'Secrets of the Clouds' 2002.
[97] Dugatkin 2006, 61.

> If the child is your own child or your brother or sister, there is an even chance that the child will also have the gene, so five such genes will be saved in children for one lost in an adult. If you save a grandchild or nephew the advantage is only two and a half to one. If you only save a first cousin, the effect is very slight. If you try to save your first cousin once removed the population is more likely to lose this valuable gene than to gain it. But on the two occasions when I have pulled possibly drowning people out of the water (at an infinitesimal risk to myself) I had no time to make such calculations.[98]

It has been noted by some that the wording in the article is sufficiently different from the quip reported by Maynard Smith,[99] whereas Maynard Smith himself thought it was close enough to trace his version back to his mentor. However, it is Maynard Smith's version that made it into later literature, the witty one-liner rather than Haldane's more elaborate phrasing. On the other hand, Maurice Dow from the Department of Zoology at Edinburgh University reacted to Hamilton's response to Maynard Smith's *Sociobiology* review exactly by quoting Haldane's *New Biology* article:

> Sir,—With reference to the letter by W. D. Hamilton (1 July, p 40) suggesting that J. B. S. Haldane might not have said that he was "prepared to lay down his life for eight cousins or two brothers", I should like to quote from Haldane's article in the *New Biology* series (vol 18, p 44).[100]

For Dow, this was enough evidence that Haldane had had such ideas and may have talked about them in the pub. But Hamilton was not convinced and deeply resented the story and, by extension, Maynard Smith:

> I do not believe your anecdote about what J.B.S. Haldane supposedly said in a pub about the kin-ship principle. This means that while I continue to have considerable respect for your versatility as a scientist and for your contribution in making our common field of interest advance as rapidly as it has, I am unable to respect you as a person. […] Either you are some kind of amnesiac capable of unconsciously fabricating an anecdote harmful to the reputation of a fellow scientist or else you are a person capable of fabricating such an anecdote consciously as part of an attempt to avoid the discomfort of admitting intellectual indebtedness to a younger man. The first supposition is the best that I can think of you.[101]

It is worth pointing out that it is over a decade after the "inclusive fitness" and "kin selection" papers which first caused Hamilton's ill feelings towards Maynard Smith – his

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[98] Haldane 1955, 44.
[99] O'Toole 2016.
[100] Dow 1976, 195.
[101] Hamilton to Maynard Smith, 19 October 1977. JMSA Add MS 86764.

'life-long "Maynard Smith paranoia"', as Segerstråle has called it[102] – and that only now he addressed them directly and in person. Throughout the letter we learn that at some point, Hamilton had already wondered if his grudge against Maynard Smith was unjust, given that the latter was publicising him so much on kin selection, but that the Haldane anecdote brought all his misgivings back into focus. He listed four reasons for disbelieving Maynard Smith on the story – the wording being similar to his papers; the fact that no one mentioned the story or seemed to have heard it before; that Maynard Smith had not mentioned Haldane's interest in altruism when they met in the 1960s; and that Haldane could impossibly have worked it all out on the back of an envelope.[103]

We may leave aside for a moment the question of whether Maynard Smith fabricated the anecdote. In reply to Hamilton he stated that 'there is no defense' if he did invent it, but he was 'quite certain' that he did not. He then brought the *New Biology* article back into play: 'Further, I do not think I need any evidence in support of my memory beyond Haldane's New Biology article. Although not identical, the two things are so similar it really makes no odds.'[104] It is important to look more in detail at what the anecdote and reference to Haldane's 1955 work do in the context of the priority dispute. There is a sense in which it has been shifted back by these remarks and references, away from Maynard Smith and onto Haldane, but leaving Hamilton in a similar position as before. We can draw parallels to the priority dispute surrounding genetics around 1900. Referring back to Augustine Brannigan, Berris Charnley and Greg Radick explain that the reason Gregor Mendel has been sharply brought into focus and "rediscovered" in 1900 by the German botanist and geneticist Carl Correns was a simmering priority dispute between Correns and the Dutch botanist Hugo de Vries.

> Correns' generous gesture toward Mendel was at the same time a bid to undermine De Vries. Correns might have lost out to De Vries in the publication race; but now, in stressing how much both men's work shared with Mendel's, down to the "strange coincidence," in Correns' phrase, of De Vries replicating the abbot's vocabulary of "dominant" and "recessive," Correns got his revenge. If he would get no credit for the discovery, neither would De Vries. (Intriguingly, both the word and the quotation marks around "rediscovery" are Correns'. Even so, he, like De Vries, owed a larger and earlier intellectual debt to the 1866 paper than he would ever

102 Segerstråle 2013, 181.
103 Hamilton to Maynard Smith, 19 October 1977. JMSA Add MS 86764.
104 Maynard Smith to Hamilton, 27 October 1977. JMSA Add MS 86764.

> admit.) So Mendel entered the wider biological consciousness, at the time that he did, as a means to the end of resolving a priority dispute.[105]

Whether Maynard Smith's (re)introduction of Haldane into the history of genetic altruism was intended to resolve the dispute with Hamilton, it did shift attention away from kin selection and onto Haldane. In fact, what Maynard Smith did emphasise was that Haldane was prone to having ideas but not following up on them. In a collection of popular Haldane essays edited by Maynard Smith, he added an appendix entitled "Adumbrations". 'Scattered through Haldane's writings,' Maynard Smith wrote, 'there are hints of things to come.'

> He sketches some experiment, or theory, or field of investigation which later and in other hands has become important. There are many possible reasons why he failed to follow up these hints himself: he was too impatient to be good at raising grants to support experimental work, the techniques needed to test an idea were not yet developed, or he simply had too many other things to think about. I give three examples, each followed by an explanation and an account of what has happened since.[106]

The examples are first, how a gene reproduces itself, second, the evolution of altruism and third, disease and evolution. Maynard Smith quoted the relevant passages from the 1955 *New Biology* article, explaining that it contained 'the seeds of an idea which was developed by Hamilton.' R.A. Fisher had a similar idea, he added, and Haldane 'grasped the essential arithmetic' – but neither of them followed up on their hunches.[107] Nor did Maynard Smith see how social behaviour could have evolved: 'When I first came across this point in Hamilton's 1964 paper, I felt furious with myself for not having seen it too, but slightly comforted that Haldane had missed it too.'[108] This genealogy has been re-affirmed over the last ten years by other biologists and others writing historically on evolutionary genetics. Thus Marek Kohn, without going into detail, mentions both Haldane and Hamilton as predecessors for Maynard Smith's "kin selection".[109] More extensively, Brian Charlesworth, a colleague of Maynard Smith's at Sussex for several years, has written on

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[105] Charnley and Radick 2013, 227.
[106] Maynard Smith in Haldane 1986a, 178.
[107] Maynard Smith in Haldane 1986a, 182f.
[108] Maynard Smith in Haldane 1986a, 182.
[109] Kohn 2004, 229.

Haldane and modern evolutionary genetics, referring to the 1955 *New Biology* article, kin selection and Hamilton:

> Haldane introduced the concept of "altruistic behaviour" into evolutionary biology, where a behaviour such as an alarm call may harm the individual but benefit other members of the population (Haldane 1932, 1955b). He suggested two processes by which it could evolve. The first was the process of intergroup selection, whereby groups that acquire a genotype promoting the behaviour by genetic drift in opposition to selection within groups out-compete nonaltruistic groups. The second was what is now known as "kin selection" (Maynard Smith 1964), where altruists benefit their relatives who tend to share the same genotype as themselves. (Both of these ideas were also discussed by Fisher (1930b).) In the hands of William Hamilton (1964a, b) and his followers, the theory of kin selection became a cornerstone of behavioural ecology, providing a crucial framework for relating observations to theory (West et al. 2006).[110]

Charlesworth does not use the term "inclusive fitness" – and neither does Anthony Edwards (a student of Fisher's) who, more decisively than Charlesworth, moves the discussion back to Fisher (see Charlesworth's parentheses). Chapter 7 of Fisher's 1930 *The Genetical Theory of Natural Selection*

> is notable particularly for the section "The evolution of distastefulness" [in insects] which he explains by what is now known as "kin selection", often attributed to Haldane but in fact suggested by Fisher *already in a student talk in 1912 published in 1914* when he considered how a childless man killed in war could be replaced genetically speaking by his nephews.[111]

It is fair to say, then, that other biologists have hinted at the solution to the altruism problem before Hamilton but also that, as Maynard Smith repeatedly pointed out, no one developed these hints into anything useful for biology.

Ludwik Fleck made two interesting points in this respect. First, he talks about ur-ideas, or pre-ideas, ideas that in a sense describe what later becomes scientific.[112] He emphasised, however, that not every discovery can be traced back to such an ur-idea, nor that scientists just pick "the right ideas" from amidst a pool of available ur-ideas, discarding the "wrong" ones.[113] Second, he thought of 'every scientific work as collective work' – often, the person

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110 Charlesworth 2017, 776.
111 Edwards 2011, 425 (emphasis added).
112 Fleck 1935/2017, 35.
113 Fleck 1935/2017, 36f.

we know as "the discoverer" of a scientific fact is more often 'standard-bearer of the discovery rather than its sole achiever.'[114]

The question remains why no one ever referred Hamilton to the Haldane 1955 article, as Hamilton noted, still rather upset, in 1980.[115] But the problem with Hamilton's anger that no one pointed him in this direction is that he had actually read it. Not only had he read it, he had quoted it in his 1963 *American Naturalist* article summarising his work on "The evolution of altruistic behavior":

> To put the matter more vividly, an animal acting on this principle would sacrifice its life if it could thereby save more than two brothers, but not for less. *Some similar illustrations were given by Haldane (1955).*'[116]

It seems that at this point, after almost two decades of nourishing this grudge and priority dispute, Hamilton was set in his specific claims towards his own priority. From his point of view, he had given credit where credit was due to any predecessors and his intellectual property and originality should therefore be safely established by his 1963 and 1964 papers.[117] But he shifted from saying that Haldane had done something that did not go as far as what he was suggesting – which is the point that Maynard Smith kept making – to wanting to take Haldane out of the equation completely. In 1976 he had still argued that he knew the passage quite well but that '[i]n my own approach I was not consciously helped by Haldane's comments although I must have read them since I used to read his articles in *New Biology* as they came out.'[118] It is interesting that he says he was not 'consciously' influenced – but what about unconsciously? According to Fleck, 'knowledge lives in the collective and is constantly being reworked.'[119] In 1996, this has shifted to:

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114 Fleck 1935/2017, 57.
115 Hamilton to Maynard Smith, 23 October 1980. WHP Z1X97/1/4.
116 Hamilton 1963, 355 (emphasis added).
117 He told Maynard Smith that 'so far I am only aware of having given slightly less than due credit to Darwin […] and to Sewall Wright.' Hamilton to Maynard Smith, 19 October 1977. JMSA Add MS 86764.
118 Hamilton 1976b, 195; see also Segerstråle 2013, 39: Hamilton 'read and discussed the essays published in the semi-popular journal *New Biologist* [*sic*] by Haldane and others. For budding biologists, it was that journal, rather than the textbooks studied in class, that was their real source of knowledge. Bill also used to discuss recent journal issues with his sister Mary.'
119 Fleck 1935/2017, 125.

> While I was still an undergraduate at Cambridge, and just beginning to try to devise models that would support altruism under natural selection, I did not have Fisher's remark on distastefulness consciously in my mind even though I had probably read it, nor did I have J. B. S. Haldane's equally brief discussion that he put into a popular paper in *New Biology* even though I know for certain that I had read that.

Hamilton continued that '[o]ne reads and forgets. Hints not understood probably leave their traces, but one has to return to the topic in a better state of preparation and to re-read before such throwaway items become meaningful.'[120] He was acknowledging that he had read the works but was diminishing their influence on his thought-processes. The non-specialist nature of the *New Biology* article plays an important role in the ambiguous and shifting attitudes towards Haldane's contribution. Hamilton made a point of calling it a "popular paper". 'Population genetics', as it was titled, was published in *New Biology* which, as we learned in Chapter 1, targeted mostly non-specialist audiences and functioned as an introduction to biology. Maynard Smith himself suggested this was a reason why no one – including Haldane – took his views on altruism to be important. He wrote to Hamilton that quite possibly, Haldane did not think 'the idea more than entertaining. […] He published it as a throw-away paragraph in a popular article.'[121] Notwithstanding the fact that he himself was comfortable publishing in non-specialist outlets, even used them to introduce new ideas (see Chapter 4), in this situation he clearly emphasised that this is not a place to go to for priorities. Of course, priorities did matter to Maynard Smith as well although, like Hamilton, he unsuccessfully tried 'not to be unreasonable about it.'

> I fully understand and sympathise with your feelings of protectiveness about inclusive fitness. I even understand your resentment towards myself, although I think you are in some ways unjust to me. I cannot think of anything in my scientific career which would give me greater pleasure than if you and I could somehow learn to discuss science without any feeling of distrust. I do not ask you to think that I have always behaved well – only that I am not more dishonourable than most men.[122]

4.4 1980: moral of the story

After its brief outing in the pages of the *New Scientist* in 1976 and the letters between Hamilton and Maynard Smith from 1977, the dispute went back underground yet Maynard

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[120] Hamilton 1996, 22.
[121] Maynard Smith to Hamilton, 14 November 1980. JMSA Add MS 86764.
[122] Maynard Smith to Hamilton, 27 October 1977. JMSA Add MS 86764.

Smith remained troubled. In the late 1970s, he wrote to Robert Trivers, an American evolutionary biologist, and asked him for a reconstruction of the 1963-65 events surrounding kin selection. Trivers, however, replied that even though he had once promised this, it

> seems so distant in the past and any damage to Hamilton now so trivial that I feel like letting dead dogs lie, or at least, dying dogs succomb [*sic*] on their own. We all know of his unique value to our field, and what's more, he knows we know.[123]

Although he wished not to get involved[124] and his feelings of Hamilton are unclear, his signature – and Maynard Smith's approaching him on this delicate matter in the first place – indicates their good relationship: 'Wishing you, as always, all the best'. Hamilton too, in his long 1977 letter to Maynard Smith listing his four grounds for disbelieving the Haldane story, had had to admit that his view of Maynard Smith was not shared: 'My suspicion and low estimate of you runs counter to that of colleagues.'[125] Some of these testimonies can be found in the Hamilton archive itself, in letters of other scientists reacting to Hamilton's views on Maynard Smith. Thus Robin Holliday, a British molecular biologist, told Hamilton that he knew 'John Maynard Smith well and […] would have thought that he was the last person one could accuse of plagiarism.'

> He is well aware of the originality of your ideas and once told me that it was embarrassing at the oral examination for your PhD because it was evident on both sides that you knew more than he did about the subject under discussion![126]

George Price's first opinions of Maynard Smith had been strongly informed by Hamilton, as Price met Hamilton first. But Price changed his views completely after having met Maynard Smith. He told Maynard Smith so himself in a letter in 1972:

> to about four people I made rather unkind comments about how you had delayed the paper.[127] One person I said this to was Richard Andrew. Then when I visited Falmer I found that you were not at all as I had pictured you, and you were extremely kind and considerate toward me. Therefore I remarked to Richard during the afternoon that I was sorry I had said that about you, and you were so

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[123] Trivers to Maynard Smith, 30 April 1979. JMSA Add MS 86764.
[124] In 1985, Trivers published a possible explanation as to why Haldane never followed up on his kinship ideas. According to his interpretation, 'Haldane would have understood quite well the underlying principle (which Hamilton was later to develop), but he deliberately stopped himself from producing a full-fledged theory because of the political consequences he saw with the theory' (Segerstråle 2013, 183).
[125] Hamilton to Maynard Smith, 19 October 1977. JMSA Add MS 86764.
[126] Holliday to Hamilton, 24 April 1978. WHP Z1X97/1/4.
[127] He is talking about his 'Antlers' paper; see Chapter 4.

> considerate that I thought probably it was another referee who was responsible for the delay, or if it was due to you, then you had some good reason for it. (He looked at me with a rather serious expression on his face, nodded, and said, "Yes, that's right".)[128]

Similarly, Price wrote to the American biologist Richard Lewontin in September 1970: 'Last month I finally met Maynard Smith, and I found him to be so kind and considerate a man that I believe I must have been mistaken […] about him.'[129]

Hamilton remained 'stubborn' when it came to Maynard Smith[130] and 'rather resentful about the matter in a general way',[131] but eventually had to concede at least that the Haldane anecdote was not fabricated.

> Very recently E. [*sic*] Eysenck has written in a book review that he heard substantially the same statement by Haldane when he was a student under him. It can't have been the same occasion because the wording is slightly different (3 and 9 instead of 2 and 8 and no back of envelope) and in fact Eysenck goes out of way to add that, as with some other sayings of his that he knew to be important, Haldane repeated it to different groups of students in various pubs. […] So I am very sorry that I doubted your veracity on this.[132]

It is worth pointing out that Maynard Smith continuously tried to make sure that the fire was not rekindled. Two years later, in 1982, he was asked to comment on a draft manuscript. It had been sent to him by Neil Tennant from the University of Sterling, and Richard Dawkins was one of the co-authors. Maynard Smith told Tennant that there was 'One minor (but to me important) question':

> I share Dawkins' wish that you should not quote the Haldane remark. I'm responsible, I'm afraid, for the remark being so widely known, but have subsequently realized that it has given Hamilton a good deal of distress, and, worse in a way, has made relations between us very strained. I may be locking the stable door, but I would like to discourage people using the quote too.[133]

The remark was not only widely known, both popularly and professionally, it also fitted very well with an image of Haldane. Haldane was a larger-than-life character. During World

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128 Price to Maynard Smith, 19 October 1972. JMSA Add MS 86764.
129 Price to Lewontin, 15 September 1970. WHP Z1X102/1/4.
130 Segerstråle 2013, 151.
131 Hamilton to Maynard Smith, 23 October 1980. WHP Z1X97/1/4.
132 Hamilton to Maynard Smith, 23 October 1980. WHP Z1X97/1/4.
133 Maynard Smith to Tennant, 18 October 1982. JMSA Add MS 86590.

War I (which he rather enjoyed[134]), he ran a bomb-making workshop and made smoking compulsory. That weeded out the wrong sort of chaps, and presumably kept the remaining ones on their toes.[135] He also recorded his own obituary for the BBC, which was broadcast as a *Horizon* episode after his death in 1964. And he was well known for witty one-liners. For instance, '[l]egend has it that when asked […] about what evolutionary biology might tell us about God, Haldane cracked that God must have "had an inordinate fondness for beetles".'[136] Stephen J. Gould has written a whole essay on Haldane and quotable one-liners.[137]

One-liners are 'a mainstay of culture' and have the power to 'grasp the eternal truths of nature and humanity' and not a recent invention. Haldane's line is one of the most famous, at least among biologists. Gould set out to trace this 'inordinate fondness for beetles' back to its origins: 'did Haldane utter it—and if so, when, where, and how?' He probably did, is the conclusion, though not quite in the setting originally suggested and worded differently. There is no written record of it: 'Haldane was a brilliant and copious writer, but he was an even more fluent barroom wit—and great comments in this venue end up either scratched into soggy napkins or dimly remembered in the midst of a hangover.' But he did make 'the quip several times, but always among friends.'[138]

Thinking of Eysenck's review that led Hamilton to concede the quip about jumping into rivers was not a fabrication of Maynard Smith's, it seems indeed likely that Haldane repeatedly made it. That does not resolve the question of how much exactly he understood what he was hinting at, but at least it supports the likelihood of Haldane having repeated it several times in several versions but without necessarily taking it to mean much.

It is easy to see why Hamilton felt so strongly about the issue at first, and maybe also why he was unable to let go entirely. In 1964, he had been at the very beginning of his scientific career and had worked on the problem for years. After all, '[t]he reason scientists care so

134 Haldane 1986, 170.
135 Kohn 2004, 152.
136 Dugatkin 2006, 61.
137 Gould, S.J. (1993). A special fondness for beetles. *Natural History 102*(1), 4-8.
138 Gould 1993.

much about priority [is that] the main reward in science is recognition, bestowed in prizes and the naming of discoveries.'[139] He had expected help from the scientific establishment but did not receive any. This did not sit very well with Maynard Smith either; being a good teacher had always been important to him.[140] Whether or not Hamilton ever fully forgave Maynard Smith is hard to determine. Segerstråle suggests that the wounds may eventually have healed – although as we have seen, it took a long time.[141] Maynard Smith felt, or at least hoped, that they had resolved the dispute. In an interview given in 1997, three years before Hamilton's sudden death after an expedition to the Congo, Maynard Smith and Richard Dawkins touched upon the controversy once again.

> *Maynard Smith*: I can understand his feelings on this. He was a young man, he had no name, his ideas were not taken seriously. I think it's one of these horrid misunderstandings.
>
> *Dawkins*: I don't think he thinks that anymore.
>
> *Maynard Smith*: I don't think he does. […] I think Bill and I are fine now, I mean, I think we understand one another very well and admire one another. I admire him enormously and respect him. But no doubt, that from 1964 to the late 1970s, it was a problem.[142]

In terms of overall conclusions, it is possible to say that perspective on and interpretation of the events played an important role in this controversy. Concerning inclusive fitness, Maynard Smith interpreted it in relation to the Wynne-Edwards' book with its explicit group-selectionist focus. His definition of the term "kin selection" was necessary: Hamilton's work and Haldane's ideas needed to be differentiated from group selection which in the eyes of Maynard Smith and others was wrong and misleading. But from Hamilton's perspective, this had nothing to do with group selection. Instead, it was about a senior researcher appropriating his ideas and giving them a different name. Being young and at the beginning of his career, he was worried that his work and insight would be unrecognised by the scientific establishment – which, he had felt during his time at UCL, had done nothing to help him before.

139 Pinch 2015, 281.
140 Cf. for example his interview for the BBC Radio "Eureka" programme (Myers 1998).
141 Segerstråle 2013, 109.
142 Maynard Smith and Dawkins 1997, https://www.webofstories.com/play/john.maynard.smith/37.

Similarly, Segerstråle points out that much rests on angle and point of view with regard to the Haldane quip and 1955 article: Hamilton preferred to think of the Haldane article as only talking about rare genes, Maynard Smith pretty much agreed but still gave Haldane some credit for the idea (but probably not as much as Hamilton thought). Segerstråle herself reframes the Haldane passages as wanting to make a larger point, that he 'really wants to talk about […] the so-called Sewall Wright effect'[143] and concluding 'that it takes (or took) small populations for altruism to develop'.[144]

We have also seen that there are two different takes on scientific priority, revolving around the question of which is more important – who thought of something "first" or who did most with it, following through with an idea?[145] Hamilton, on the one hand, felt slighted because he was afraid that people would always think of Haldane as having thought of the essential idea of inclusive fitness first. On the other hand, Maynard Smith tried to assure him that it is more important that Hamilton actually formalised the idea. It was Hamilton who lifted it from mere anecdotal status to becoming a successful research tool and founding a new way of thinking in evolutionary biology. Maynard Smith always emphasised that this was the hard part: realising first that the idea Haldane had was in fact a clue to understanding the evolution of social behaviour, and second, mathematically figuring out and proving how this worked.[146] This interpretation will become important when we look at the collaboration between Maynard Smith and George Price in the following chapter: again, Maynard Smith came across an idea in a paper he reviewed and then started developing it.

Group selection, or the level of selection question as such, the background against which the controversy developed, is an ongoing issue in evolutionary biology. Repeatedly proclaimed "dead", it has a habit of re-emerging. Mark Borrello, in a 2005 review article, concluded that it 'appears that a hierarchical approach to evolutionary phenomena is now

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143 Segerstråle 2013, 184.
144 Segerstråle 2013, 185.
145 While developing a performance piece based on the kin selection controversy with me, Laura Farnworth, artistic director of Undercurrent Theatre, the British Library's first affiliated theatre company, pointed out the similarities in priority issues between science and the arts. She has encountered similar cases of (especially young) artists who were very careful to establish and keep track of which ideas and pieces were theirs.
146 Maynard Smith and Dawkins 1997, https://www.webofstories.com/play/john.maynard.smith/38.

more commonplace than at any time since the early 20th century.'[147] It has in fact be argued that Maynard Smith's later work on evolutionary game theory (see next chapter) *is* group selection and that the *Major Transitions in Evolution*, co-written with Eörs Szathmáry, is a sign of the acceptance of hierarchical views of evolution.[148] Maynard Smith and Szathmáry however perceived their work as strictly neo-Darwinian and gene-centric: 'the transitions must be explained in terms of immediate selective advantage to individual replicators: we are committed to the gene-centred approach outlined by Williams (1966) and made still more explicit by Dawkins (1976).'[149]

147 Borrello 2005, 47.
148 E.g. Okasha 2001, 2005; Borrello 2005.
149 Maynard Smith and Szathmáry 1995, 8.

5 A decade of games

5.1 A game-changing idea

In 1972 John Maynard Smith published his first collection of essays, *On Evolution.*[1] It was a way of taking stock of the development and status of the theory of evolution – particularly from the point of view of and through the lens of neo-Darwinism. Just over a dozen years after Maynard Smith's first book, the non-specialist *Theory of Evolution* and a similar time into his career as a broadcaster, the collection did not only look back. It also reflected on the present and was to shape the future of evolutionary studies by presenting a game-changing idea: evolutionarily stable strategies, ESS for short. A decade later, in 1982, Maynard Smith was to carve his idea into stone by publishing *Evolution and the Theory of Games.* (And in 2013, the ESS made it to number 61 of 87 in the Great British Innovation Vote,[2] in which the public was asked 'what they thought was the most important innovation of the last 100 years'. Over 50,000 votes were cast; the winner was Alan Turing's Universal Machine, followed by the Mini and X-ray crystallography.[3])

Games and ESS are further examples of Maynard Smith looking beyond biology. As seen in Chapter 1, he had used his engineering background in his first papers and research, analysing animal flight by thinking about the aerodynamics of aeroplanes. His *Mathematical Ideas in Biology* (1968) underlined the importance of mathematics for the study of biological phenomena, an issue that was close to his heart. In Chapter 2 we saw that Maynard Smith not only discussed science in non-specialist spaces but also wider implications of science and scientific thinking. Now we will follow him as he took an idea from economics and brought it into the study of evolution. This idea was game theory, originally developed by John von Neumann and Oskar Morgenstern with the aim to analyse economic behaviour.

The development of evolutionary game theory and ESS highlights two important aspects. Similar to the Hamilton case of the previous chapter, it deals with the outcomes of Maynard Smith being inspired by a manuscript he reviewed. Rather than resulting in a

[1] A second, *Did Darwin Get It Right?,* followed in 1988.
[2] 'Top British Innovations', ESS.
[3] 'Top British Innovations', About this vote.

controversy, this time the inspiration resulted in the collaboration with the original author, George Price. This case also elucidates how non-specialist and specialist publications function to establish priority and intellectual property claims, as well as how the idea of evolutionary game theory travelled through different types of media with different audiences. This really is "knowledge in transit", looking at how different contexts and media of communication have shaped a scientific idea and created the link to Maynard Smith as the one man behind it.

At the same time, this is an example of how the continuity model of science communication, which developed in reaction to the deficit model, is not reflective of science communication in action either. As Massimiano Bucchi said, it can be a 'useful frame of reference' but it still describes 'some sort of ideal flow of communication in routine circumstances' only.[4] The idea that science is communicated at various levels, moving from the specialist to the non-specialist stage (with a feedback loop back to the specialists) neglects deviations like scientists directly addressing non-specialists (for example with a view to influence policy, settle a controversy, or convince other specialists of new ideas).[5] Evolutionary game theory deviates from both the deficit and the continuous models of science communication and uncovers how the stages and levels between specialist and non-specialist are much more loosely organised: the idea is introduced in non-specialist spaces and keeps making appearances there before and during its discussion in specialist journals. Thus magazines, television and radio step in very early on in the history of evolutionary game theory (EGT) and evolutionarily stable strategies (ESS), and it would take a decade before the first textbook is written on the topic.

5.2 The first games

The history of game theory and its application to biology does not start with Maynard Smith. In some form it can be traced back to R.A. Fisher, and similar ideas were present in works by Hans Kalmus, Richard Lewontin, Bill Hamilton, Robert MacArthur and George Williams.[6] Fisher anticipated the way in which evolutionary game theory thinks about

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[4] Bucchi 2008, 63.
[5] Bucchi 2008; see also Sepkoski 2014.
[6] E.g. Maynard Smith 1972, Maynard Smith 1974, Maynard Smith 1982b, Rapoport 1985, Hammerstein and Selten 1994, Harman 2011, Erickson 2015.

phenomena in as early as 1930. At that time, game theory, in its original economic form, had not been formulated. So Fisher did not, and could not, use game theoretic terminology, but in writing about his sex ratio theory he made use of similar ways of thinking.[7] In *The Genetical Theory of Natural Selection* he argued, among other things, as to why many species have an almost equal number of males and females. As Anthony Edwards points out, it was an early argument against group selection and

> it was hailed as the first example of an evolutionarily stable strategy (ESS) by those who later christened the concept (see Maynard Smith 1982); and it has frequently been he quoted as a key example by those to whom such an approach appeals (e.g., Maynard Smith 1978, 1982; Williams 1996b).[8]

Peter Taylor, from the Department of Mathematics and Statistics at Queen's University in Kingston, Canada, wrote to Maynard Smith in the late seventies, differentiating between what he called "Fisher's method" and the "ESS method" which Maynard Smith had pioneered. 'I agree completely with you,' he wrote in reply to comments Maynard Smith had sent him on a manuscript of his (which he acknowledged he would have to rewrite),

> that to distinguish the two methods with these names is quite misleading. The ESS idea is what is behind both methods, even if the formal definition was not around in Fisher's day. The methods are better distinguished as follows. The first might be called Fisher's equilibrium condition. In general, it attempts, by an analysis of the genetic relationship among the principal actors in the life cycle, to write down a condition of the form
>
> genetic payoff of a male = genetic payoff of a female
>
> and solve this equation for the sex-ratio r. The second is completely mechanistic.[9]

Fisher was aware of his connections to game theory. He died in 1962 but, as P.G. Martin (in the 1980s professor at the Department of Botany, The University of Adelaide) remembered, a couple of months previously he had attended a seminar organised by a group of biologists around a visit by Richard Lewontin.

> First our professor of mathematics explained to us the Theory of Games, then Lewontin discussed the subject along the lines of his 1961 paper "Evolution and the theory of games" (J. Theoret. Biol. I, 382-403), and finally Fisher spoke to us on this topic. If my memory serves me correctly, Fisher did not attend the first two seminars.

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[7] Sigmund 1993, 168.
[8] Edwards 1998, 564.
[9] Taylor to Maynard Smith, 10 April 1979. JMSA Add MS 86597A.

> The final seminar was "real Fisher". He pointed out that he had expounded the so-called Minimax Principle ten years before von Neumann and gave us the reference (collected papers 111 of 1934). He had also anticipated Lewontin's application of the principle to evolutionary theory in a paper which appears to have been published twice (No. 277 of 1958)but [*sic*] to which Lewontin did not refer.[10]

The quote also shows that Lewontin is one of the other figures who applied game theory to evolutionary biology before Maynard Smith and Price. But according to Paul Erickson, writing on *The World the Game Theorists Made*, Lewontin and his colleagues' work was the 'most prominent of […] unsuccessful attempts' to establish evolutionary game theory.[11] Similarly, Oren Harman noted that Lewontin's attempt 'proved too complicated a task.'[12] Lewontin hoped that applying game theory to evolutionary questions would help address some shortcomings in population genetics, in particular the fact that there is no 'adequate theory of evolutionary dynamics' and that it is 'not genetics of populations, but genetics in populations'.[13] His game is a "game against nature", in which the two players are a population on the one hand, and nature on the other. Nature will have the first move and populations will adopt a "maximin criterion of optimality". That is, they will 'attempt to maximize the minimum possible reproductive utility payoff (in terms of collective reproductive success), an assumption that Lewontin justified by noting that the environment is "capricious," like a clever poker-player, constantly changing and lacking in statistical regularities.'[14] A maximin, or minimax, strategy implies that one is thinking in terms of worst-case scenarios and trying to maximise one's minimal payoff against these (or minimising the maximal payoff of the opponent).[15] Lewontin concluded his paper by noting that these ideas would have to be supported by 'experimentation and observation', which would serve to identify what kind of strategies populations and species really adopt and 'thus to define *biologically* the meaning of an optimal strategy.'[16]

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[10] Martin to Box, 14 January 1980. JMSA Add MS 86597A.
[11] Erickson 2015, 205.
[12] Harman 2011, 5.
[13] Lewontin 1961, 382f.
[14] Erickson 2015, 215.
[15] Sigmund 1993, 163 and 168.
[16] Lewontin 1961, 403. Erickson argues that Lewontin's attempt at evolutionary game theory might have failed because he understood game theory too well – the transferral from the social and behavioural sciences with its terminology around rationality and choice was difficult to use in the context of individual animals, even more so in that of whole species or populations (Erickson 2015, 216).

There is at least one later instance of game theoretic ideas being used in biology. In 1967, Hamilton published a paper on 'Extraordinary sex ratios' which re-appraised the Fisherian sex ratio theory. It anticipated the idea of stable states which became central as equilibria in Maynard Smith's evolutionarily stable strategies. Hamilton also discussed "unbeatable strategies", which resemble Maynard Smith's ESS: an unbeatable strategy is one 'which, if all members adopt it, offers no scope for individual improvement.'[17] In comparison, Maynard Smith and Price defined an ESS as 'a strategy such that, if most of the members of a population adopt it, there is no "mutant" strategy that would give higher reproductive fitness.'[18]

In his 1982 book on *Evolution and the Theory of Games*, Maynard Smith acknowledged that Hamilton's and his and Price's strategies are 'essentially the same'.[19] He had already brought up the matter in correspondence. In the same letter discussing Hamilton's feelings on priority in the inclusive fitness/kin selection matter, Maynard Smith pointed out that there was

> one other matter between us which you do not mention, but which has been on my mind. That is the origin of the idea of an ESS. When George [Price] and I published the idea, we did not quote your 1967 use of an "unbeatable strategy", although I had read your paper, and the idea is basically the same. Since I became aware of this, I have tried to put this right (e.g. in the American Scientist last year). There are really two points here. One is that I must have been influenced by your paper, but was not conscious of it at the time. Although I am not a complete amnesiac, I don't always know where my ideas come from. The other is that I think I did a good deal more with the idea than you did, and feel I deserve the credit for seeing its generality.[20]

This, of course, is exactly the same argument Maynard Smith used to justify crediting Hamilton with kin selection while at the same time establishing Haldane and, to a lesser degree, Fisher as part of the concept's history. Now he did the same for himself; Hamilton had had a similar idea, but Maynard Smith generalised it: 'The concept of an ESS, which is

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[17] Sigmund 1993, 168.
[18] Maynard Smith and Price 1973, 15. The ESS is also close to the Nash equilibrium, which Maynard Smith had not heard of until ca. 1975, when his graduate student, economist Peter Hammerstein, asked why he never cited Nash. Afterwards he tended to quote Nash even though, he said, he did not owe him anything, not having known about him (Maynard Smith and Erickson 2004. JMSA [uncatalogued].)
[19] Maynard Smith 1982b, 2.
[20] Maynard Smith to Hamilton, 27 October 1977. JMSA Add MS 86764.

similar to but more general than Hamilton's "unbeatable strategy", was developed *independently* by Maynard Smith & Price (1973)'.[21]

Despite Hamilton's long, possibly even life-long, "Maynard Smith paranoia", the ESS matter appears not to have caused any more conflict. Similarly, no priority dispute arose between Maynard Smith and Price even though the case had all the potential for it: Maynard Smith refereed a paper by Price which inspired him to consider game theory.

5.2.1 Price's 'Antlers' paper and Chicago 1970

Figure 17. George R. Price. London 1974. © Estate of George Price.

George R. Price (1922-1975) was an American polymath with a PhD in chemistry for work done on the Manhattan Project. He then worked in a variety of fields, not quite finding his vocation, before moving to the UK in 1967.[22] In London, he began thinking and working on the evolution of altruism, further stimulated by correspondence with Hamilton. Price had come across Hamilton's 1964 'The genetical evolution of social behaviour' papers in the library but found it too dense for library reading. He asked Hamilton for reprints, but Hamilton had none left. Instead he sent his paper on extraordinary sex ratios, admitting: 'So

[21] Maynard Smith 1978, 147 (emphasis added).
[22] Harman 2010.

far I haven't arrived at any clear idea even as to what sort of "game" the genes are expected to be playing when operating together'.[23] The notion of games in the animal world stuck with Price who – for a different project – had read von Neumann and Morgenstern's book. He eventually connected the dots and realised that animal conflicts could be thought of as games.

Price started going through the literature and composed a long manuscript on intraspecific combat, submitting it to *Nature* in 1968. *Nature* forwarded it to Maynard Smith for review. Maynard Smith liked Price's ideas and suggested the paper should be published as an abstract (it being too long for *Nature*). But a long version could be sent to, for instance, the *Journal for Theoretical Biology*.[24]

The 'Antlers' paper, as Maynard Smith dubbed his files ("Price—Antlers"; the full title was 'Antlers, intraspecific combat, and altruism'), has been discussed by Oren Harman.[25] Antlers were the main example and starting point for the paper and its argumentation. They presented a problem in that they are expensive in evolutionary terms but not very effective as weapons. They also could not (just) be accessories for sexual selection: in some species, both males and females have antlers. Another solution had been put forward in a paper by Bernard Stonehouse.[26] Stonehouse claimed that antlers were neither but instead a means for heat dissipation. Price's paper specifically argued against that because Price thought antlers must have evolved in the context of limited combats.[27] Limited combat means that individuals would fight but avoid injury. 'I develop an explanation that I believe to be new, of how combat limitation behaviour and non-injurious weapons can be advantageous not only to a group or species, but also differentially advantageous to individuals and thus stable against evolutionary change.'[28] Price then simulated several rounds of male deer fighting and their following mating probability.[29] He discovered that limited combat strategies are more successful than escalating fights when thinking about the long term.[30] Like Hamilton in his

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23 Harman 2011, 2.
24 Maynard Smith and Dawkins 1997, https://www.webofstories.com/play/john.maynard.smith/42.
25 Harman 2011; see JMSA Add MS 86597B for the manuscript.
26 Stonehouse, B. (1968). Thermoregulatory function of growing antlers. *Nature 218*, 870–872.
27 'Antlers' manuscript, p.1. JMSA Add Ms 86597B.
28 'Antlers' manuscript, p.2. JMSA Add MS 86597B.
29 'Antlers' manuscript, p.13ff. JMSA Add MS 86597B.
30 Harman 2011, 3.

1967 paper, Price too came up with an early formulation of an ESS, which he needed to explain why a stag with deviant behaviour, always escalating fights and injuring opponents, would not be more successful:

> A sufficient condition for a genetic strategy to be stable against evolutionary perturbation is that no better strategy exists that is possible for the species without taking a major step in intelligence or physical endowment. Hence a fighting strategy can be tested for stability by introducing perturbations in the form of animals with deviant behaviour, and determining whether selection will automatically act against such animals.[31]

Price concluded that nature was necessarily more complex than his model. But he hoped that his theoretical work could be tested experimentally and observationally,[32] as did Michael Simpson who had read the draft. He hoped it would be 'published soon, because it could give ethologists who study social organisation in the field new ideas. [...] Although, as I am sure you will already have discovered, ethologists are rather shy of abstractions and simplifications.'[33] Price himself, after sending his draft to *Nature,* then attempted to come up with computer simulations to find a truly unbeatable strategy, but he soon 'reached a dead end and was thinking of giving it all up.'[34]

Problems relating to animal behaviour and conflicts were not new to Maynard Smith when *Nature* sent him Price's manuscript to referee. He had been thinking about them ever since his time as an undergraduate at UCL in the late 1940s. He had read Konrad Lorenz and others on ritualised behaviour in fighting and the avoidance of escalation, thinking that the explanation in group-selectionist terms had to be wrong. Avoiding injuries "for the good of the species" was not a viable Darwinian explanation for him, but animal behaviour also was not his area of research (although one of his papers on fruit fly genetics presents an important observation of animal behaviour, i.e. female selection of mates related to their

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31 'Antlers' manuscript, p.16. JMSA Add MS 86597B.
32 'Antlers' manuscript, p.28. JMSA Add MS 86597B.
33 Simpson to Price, 25 July 1970. JMSA Add MS 86597B.
34 Harman 2011, 5.

fitness[35]). Yet animal conflict stayed 'in my mind as a puzzle, you know. And I didn't think about it seriously until […] round about 1970'[36] – when he was sent the 'Antlers' paper.

One major point Maynard Smith picked up in the paper was that it supplied an individual-selectionist explanation for altruism and other animal behaviours. But two years passed before he started thinking about this issue seriously. In 1970, Maynard Smith took some time off from his duties at Sussex. He had been dean for five years and 'really pretty well been devoted to setting up a new school of biology, of filling it with apparatus and people and students and getting the courses going and so on, it's a pretty heavy job.' Maynard Smith 'got [himself] paid elsewhere' and went to the Committee on Mathematical Biology at the University of Chicago.[37] The Committee on Mathematical Biology had been set up in 1948 by Nicolas Rashevsky, a Ukrainian-born theoretical physicist who moved into biology and coined the term "mathematical biology" (as opposed to bio-mathematics or theoretical biology).[38] The Committee was an 'interdisciplinary departmental Committee [...] with the power to grant PhD's in the Division of Biological Sciences' and was meant to train mathematical biologists.[39] By the early 1960s it was functioning more or less like a fully-fledged department, with its own budget, power to appoint positions, and in its own building. But in 1964 Rashevsky resigned a year prior to retirement over difficulties finding a successor for the position of the Committee's chairman.[40] According to Lewontin, a critic of Rashevsky's and his approach, '[t]he work of the school was regarded as irrelevant to biology and was effectively terminated in the late 1960s, leaving no lasting trace.'[41] The primary tone of accusations was that Rashevsky failed to interact with biologists – although, as Evelyn Fox Keller has pointed out, 'dialogue is a two-way process, and some degree of responsibility for that failure lies with the biologists themselves.'[42]

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[35] Maynard Smith 1956.
[36] Maynard Smith and Erickson 2004. JMSA (uncatalogued).
[37] Maynard Smith and Dawkins 1997, https://www.webofstories.com/play/john.maynard.smith/42.
[38] Shmailov 2016, xi-xii.
[39] Shmailov 2016, 91f.
[40] Shmailov 2016, Chapter 5.
[41] Lewontin 2003a, cited in Shmailov 2016, 159. Lewontin had been chairman of the Program in Evolutionary Biology at Chicago between 1968 and 1973 (Aronson 2001).
[42] Keller 2003a, 84.

Maynard Smith joined this environment in 1970. As he recalled, 'the only thing you can say for Chicago is that it's so awful, there's nothing to do there except work.'[43] Stimulated by the 'curious manuscript' of Price that he had reviewed earlier, he decided to learn 'some game theory.'[44] When he set out, he knew virtually nothing about game theory except that von Neumann and Morgenstern's book existed, and that the theory might offer some helpful insights. He wanted to know if game theory could help him understand animal conflict. However, as he attempted to read *Theory of Games and Economic Behavior* he found it 'totally incomprehensible' and 'deeply obscure'. Certain that this book could not be the only one discussing game theory he went looking for some further, elementary texts. Someone recommended Robert D. Luce and Howard Raiffa's *Games and Decisions: Introduction and Critical Survey* (1957), of which he read the first chapter. ('I should have read the whole book, but I didn't. You know how life is.') Maynard Smith took the concept of the payoff matrix from it. Once he had that and knew that the payoff was individual fitness, he could use it to ask questions about the evolution of behaviours.[45]

> And the one thing that reading the sort of text books of classical game theory did for me, was to provide me with a notion of a pay-off matrix, which is a very simple notion, and anybody can write down a pay-off matrix once they know what it is. I mean, you just write down a list of the strategies on the bottom and a list of strategies across the top and you have a whole series of entries, and in each hole you put what would the pay-off be to me if I do this and he does that.[46]

Table 1. *Payoffs for the Hawk–Dove game*

	H	*D*
H	$\frac{1}{2}(V-C)$	V
D	0	$V/2$

Figure 18. Payoffs for the Hawk-Dove game (Maynard Smith 1982, 12)

43 Maynard Smith and Dawkins 1997, https://www.webofstories.com/play/john.maynard.smith/42.
44 Maynard Smith 1985, 352.
45 Maynard Smith and Erickson 2004. JMSA (uncatalogued); cf. also 'Some Notes on Game Theory', referencing the Luce and Raiffa book, in JMSA Add MS 86749 (the folder is dated 1972 however, the year that he first published on evolutionary game theory).
46 Maynard Smith and Dawkins 1997, https://www.webofstories.com/play/john.maynard.smith/50.

Thinking about game theory and further developing his ideas, Maynard Smith finally gave it to his class of graduate students at Chicago to try out. Suppose you have a payoff matrix like this, he asked them, and then gave them the Hawk-Dove game, what would happen?

The Hawk-Dove game is, in its simplest form, depicted in Figure 18. Hawk and Dove[47] are strategies, or 'behavioural phenotype[s]; i.e. [they are] a specification of what an individual will do in any situation in which it may find itself.'[48] In the Hawk-Dove game, you may have two animals contesting a resource with the value *V*. *V* will be added to the Darwinian fitness of the animal winning the contest.[49] There are three possible behaviours – display, escalate, retreat – which make up two distinct strategies in the game as shown in above illustration. A Hawk will 'escalate and continue until injured or until opponent retreats', whereas a Dove will 'display [and] retreat at once if opponent escalates'.[50] Any injury will reduce the individual's fitness, and this cost is represented in the payoff matrix as *C*. *C* will be deducted from the injured individual's fitness. The payoffs are then defined as 'changes of fitness arising from the contest'.[51] That is, in its most basic form, fitness is measured in 'the expected number of offspring' which is ranked against each other.[52] Added *V* means more offspring than otherwise, deducted *C* means fewer.

Another game Maynard Smith came up with is the 'war of attrition' game. In this game, one essentially has an ongoing contest which no contestant can win but where it is also not worth – or possible – to share the resource. So you have to introduce an asymmetry between the two players; the asymmetry will define who wins the contest. One such asymmetry – and the reason why this strategy came to be known as the 'Bourgeois' strategy – is ownership. It means that whoever got to a territory first, or whoever got the resource first, wins, and the intruder will back down.[53] Initially, however, Maynard Smith thought of

[47] The terminology has a political and military background: 'Politically, and generally, the hawks are those who favour war and resolute military action, the doves those who support peace or compromise and negotiation. In the USA the term "Warhawk" came into particular prominence for those agitating for war with Britain in 1811–12.' ('Hawks and Doves' 2013). See also Sigmund 1993, 167.
[48] Maynard Smith 1982b, 10.
[49] Maynard Smith 1982b, 11.
[50] Maynard Smith 1982b, 12.
[51] Maynard Smith 1982b, 13.
[52] Sigmund 1993, 167.
[53] Maynard Smith and Dawkins 1997, https://www.webofstories.com/play/john.maynard.smith/46; for a detailed description see Maynard Smith 1982, 22f, and chapter 3.

these games more as a theoretical possibility rather than something that happened in nature. It was only when he gave a seminar in Austin, Texas, that things sped up. He presented his theoretical musings on game theory and finished with his ideas about ownership and a bourgeois strategy.[54] 'Of course, I don't believe animals actually do this, but, you know, if they'd read my paper I'm going to write, they should do, you see.'[55]

At this point, a postdoc called Larry Gilbert got up and said he would like to tell them about his PhD work. Gilbert, who is now professor at the Department of Integrative Biology at the University of Texas at Austin, had been studying anise swallowtail butterflies (*Papilio zelicaon*) in California. He had observed that during mating season, the males would occupy territories, hilltops, and the females would fly uphill to mate. As there are more male butterflies than hilltops, the 'owners' would be challenged by 'intruders', to use Maynard Smith's language. Gilbert saw that it was always the owner who won these conflicts. But he had also undertaken an experiment: he had made two male butterflies believe they owned the same hilltop by letting them occupy it on alternate days. Then one day, 'they were both loosed on the same hilltop. And they went in for a great long fight, they both thought it was theirs'.[56] The butterflies behaved exactly as Maynard Smith had predicted: without the asymmetry of ownership, the males kept fighting. This interaction proved to Maynard Smith that he was actually on to something, and that his abstract reasoning had a place in nature. (Gilbert, however, was known as 'John's imaginary biologist' at Sussex because he never published his PhD research; Maynard Smith finally 'produced him in the flesh' but still could only refer to the episode anecdotally.[57])

While Maynard Smith was in the United States learning game theory and testing out his ideas, Price was in London at the Galton Laboratory, trying to program computer simulations for "INTRASPECIFIC CONFLICT, POPULATION EFFECTS". After confirmation by John Maddox, the editor from *Nature,* to publish Price's Antlers paper if he

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54 Maynard Smith and Erickson 2004. JMSA (uncatalogued).
55 Maynard Smith and Dawkins 1997, https://www.webofstories.com/play/john.maynard.smith/47.
56 Maynard Smith and Dawkins 1997, https://www.webofstories.com/play/john.maynard.smith/47.
57 Maynard Smith and Dawkins 1997, https://www.webofstories.com/play/john.maynard.smith/49. See, for instance, Maynard Smith 1976, 45, for a reference to 'L. Gilbert (pers. comm.) on the swallowtail butterfly, *Papilio zelicaon*.'

shortened it, Price had wanted to add some computer simulation.[58] The John Maynard Smith Archive contains several papers sent to Maynard Smith by the Galton Laboratory after Price's death on the paper they were to collaborate on, amongst which are computer printouts dated 25 September 1970, Galton Laboratory, UCL.[59] But Price failed to make his simulation work and stopped working on the Antlers paper.[60] Erickson suggests that his religious conversion may have distracted him from his work,[61] but Price also admitted to Hamilton that it was simply more difficult than he had imagined – although he also thought it was 'almost at the point where I can return to writing the paper':

> Currently I am working on the animal combat paper. The children brought about much interruption in my work schedule, and I have mostly lately been working on computer programs. One program for a population model for gene frequency changes from various patterns of fighting, went pretty easily. A second paper, simulating two-animal combat, has turned out to be much more difficult than I anticipated. It indicates that my ideas on mechanisms weren't as clear as I thought.[62]

5.2.2 Mice, doves, and hawks in the computer

We have already introduced the Hawk-Dove game above, but the actual publication of these ideas took a few more years. After his return from Chicago, Maynard Smith wanted to write up his ideas but needed to refer to Price. They met about August 1970.[63] In 1972, Maynard Smith suggested in correspondence that Price's name should be on his paper as well.[64] But the first publication containing the idea of an ESS – and the first use of the term "evolutionarily stable strategy" – were by Maynard Smith alone and published in *On Evolution*. Maynard Smith mentioned Kalmus, Lewontin and Hamilton as biologists who had applied versions of game theory to evolutionary biology before him. He credited Price in the introduction to his essay collection:

> I would probably not have had the idea for this essay if I had not seen an unpublished manuscript on the evolution of fighting by Dr George Price, now working in the Galton Laboratory at University College London. Unfortunately, Dr Price is better at having ideas than at publishing them. The best I can do therefore is

[58] Price to Geist, 24 March 1974. JMSA Add MS 86597B.
[59] George Price, "INTRASPECIFIC CONFLICT, POPULATION EFFECTS", 25 September 1970. JMSA Add MS 86597B.
[60] Harman 2011, 5.
[61] Erickson 2015, 235.
[62] Price to Hamilton, 21 September 1970. GPP Add MS 84116.
[63] Price to Lewontin, 15 September 1970. WHP Z1X102/1/1.
[64] Price to Maynard Smith, 20 April 1972. JMSA Add MS 86764.

> to acknowledge that if there is anything in the idea, the credit should go to Dr Price and not to me.[65]

Even though it was followed by reprints of essays and talks originally given in various professional environments, this essay-collection was aimed at a non-specialist audience. Intended audiences are central in this case in relation to scientific priority claims and intellectual property. As we have seen, evolutionary game theory had by 1972 quite a varied history including published and unpublished attempts to integrate or make use of game theory in evolutionary biology. Now Maynard Smith introduced his take on evolutionary game theory not in a peer-reviewed scientific journal but in *On Evolution.* This offered quick publication and may have been a way of trying out an idea not quite ready for a journal. Non-specialist writings are used to 'define boundaries of a new field'.[66] Even if purportedly addressed to "the public", they can carry hidden (or less hidden) agendas meant to convince other specialists.[67] At the same time, if we remember the rhetoric about Haldane's 1955 publication touching on genetic altruism, both Maynard Smith and Hamilton made a lot of the fact that it was a "popular" article when discussing Hamilton's priority over Haldane's.

Maynard Smith started the essay with Price's example of antlers and a section about his issues with group selection as an explanation for ritualised animal fights. He explained his interest in game theory before turning to discuss two levels of fighting (conventional and escalated) and the related strategies. The first two of his five explored strategies, reminiscent of the Hawk and Dove strategies (the terms are not introduced in this essay), are written as follows:

> $C \rightarrow C$ Fight conventionally. Retreat if one's opponent proves to be stronger (or to display with greater vigour) or if one's opponent escalates.
>
> $E \rightarrow E$ Fight at escalated level. Retreat only if injured.[68]

'A strategy qualifies as an ESS' as first defined by Maynard Smith here 'if, in a population in which most individuals adopt it, there is no alternative strategy which will pay better.'[69]

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65 Maynard Smith 1972, vii-viii.
66 Gregory and Miller 1998, 86.
67 Cf. Sepkoski 2014.
68 Maynard Smith 1972, 19.
69 Maynard Smith 1972, 21.

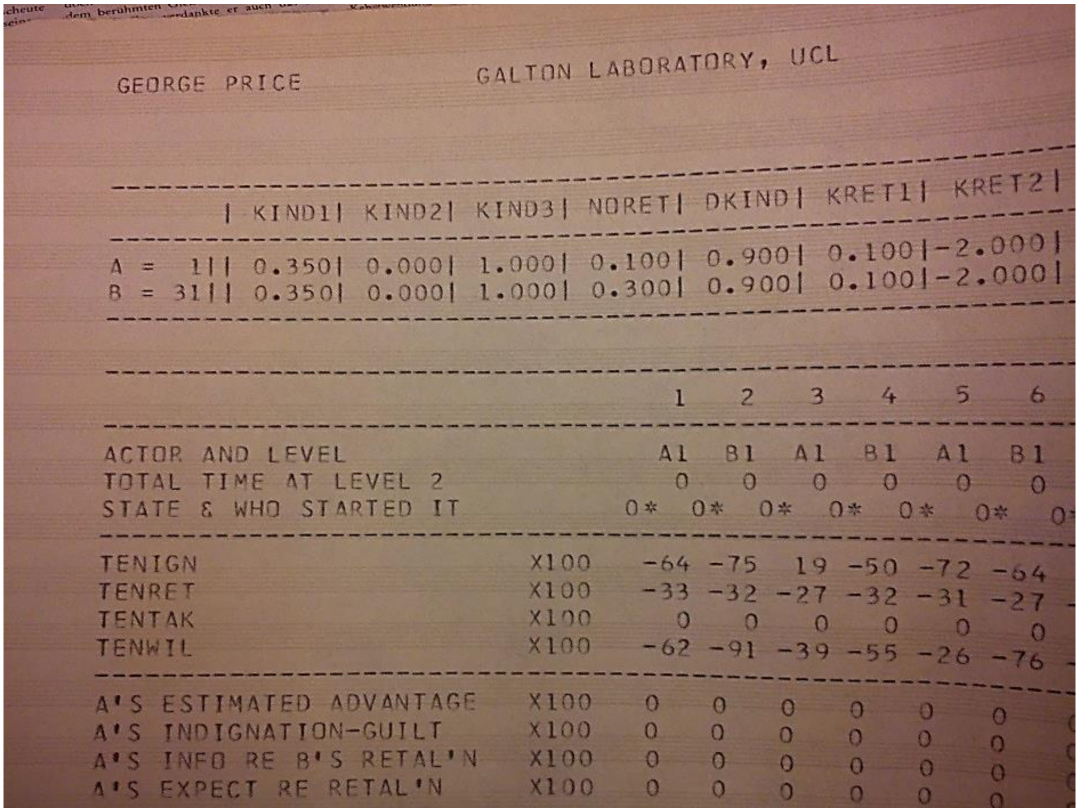
The situation in which Price and Maynard Smith found themselves in the early 1970s had the potential of becoming a priority dispute. Maynard Smith's work undertaken during and after his visit to Chicago was, on the one hand, the result of a career-long fascination with the problem of animal behaviour and an aversion to group-selectionist explanations for behaviour.[70] On the other hand, it had been brought back into focus and been inspired by Price's manuscript, formalising some of Price's verbal ideas. (Price's paper does not contain a payoff matrix.) Indeed, in parallel with this first essay aimed at a popular audience, Maynard Smith had been working on a version aimed at professional audiences, and it was in the context of this that he originally tried to locate Price's work. As it turned out, the Antlers paper had not been published. In fact, Price had moved on to work on something else.[71] Returned from Chicago in 1970, Maynard Smith tracked down Price in London.[72]

They started collaborating and in 1972, Price tentatively agreed to joint authorship, but only if Maynard Smith's name went first – and only after he had another look at the program Maynard Smith was using.[73] He was insisting they needed the simulations to back up the theory and sent his earlier, failed simulations to Maynard Smith, commenting that it was 'hard to remember the details when I hadn't looked at that program for months.'[74] He recalled his aim and his main problem however:

> To get an interesting result, one has to get a simulation that shows adaptive behaviour even if one or both combatants deviate slightly from mathematically exact "get even" strategy. For example, after a sequence like this, abababababAB, suppose animal A does not immediately deescalate, but tries another Level II act: ababababABA. Then B has to retaliate again at Level II. So we might have sequences like abABABab. The trouble was that I found a tendency to get only certain extreme cases. Thus, with one adjustment of parameters (shown in the "A = …", "B = …." table near the top of the page),[75] there would be no escalation to Level II. With a second adjustment, one would get only 1-round bouts, ababABabab. With another adjustment, there would be no deescalation, i.e.:

[70] Maynard Smith and Erickson 2004. JMSA (uncatalogued).
[71] Maynard Smith 1976b, 42.
[72] Maynard Smith and Dawkins 1997, https://www.webofstories.com/play/john.maynard.smith/43; Price remembered getting a letter from Maynard Smith about it: 'After a year or so Maynard Smith wrote to me telling me he had refereed my paper and recommended publication in Nature, and now he wanted to cite it in something he was writing, and he wondered what had happened to it.' Price to Geist, 24 March 1974. JMSA Add MS 86597B.
[73] Price to Maynard Smith, 20 April 1972. JMSA Add MS 86764.
[74] Price to Maynard Smith, 13 February 1972. JMSA Add MS 86597B.
[75] Cf. Figure 19.

> abababababababababababaBABABABABABABABABABABABABABABABABA BABABABABA[76]


GEORGE PRICE GALTON LABORATORY, UCL

	KIND1	KIND2	KIND3	NORET	DKIND	KRET1	KRET2
A = 1||	0.350	0.000	1.000	0.100	0.900	0.100	-2.000
B = 31||	0.350	0.000	1.000	0.300	0.900	0.100	-2.000

		1	2	3	4	5	6
ACTOR AND LEVEL		A1	B1	A1	B1	A1	B1
TOTAL TIME AT LEVEL 2		0	0	0	0	0	0
STATE & WHO STARTED IT		0*	0*	0*	0*	0*	0*
TENIGN	X100	-64	-75	19	-50	-72	-64
TENRET	X100	-33	-32	-27	-32	-31	-27
TENTAK	X100	0	0	0	0	0	0
TENWIL	X100	-62	-91	-39	-55	-26	-76
A'S ESTIMATED ADVANTAGE	X100	0	0	0	0	0	0
A'S INDIGNATION-GUILT	X100	0	0	0	0	0	0
A'S INFO RE B'S RETAL'N	X100	0	0	0	0	0	0
A'S EXPECT RE RETAL'N	X100	0	0	0	0	0	0

Figure 19. Printouts, 25 September 1970. (JMSA Add MS 86597B)

But Price needed his simulations to show that animals did *not* escalate into fights like this, and he was puzzled as to why he could not. So Maynard Smith set about to do some programming himself. 'George was a perfectionist,' he remembered,

> and he wanted me to do more mathematics to show that some of the things he claimed were correct, and I had to teach myself some computer programming, because it wasn't analytically solvable, and I had to solve some of it by computer simulation.[77]

Their collaboration worked primarily by splitting the work load, with Maynard Smith tackling the simulations and Price doing the literature review. (Although Price at one point told Maynard Smith, 'You've done much more than your share of work on this paper, so let me try putting together a slightly expanded version […].'[78]) The computer printouts of

[76] Price to Maynard Smith, 13 February 1972. JMSA Add MS 86597B.
[77] Maynard Smith and Dawkins 1997, https://www.webofstories.com/play/john.maynard.smith/44.
[78] Price to Maynard Smith, 19 October 1972. JMSA Add MS 86764.

Maynard Smith's simulations are filed under "Hawk and Dove" in his archive, and throughout their correspondence and for the simulations, the strategies for their game are called Hawks and Doves. The published paper of 1973, however, talks of Hawks and Mice. Price, after an earlier religious conversion, was uncomfortable using the word Doves because of its Christian and theological connotations[79] – although he had originally suggested Dove: 'You also ask for suggestions about names for combatants. My own feeling is that it will be most helpful to readers to use easily-understood descriptive names like Dove, Hawk, and Prober.'[80] Thus one of the first reports on evolutionary game theory in the *New Scientist* is titled, 'When a mouse defeats a flock of hawks'.[81] Afterwards, in his single-author paper of 1974, Maynard Smith changed the name back to Dove.

Some printouts in the "Hawks and Doves" folder indicate that Price ran the simulations as his name is on them. But Erickson, who interviewed Maynard Smith in 2004, notes that they were in fact run at the University of Sussex,[82] and it was Maynard Smith who wrote them – indeed, we know that Price specifically suggested he do so, since he himself had been unable to get results.[83] It is also Maynard Smith's handwriting on the printouts, noting difficulties that needed ironing out in a second, third or fourth run. Thus Maynard Smith noted on the printout for the second run of the program B 31 L (11 April 1972) – which, overall, was 'Fairly sensible' – that it appeared a 'bit artificial that first player, A, always runs out of motive first,' or that it is 'v. puzzling that first 14 unprovoked escalations are from B?!'[84] The third run of the same program (which they did the following day, 12 April) '[l]ook[ed] OK' but A still seemed to run 'out of motivation just before B, and so loses.'[85]

This tinkering questions the nature and role of the computer simulations. Maynard Smith and Price argued that a 'main reason for using computer simulation was to test

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[79] Harman 2011, 8. Maynard Smith recalled that 'when we were halfway through writing the […] *Nature* paper, he underwent this, he fell off a donkey on the way to Damascus or something. I don't know what happened' (Maynard Smith and Erickson 2004. JMSA [uncatalogued]).
[80] Price to Maynard Smith, 20 April 1972. JMSA Add MS 86764.
[81] Anonymous (1973). When a mouse defeats a flock of hawks. *New Scientist 60*(871), 390.
[82] Erickson 2015, 235.
[83] Price to Maynard Smith, 5 August 1972. JMSA Add MS 86764. See also Price to Geist, 24 March 1974. JMSA Add MS 86597B.
[84] B 31 L – Run 2 (11 April 1972). JMSA Add MS 86749.
[85] B 31 L – Run 3 (12 April 1972). JMSA Add MS 86749.

whether it is possible even in theory for individual selection to account for "limited war" behaviour.'[86] Maynard Smith had carried over an appreciation for models and simulations from his years as an engineer. He knew that even though models would require simplifications, they would still work, telling you something that could be translated back into the real world.[87]

> Maynard-Smith's [*sic*] game theory attack on animal behaviour is starting to pay dividends. We now begin to understand the forces behind animal competition. Some sceptics were worried by the apparent simplicity of the models and found it difficult to believe that this simple approach could throw any light on the complicated business of real life. Maynard-Smith had the last laugh: "When I was an aircraft designer," he told us "we built our planes on the assumption that air was incompressible. We all knew that air was *not* incompressible, but the planes flew nevertheless."[88]

With the advance of computer technology, simulations were increasingly used in the sciences. 'Of the many differences made by this turn to computers in biology, one of the most prominent has been to render the conceptual work performed by these models easier to recognize as theoretical'[89] – theoretical being defined as 'the analysis of a set of facts in their relation to one another'.[90] Simulations can have epistemic power, and Maynard Smith later pointed to the heuristic value of his game-theoretic models.[91] At the same time, the problems he and Price were facing were not soluble with traditional analytical methods.

> In the types of systems with which the simulation modeler is concerned, it is mathematically impossible to find an analytic solution to these equations—the model given by the equations is said to be analytically intractable. In other words, it is impossible to write down a set of closed-form equations.[92]

The computer simulations were the only way to prove their point.[93] But as the above-mentioned tinkering implies, as well as Price's difficulties with his original program from

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86 Maynard Smith and Price 1973, 15.
87 Kohn 2004, 211.
88 Cherfas 1977, 673 (emphasis in original).
89 Keller 2003a, 237.
90 *Webster's Seventh New Collegiate* (1967) cited in Keller 2003a, 236.
91 Maynard Smith 1982b.
92 Winsberg 2010, 7.
93 Maynard Smith later made regular use of simulations in his teaching at Sussex, setting advanced undergraduate and graduate students computer projects to solve, e.g. in his textbook *Evolutionary Genetics:*

> Some of the projects are aimed at solving problems that can be solved analytically. This is not as silly as it sounds. Most theoreticians nowadays check their results by simulation, or use simulation to suggest results that might be provable analytically. Also, if you write a program to

1970, this was not a straightforward process. Using a limited comparison with experiments – without 'embracing the […] overly grandiose intuition: that simulation is a radically new kind of knowledge production, "on par" with experimentation'[94] – we can draw on Harry Collins' concept of the "experimenter's regress": '"facts" can only be generated by "good" instruments but "good" instruments can only be recognized as such if they produce "facts".'[95] Similarly, Maynard Smith and Price only knew their simulation "worked" once it produced the results they were expecting. None of this tinkering made it into the 1973 paper, which simply states that '[t]wo thousand contests of each type were simulated by computer'.[96] There is no sign in the archives or the Maynard Smith-Price correspondence that either of them was concerned with the implications of the processes behind developing a working simulation. Maynard Smith, with his previous experience as an experimental biologist, may have taken them to be like experiments in the laboratory.

Computer simulation was also still in its infancy. Its history goes back to the United States and World War II.[97] Originally, computers were mainly used for data-logging in laboratories,[98] while 'the first and most obvious use of "computer simulations" (in the widest sense of the term) was to provide mechanized schemes of calculation that vastly expanded the reach of available methods of analysis.'[99] These were initially limited to the physical sciences, in particular nuclear weapons research, and meteorology.[100] In biology, computers have been used since the 1960s. Richard Dawkins describes using Oxford's only computer in the 1960s[101] and Russian ecologists had first published work that used computers to model populations in 1963; similar Canadian work was published in 1964.[102] In palaeontology, computers had been used by a few pioneers like David Raup since the

> solve a problem that cannot be solved analytically, it is essential to check the program by running some special cases (e.g. a case with no selection) whose results are known analytically: otherwise there is no way of being sure that the program is doing what it is intended to do (Maynard Smith 1998, viii).

94 Winsberg 2010, 136.
95 Godin and Gingras 2002, 137f; Collins and Pinch 2004, 97f.
96 Maynard Smith and Price 1973, 16.
97 Winsberg 2010, 4.
98 Hamilton 1995, 85.
99 Keller 2003b, 201.
100 Winsberg 2010, 135.
101 Dawkins 2013, 191ff.
102 Menshutkin, Kazanskii and Levchenko 2010, 538.

early 1960s.[103] Raup used computers to produce images of morphological structures for his papers and for geometric analyses in the early and mid-sixties. In 1969, a meeting on "Computers in Paleontology" took place in Chicago, at which several papers 'examined the potential for computers to assist in the actual formation and testing of new hypotheses.'[104]

The speed with which computer simulations were taken up in the sciences was determined partly by access to computers in the first place. It had been 'only in the mid-1950s that the UGC [University Grants Committee] became aware of computers as tools of academic research for which funds might have to be found on a regular basis.'[105] By 1965, 23 universities were to be provided with computers,[106] and the Flowers Report of 1966 recommended that over the following five years, every university 'would be provided with small to medium-sized installations'.[107] Price only had had access to UCL's IBM 360 Mod 65 computer thanks to Hamilton, who had given his 'permission to use his job number (UMBSV19)'.[108] (Hamilton and Price had been collaborating on simulations around 1970.[109]) Whereas Price mostly used the computer language FORTRAN,[110] Maynard Smith seems to have used ALGOL.[111] The University of Sussex had its own on-site ICL (International Computers Limited) computer since 1966, with more facilities becoming available in 1970.[112]

Although the 1973 paper relied on computer simulations to back up its theory, the archive shows that Maynard Smith relied on further pen and paper analyses. Next to the printouts of tournaments and programs run in 1972, there are hand-drawn flow charts of the moves that A makes – presumably to check why it seemed to always lose. Price asked Maynard Smith to let him take a look at some of these because he wanted to check where he had gone wrong in his own programs. Overall, he was thrilled with Maynard Smith's results. 'Fascinating. Congratulations!' he wrote. 'Thus far I've had only a little glance at it,

103 Sepkoski 2012, chapter 3.
104 Sepkoski 2012, 108.
105 Agar 1996, 630.
106 Agar 1996, 637.
107 Agar 1996, 640.
108 Hamilton 'To Whom it may concern', undated. GPP Add MS 84117.
109 Erickson 2015, 234.
110 Price to CPL Recruitment, 27 August 1974. GPP Add MS 84115; see also Price to Maynard Smith, 13 February 1972. JMSA Add MS 86597B.
111 Price to Maynard Smith, 20 April 1972. JMSA Add MS 86764.
112 'History of IT at Sussex' 2012.

but so far as I can understand it, it looks as though you've gotten well beyond the point I reached.'[113] In fact, Price had anticipated Maynard Smith would fail:

> Incidentally, I should tell you that when I urged you to try the animal combat simulation I felt pretty sure that you would fail as I did – but I thought something might still be gained from that […]. Thus it was a considerable surprise to me when I received the print-out.[114]

While Maynard Smith was busy formalising the arguments and working on the simulations, Price was responsible for reviewing the ethology literature.[115] This resulted in a second issue surrounding priority claims, or at least of acknowledging other people with the 'Logic of animal conflict' paper: Valerius Geist complained that he had not been acknowledged for having the idea of retaliation first. Geist is an ethologist with a 1966 PhD on American mountain sheep in Canada.[116] Later that year, Geist published a long and detailed paper on 'The evolution of horn-like organs' in *Behaviour*. He discussed various types of horns and their possible evolutionary function, surveying much of the existing ethological literature and adding substantially from his own field work. 'There is little argument that horns can function as weapons and inflict wounds on opponents,' he wrote.

> Yet this statement is a far cry from the generalization that horns evolved as weapons. [...] it appears unlikely that horns evolved in response to predators […]. Interspecific engagements appear hence unlikely as an impetus to horn evolution. Intraspecific contacts therefore remain as the most probable functional influences.[117]

Another possible function of horns lay in their display to intimidate an opponent.[118] Another option was that they function as rank indicators and are related to territoriality.[119] Here, Geist talked about aggression and adaptation:

> Aggression arises from self assertion when one individual attempts to displace another during conflict of mutual interests. Aggression is adaptive. It ensures the more aggressive having priority in satisfying its basic appetite; dominance hierarchies establish such priorities in groups of individuals. An individual without

113 Price to Maynard Smith, 20 April 1972. JMSA Add MS 86764.
114 Price to Maynard Smith, 5 August 1972. JMSA Add MS 86764.
115 Price to Geist, 24 March 1974. JMSA Add MS 86597B.
116 Willeke 2015, 'Wie weit darf Naturliebe reichen?'
117 Geist 1966, 183.
118 Geist 1966, 196.
119 Geist 1966, 205ff.

> self assertion is not only mal-adaptive but unthinkable. *Yet, overt aggression, fighting, is for most mammals highly unadaptive.*[120]

This last sentence captures the point made in the Maynard Smith and Price paper: that pure fighting strategies are not evolutionarily stable because of the risk of injury which would give advantage to less aggressive animals who may not win fights but, by avoiding them, do also not get injured. 'Display or threat are mechanisms achieving the same end as overt aggression, but not the same consequences,' is one of Geist's conclusions.[121] After reading Maynard Smith and Price's paper, Geist sent a manuscript to *Nature* in early 1974, twelve pages long (fifteen with references) and angry. Geist repeatedly referenced his own field work and observations, calling attention to his efforts and practical rather than theoretical biology. 'The paper by Maynard Smith and Price entitled "The logic of animal conflict" increases one's awe of computors [*sic*], for how can a program based on invalid and unrealistic assumptions come to valid conclusions about animal combat?'[122] After ten pages of criticism, he conceded that the model 'leads them (Maynard Smith and Price) to conclusions that can be accepted as valid and *that have been reached by others, but which were not acknowledged*.'[123]

The manuscript appears to have been forwarded to Price, who in March 1974 wrote a long letter to Geist. He picked up on Geist writing in a style that implied Maynard Smith and himself had intentionally withheld credit: 'I do not know whether this was your meaning or not, but your use of the word "acknowledge" is likely to suggest to many readers that we were familiar with your work but refused to give you credit.' Price therefore wished to clarify that neither Maynard Smith nor he had been aware of Geist's work on the retaliation principle, and that if they had been, they would 'most certainly have given you credit.'[124]

In the end, Geist wrote to Price that while he was still 'not terribly pleased' and held them accountable for not doing their literature search thoroughly enough, he had 'mellowed somewhat'. He also conceded that if he had titled his article differently, it might have been

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120 Geist 1966, 207f (emphasis added).
121 Geist 1966, 208.
122 Geist, January 1974, p.1. JMSA Add MS 86597B.
123 Geist, January 1974, p.10 (emphasis added). JMSA Add MS 86597B.
124 Price to Geist, 24 March 1974. JMSA Add MS 86597B.

easier to find.[125] Maynard Smith decided not to reply to Geist's *Nature* letter, even though the journal had invited him to do so.[126] Instead, he mentioned and cited Geist's paper in his 1974 paper 'The theory of games and the evolution of animal conflicts', which was a much more extensive discussion of evolutionary game theory as envisaged by Maynard Smith (and which also reintroduced the doves): 'The importance of retaliation in the evolution of animal conflict was emphasized earlier by Geist (1966).'[127] Geist's paper got an additional mention in Maynard Smith's brief history of evolutionary game theory written two years later for the *American Scientist*.[128]

The issue with Geist got resolved, and rather amicably, although a letter from unrelated correspondence shows that some resentment remained between Geist and Maynard Smith. Commenting on the proposed "Selfish Gene" *Horizon* episode (see below), Geist informed the producer that he 'did criticize Professor Maynard Smith in Nature 259, 354 (1974), for falling victim too readily to the dichotomy of ritualized versus unritualized fighting. He may not have forgiven me.'[129] More pertinent to this chapter, there never much arose any conflict between Price and Maynard Smith on the question of scientific priority or intellectual property. Firstly, Maynard Smith tracked down Price to credit him and offered joint-authorship. Moreover, Maynard Smith was building on Price's *verbal* arguments, formalising them mathematically, successfully running computer simulations (which Price had failed to do) and introducing the idea of an evolutionary stable strategy. Richard Dawkins has remarked on the Price-Maynard Smith collaboration: 'I think you were generous to him if I may say so. I hadn't appreciated before that the whole importation of game theory in ESS was entirely your contribution rather than his.' Maynard Smith replied,

> The idea of introducing game theory and the definition of an ESS was mine, yes. And I think had he published his paper, which was an argument that ritualised behaviour is stable because of the dangers of retaliation – using, I think, no algebra,

[125] Geist to Price, 22 April 1974. GPP Add MS 84116.
[126] Maynard Smith to Price, 17 June 1974. GPP Add MS 84116. The letter was published on 26 July 1974 as 'On fighting strategies in animal combat' (Geist 1974); it is considerably shorter and sounds less angry than the January manuscript.
[127] Maynard Smith 1974, 210.
[128] Maynard Smith 1976, 42.
[129] Geist to Jones, 24 June 1976. BBC WAC T63/109/1.

> entirely a verbal argument – had he published that, then I think I would not have made him a joint author and I would just have quoted the paper.[130]

The 'Antlers' paper is mostly verbal, and it does not contain a payoff matrix, the essential point Maynard Smith took from classical game theory. It does talk about probabilities and games, though in a more indirect manner and without referring to game theory: 'it is likely that, in a species that does not form coalitions, the basic strategy that has been outlined actually is unbeatable within capabilities of animal brains – since this same strategy characterizes human "two-person game" conflict at all levels from kindergarten children to nations.'[131]

Maynard Smith added that, 'to put it quite brutally, [Price was] a guy in much greater need of publications at that time, than I was,' revealing the imbalance in scientific status between the two. Price was quite aware of this too, and his respect for Maynard Smith and his work is apparent in their correspondence. On acceptance of their paper by *Nature*, Price noted that 'this [was] the happiest and best outcome of refereeing I've ever had: to become co-author with the referee of a much better paper than I could have written by myself.'[132]

5.3 Establishing the games

Evolutionary game theory was to take hold of the biologists' imagination, and not just in the specialised journals. It was presented popularly to a wider audience right from the start, and all along the way. Maynard Smith himself did much to push his ideas in specialist and non-specialist spaces but he was not the only one. As noted above, Maynard Smith's first publication dealing with evolutionary game theory and ESS was in an essay collection of 1972. The following year, after the Maynard Smith and Price paper, the *New Scientist* ran a short article entitled 'When a mouse defeats a flock of hawks'.[133] In 1976, Richard Dawkins – aged thirty-five and, much like Maynard Smith when he published *The Theory of Evolution*, still a relatively early-career researcher – published *The Selfish Gene.* It was picked up even before publication and turned into an episode for *Horizon*, presented by Maynard Smith. Also in 1976, Maynard Smith wrote a short piece for the *American Scientist* on the history of

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130 Maynard Smith and Dawkins 1997, https://www.webofstories.com/play/john.maynard.smith/44.
131 'Antlers' manuscript, p.18f. JMSA Add MS 86597B.
132 Price to Maynard Smith, 19 October 1972. JMSA Add MS 86764.
133 Anonymous 1973.

the ESS.[134] In 1977, Jeremy Cherfas wrote a report for the *New Scientist* following a conference on evolutionary game theory in Bielefeld, Germany.[135] The *New Scientist* ran another piece on evolutionary game theory two years later, by Ken Yasukawa ('A fair advantage in animal confrontations'), and again in 1984 (Anthony Arak, 'Playing games is a serious business'). In 1983, the computer magazine *Acorn User*, which had been founded the previous year 'to coincide with the launch of the BBC Micro' computer,[136] ran a 'Hawks and Doves competition'. It is unclear what exactly the nature of that competition was, but the magazine was running monthly competitions that involved puzzle-solving and programming.[137] The winner of this particular competition, Miguel Angel Gonzalez Munoz, was told he had submitted 'a very fine program' and was rewarded with his 'name in print in the December issue of Acorn User!'[138] (It is possible there was another prize as well – the summaries in the content lists suggest software may have been one.) In 1985, evolutionary game theory was picked up by its roots, and *The Economist* explained 'Why butterflies are bourgeois'.[139]

5.3.1 A one man tour de force?

Maynard Smith's titles for several of his papers in the first decade of evolutionary game theory are all a variation on the same theme (Figure 20), showing how much Maynard Smith was pushing evolutionary game theory. *The Economist* too noted that he was 'the main proponent of this school of evolutionary thought';[140] Dawkins has called the early history of evolutionary game theory 'largely a one man tour de force'.[141]

year of publication	title	place of publication
1972	Game theory and the evolution of fighting.	In J. Maynard Smith, *On Evolution* (pp.8-28). Edinburgh: Edinburgh University Press.

134 Maynard Smith 1976b.
135 Cherfas, J. (1977). The games animals play. *New Scientist 75*(1069), 672-673.
136 https://en.wikipedia.org/wiki/Acorn_User, accessed 16 May 2018.
137 See http://www.acornuser.com/acornuser/index/ind1.html (accessed 16 May 2018) for covers and content lists of *Acorn User* between 1982 and 1985.
138 Milne to Gonzalez Munoz, 4 November 1983. JMSA Add MS 86749.
139 Anonymous (1985). Why butterflies are bourgeois. *The Economist*, p.92.
140 Anonymous 1985, 92.
141 Dawkins 1983, 631.

1973	The logic of animal conflict (with George Price).	*Nature 246,* 15-18.
1974	The theory of games and the evolution of animal conflicts.	*Journal of Theoretical Biology 47*, 209-221.
1976	Evolution and the theory of games.	*American Scientist 64*(1), 41-45.
1979	Game theory and the evolution of behaviour.	*Proceedings of the Royal Society London, B Series 205*, 475-488.
1980	Evolutionary game theory.	In C. Barigozzi (ed.), *Vito Volterra Symposium on Mathematical Models in Biology* (pp.73-81). Berlin and Heidelberg: Springer Verlag.
1982	*Evolution and the Theory of Games.*	Cambridge [etc.]: Cambridge University Press.
1984	Game theory and the evolution of behaviour.	*The Behavioral and Brain Sciences 7*, 95-125.
1986	Evolutionary game theory.	*Physica 22D,* 43-49.

Figure 20. Maynard Smith's publications on evolutionary game theory.

By sheer omnipresence, Maynard Smith's name is linked to evolutionary game theory. The later articles are mostly focused on evolutionary game theory itself, not its history, development, or predecessors. (The Hawk-Dove game, however, makes an appearance in all publications!) But we see a creation, even a construction, of a certain narrative of the history of evolutionary game theory that outlines and sets relations, priorities and influences in the 1976 article for the *American Scientist.* It is in fact reminiscent of the 1972 essay. Now, four years later, Maynard Smith specifically wanted 'to trace the history of an idea,' in particular that of 'the concept of an "evolutionarily stable strategy"';[142] the man who developed the idea, together with George Price, was the man writing its history. This culminates in the publication of Maynard Smith's textbook and survey of the field, *Evolution and the Theory of Games,* in 1982, exactly a decade after a first definition of the ESS.

In the 1976 article – which is reproduced in Maynard Smith's second essay collection, *Did Darwin Get it Right?* (first published in 1988) – Maynard Smith summarised earlier attempts and versions of the ESS. Unlike in his 1972 essay, he did not mention Kalmus or Lewontin but focused in particular on Fisher's sex ratio theory (1930) and Hamilton's

[142] Maynard Smith 1976b, 41.

unbeatable strategy (1967).[143] He pointed out that while they did not use game theoretic terminology – Fisher in fact could not have done so, writing before the theory's development – their ideas are essentially reflective of what game theorists would call strategies:

> Although Fisher wrote before the theory of games had been developed, his theory does incorporate the essential feature of a game—that the best strategy to adopt depends on what others are doing.[144]
>
> The important point is that Hamilton looked for an "unbeatable strategy"—that is, a sex ratio which would be evolutionarily stable. In effect, he used Fisher's approach but went a step farther in recognizing that he was looking for a "strategy" in the sense in which that word is used by game theorists.[145]

Maynard Smith then moved on to George Price, his collaborator on the 1973 paper. Price had passed away the previous year but is paid tribute to here. He had realised that there was a way to explain ritualised animal conflicts not in group-selectionist terms but as benefitting the individual. But, as we have seen earlier, his manuscript to *Nature* was too long and needed to be either resubmitted in a shorter version or to a different journal – which Price never did. 'I then thought no more of the matter,' wrote Maynard Smith, until his term at the University of Chicago where he decided to learn about the theory of games and used it to develop and generalise Price's ideas and apply it to other problems too. 'While at Chicago, I developed the formal definition of an evolutionarily stable strategy'.[146] A definition of the ESS followed, then came a description of the Hawk-Dove game and of ESS work done by others, particularly Geoffrey Parker on dung flies (one paper in collaboration with Maynard Smith) and Hans Kummer on primates.

In this article, Maynard Smith argued about the history of evolutionary game theory similarly to how he had established Hamilton's priority over Haldane (and Fisher). It was Hamilton who formalised the idea of inclusive fitness mathematically, and who published on it. Without denying any of the work done before him, Maynard Smith now assured readers that the credit for the ESS went to himself. Fisher, Hamilton, and Price had

143 Lewontin's 1961 article is referenced in the bibliography however.
144 Maynard Smith 1976b, 41.
145 Maynard Smith 1976b, 42.
146 Maynard Smith 1976b, 42.

essentially developed a form of evolutionary game theory but without explicitly using game-theoretic terminology or formally, mathematically, defining the evolutionarily stable strategy. Moreover, this history appeared in a popular science magazine, the *American Scientist*. The readership is much broader than that of the 'forbidding pages of the *Journal of Theoretical Biology*', where much of the original evolutionary game theory and ESS work was published.[147] And noted above, it was not only Maynard Smith writing on evolutionary game theory in popular magazines, especially the *New Scientist*.

At the same time, Maynard Smith spent much of the 1970s pushing evolutionary game theory in professional journals and among biologists. That is, much of the popular and professional science are happening in parallel, and even in tandem – Cherfas' *New Scientist* article was a report from a conference, for instance; Yasukawa's *New Scientist* article a report on his own research in the area. Evolutionary game theory caught the biologists' attention, and the parallelism of specialist and non-specialist publications only reinforced this. Thus, while publishing in the *American Scientist,* Maynard Smith was developing and publishing on several games, writing on contests between relatives, and discussing asymmetrical contests in scientific journals. Some of those papers appeared in *The American Naturalist,* others in *Animal Behaviour*, the *Journal for Theoretical Biology* or the *Annual Review of Ecology and Systematics*, written by Maynard Smith alone or co-authored with, for instance, Geoffrey Parker.

Overall comments on the development of evolutionary game theory in the expert community of biologists agree that Maynard Smith was the driving force behind it. Alan Grafen, a student and then colleague of Richard Dawkins' at Oxford, wrote in his review of *Evolution and the Theory of Games* that Maynard Smith 'has presided over the subsequent development of ESS theory.'[148] Similarly, Mark Ridley wrote that 'Maynard Smith himself, from his department in Sussex, has done or directed much of the work, although increasingly helped by colonies elsewhere in this country, and in Germany and Canada.'[149] As noted above, Dawkins too wrote that much of the development of evolutionary game

[147] Ridley 1983.
[148] Grafen 1983, 22.
[149] Ridley 1983.

theory was 'largely a one man tour de force.' He also pointed out that 'G. A. Parker and, more recently, others, have played significant supporting roles to Maynard Smith's lead.'[150]

Dawkins, in fact, did much to popularise evolutionarily stable strategies. In 1976 – the same year as Maynard Smith's history of evolutionary game theory and three years after the Maynard Smith and Price paper – he published his book *The Selfish Gene.* The book builds much on the works of Maynard Smith, as well as those of Bill Hamilton and the American biologists Robert Trivers and George Williams. Dawkins particularly credits Maynard Smith's work from the early 1970s as a 'major stimulus that led me to dust off my old chapter 1 and write the whole book.'[151]

The Selfish Gene not only mirrors the parallelism of non-specialist and specialist mentioned above, in several of its aims it also mirrors Maynard Smith's "little Penguin" of Chapter 1. As Dawkins's preface points out, he had three imaginary readers: first, the 'general reader, the layman', second, 'the expert', and third, 'the student'.[152] This recognition of a diverse audience was important for *The Theory of Evolution* and its aims and audiences as well. *The Selfish Gene* had, before it was published by Oxford University Press (OUP), been under discussion at Jonathan Cape publishers, but they thought 'that the present version was too intellectual for a mass readership.'[153] This was the version that the OUP editor Michael Rodgers read. Rodgers made sure that the ideas, which excited him greatly, were scientifically sound by checking with a colleague of Dawkins', David McFarland. McFarland 'confirmed that Dawkins's scientific judgement was sound. The views he was putting across, David went on, represented the picture as seen by modern biologists. So, Dawkins was not an eccentric out on a limb? No, confirmed David, he was simply a good expositor wanting to gain access to a wide lay audience.'[154] (Dawkins did not think of the selfish gene idea as revolutionary; it was the 'critics and admirers' who came to do so after the book's publication. For Dawkins it was 'implicit in the orthodox neo-Darwinian theory of

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150 Dawkins 1983, 631.
151 Dawkins 2013, 273 (again on 274).
152 Dawkins 1989, v, vi. In the sequel, *The Extended Phenotype,* the audience then shifted: 'although this book is in some ways the sequel to my previous book, *The Selfish Gene,* it assumes that the reader has professional knowledge of evolutionary biology and its technical terms. On the other hand it is possible to enjoy a professional book as a spectator' (Dawkins 1990, v).
153 Rodgers 2017, 46.
154 Rodgers 2017, 46.

evolution.'[155] At the same time, the publishers were not afraid to present it as controversial on the blurb[156] and to connect it to the sociobiology debate which was '"red hot" and […] could not but help sales'[157].)

The chapter that particularly concerns us is the fifth, 'Aggression: stability and the selfish machine', although Maynard Smith's ideas also influenced the later chapters.[158] Maynard Smith is present throughout the chapter. After introducing the issue that, and briefly why, animals do not always fight and if they do, often do so without escalating, Dawkins points out that animals do 'complex, if unconscious, "cost-benefit" calculation[s]'.

> The potential benefits are not all stacked up on the side of fighting, although undoubtedly some of them are. Similarly, during a fight, each tactical decision over whether to escalate the fight or cool it has costs and benefits which could, in principle, be analysed. *This has long been realized by ethologists in a vague sort of way, but it has taken J. Maynard Smith, not normally regarded as an ethologist, to express the idea forcefully and clearly.*[159]

The collaborations with Price and Geoffrey Parker are acknowledged in the next sentence, as is Hamilton's unbeatable strategy as a precursor for the ESS. (Dawkins adds R.H. MacArthur to that list too.[160]) The Hawk-Dove game is essentially presented as a Maynard Smith idea,[161] but Price is reintroduced for the *Retaliator* strategy[162] which he and Maynard Smith discussed in their 1973 paper.[163]

Dawkins' enthusiasm for the ESS idea is particularly visible in a sentence that he later commented on in *The Selfish Gene*'s extended edition (1989) and before that, in his review of

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155 Dawkins 2013, 269 and 268; de Chadarevian 2007, 34.
156 De Chadarevian 2007, 32.
157 De Chadarevian 2007, 33.
158 Dawkins 2013, 275; in the *Extended Phenotype*, evolutionary game theory and ESS are discussed in chapter 7.
159 Dawkins 1989, 69 (emphasis added).
160 As do Maynard Smith and Price (1973, 15): 'The concept of an ESS is fundamental to our argument; it has been derived in part from the theory of games, and in part from the work of MacArthur and of Hamilton on the evolution of the sex ratio.'
161 Dawkins 1989, 69f.
162 A 'retaliator behaves like a hawk when he is attacked by a hawk, and like a dove when he meets a dove. When he meets another retaliator he plays like a dove. A retaliator is a *conditional strategist*. His behaviour depends on the behaviour of his opponent' (Dawkins 1989, 74).
163 Strategy (4): 'Plays *C* if making the first move. If opponent plays *C*, plays *C* (but plays *R* if contest has lasted a preassigned number of moves). If opponent plays *D*, with a high probability retaliates by playing *D*.' *C* describes conventional tactics, unlikely to cause injury; *D* describes dangerous tactics; *R* means retreat. (Maynard Smith and Price 1973, 16 and 15).

Maynard Smith's 1982 book on *Evolution and the Theory of Games*: 'I have a hunch that we may come to look back on the invention of the ESS concept as one of the most important advances in evolutionary theory since Darwin.'[164] He qualified this later on, saying that

> This sentence is a bit over the top. I was probably over-reacting to the then prevalent neglect of the ESS idea in the contemporary biological literature, especially in America. The term does not occur anywhere in E. O. Wilson's massive *Sociobiology,* for instance. It is neglected no longer, and I can now take a more judicious and less evangelical view. You don't actually *have* to use ESS language, provided you think clearly enough. But it is a great aid to thinking clearly, especially in those cases—which in practice is most cases—where detailed genetical knowledge is not available.[165]

In the review he made a similar point, pointing out that most will agree with him on the ESS's seminal nature but probably took his 1976 statement as exaggerated.[166] But the idea's value for evolutionary biology stands and today, 'every school child knows' of Maynard Smith's evolutionary game theory.[167]

Maynard Smith's view of *The Selfish Gene* was positive. (As were Hamilton and Medawar's, for example.[168]) Not only did he agree to narrate the *Horizon* episode (see below), he also pushed for Dawkins to be awarded the Lakatos Award. The Lakatos Award, launched in 1986, 'is given annually for an outstanding contribution to the philosophy of science, widely interpreted, in the form of a book published in English during the current year or the previous five years.'[169] Together with David Hull, who already had Michael Ruse and Daniel Dennett on board,[170] he was trying to gather nominations in 1986. John Watkins, however, of the Department of Philosophy, Logic and Scientific Method at the London School of Economics and Political Science (which awards the Prize), told Maynard Smith that,

> Of course, I have a tremendous admiration for Dawkins's work, but I should perhaps warn you that, despite your skillful pleading to the contrary, I am

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164 Dawkins 1989, 84.
165 Dawkins 1989, 287.
166 Dawkins 1983, 631.
167 Lewontin 1989, 107.
168 Dawkins 2013, 282. Less favourable views emerged already in 1977, with critical pieces by Steven Rose, Richard Lewontin, Stephen Gould, and Gunther Stent (de Chadarevian 2007, 34).
169 'Lakatos Award'.
170 Hull to Maynard Smith, 23 September 1986. JMSA Add MS 86582.

> inclined to predict that the Committee will not regard The Selfish Gene as really a contribution to philosophy of science.[171]

Maynard Smith still tried to 'persuade some philosophers to support me. I hope you will take seriously the possibility that scientists sometimes do better philosophy of science than philosophers.'[172] But it did not help; the 1986 Award was jointly won by Bas van Fraassen and Hartry Field.[173] Maynard Smith kept defending Dawkins, saying in 1985 that Dawkins' 'widespread misrepresentation […] that has gone on has been unjust to him'[174] and that he deserves credit as both a scientist and a populariser.[175] They also fought for a common cause – against creationism – in the 1986 Huxley Memorial Debate at Oxford (see Chapter).

The medium for non-specialist communication also changed with Dawkins. Even before the publication of his book, the BBC broadcast an episode in their *Horizon* programme on the selfish gene idea. Dawkins' contact with *Horizon* was established by chance. Michael Rodgers had a meeting with mathematician Norman Gowar who was, at the time, writing what was to become his *Invitation to Mathematics* (published 1979) for OUP. Over lunch Rodgers began talking about Dawkins' book and Gowar then 'casually said that he would mention it to Vivienne King, someone he knew at the BBC.'[176] After a phone call from King, she and *Horizon* producer Peter Jones came up to Oxford for a meeting with Rodgers and Dawkins. *Horizon* decided to produce an episode on the ideas in *The Selfish Gene* and asked Dawkins

> if I would like to present a documentary on the subject, but I was much too shy at that time to dare appear on television, and I recommended John Maynard Smith instead. He did a good job – he had a wonderfully warm and engaging nature […].[177]

Rodgers' account of why Dawkins did not want to present any prospective TV programme himself adds nerves as well as the fact 'that he was not the originator of the basic ideas he

171 Watkins to Maynard Smith, 25 September 1986. JMSA Add MS 86582.
172 Maynard Smith to Watkins, 13 October 1986. JMSA Add MS 86582.
173 'Lakatos Award 1986'.
174 Maynard Smith to Taylor, 15 February 1985. JMSA Add MS 86590.
175 Maynard Smith and Erickson 2004. JMSA (uncatalogued).
176 Rodgers 2017, 48.
177 Dawkins 2013, 281; alternatively, he recalls in the second volume of his autobiography: 'I declined through sheer nerves, and recommended John Maynard Smith instead. He did an excellent job' (Dawkins 2015, 188).

described in the book. For this reason, he told me, he wished to take something of a back seat in any television presentation.'[178] If we look at correspondence from the production period, however, a slightly different, less sanitised, image emerges. Rodgers wrote to Jones that there was an imbalance in the programme, that Dawkins was not getting enough recognition for his involvement. He – Dawkins – 'was depressed after the meeting with you and Maynard Smith over the summer – feeling that Maynard Smith had completely taken over and his own part forgotten.'[179] Jones apologised to Dawkins in December 1976, to which Dawkins replied that

> I was anxious not to come over as the originator of ideas which are really common neo-Darwinian property. It would not surprise me if John himself is a bit embarrassed for having been portrayed (not by you but by the newspaper reviews) as the onlie begettor [*sic*] of neo-Darwinism![180]

Dawkins indeed makes no appearance in the episode at all. As Soraya de Chadarevian wrote in a review of '*The Selfish Gene* at 30', 'Dawkins's participation in the programme was eclipsed by Maynard Smith's charismatic performance in the role of main presenter, and in the film's acknowledgements Oxford University Press was not even mentioned.'[181] It was advertised in the *Daily Mail* as 'Professor John Maynard-Smith [*sic*] challenges the popular and romantic Konrad Lorenz view of an altruistic animal kingdom' (Figure 21).[182] Glyn Jones, a botanist from Royal Holloway College, actually referred to "The Selfish Gene" as 'your film' in a letter to Maynard Smith, asking if 'it was commercially available for use in Universities.'[183] (Maynard Smith was not sure and told Jones that the 'BBC charges a fantastic and ridiculous price for use of their programmes.'[184])

178 Rodgers 2017, 48.
179 Rodgers to Jones, 4 October 1976. BBC WAC T63/109/1.
180 Dawkins to Jones, 16 December 1976. BBC WAC T63/109/1.
181 De Chadarevian 2007, 34.
182 *Daily Mail*, 15 November 1976, p.18.
183 Jones to Maynard Smith, 11 September 1979. JMSA Add MS 86580.
184 Maynard Smith to Jones, 19 September 1979. JMSA Add MS 86580.

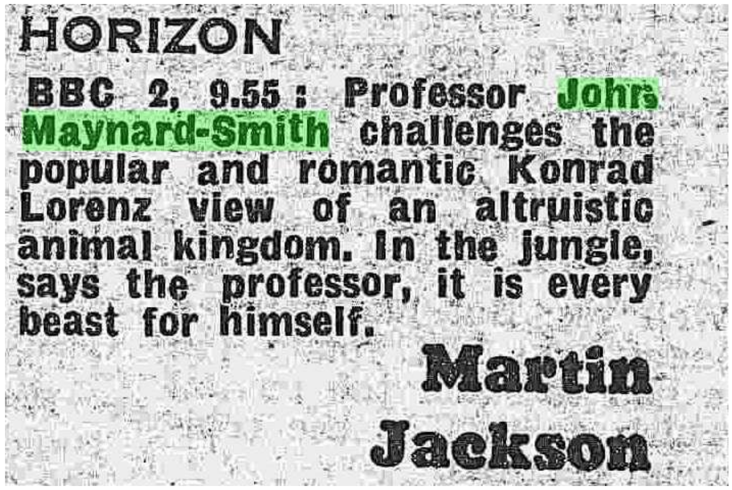

Figure 21. Advertisement for "The Selfish Gene". The Daily Mail*, 15 November 1976.*

An undated transcript of the "Genes" episode is kept in the John Maynard Smith Archive (but no further correspondence regarding, for instance, Dawkins' involvement or his vision for the programme; the episode's file at the BBC Written Archives Centre equally holds no further correspondence on the topic between Maynard Smith and producers). The gene's-eye view is prominent throughout, similarly the issue of altruism – 'What I want to do is to ask how it can be that animals can behave in such different ways, so selfishly or in such a self sacrificing [*sic*] way and that it should all be brought about by the same process of evolution by natural selection'[185] – and group selection. Maynard Smith, of course, argued against it:

> Now one of the arguments that has been used to suggest that selection really favours the species as a whole, rather than the individual, has been that very often when we see two males fighting the fight seems to be somewhat conventional, somewhat ritualised. They don't seem to be using theri [*sic*] weapons in the most effective way to wound their opponent, but more like to boxers who always hit above the belt instead of hitting in the most painful place, again I don't beleive [*sic*] this explanation I think its [*sic*] true that animals refrain from fighting at the most dangerous level very often, but the reason they do so is in their own interest, and animal who escalates too often is likely to find that his opponent will escalate back.[186]

Thus the episode finds its way to animal conflict and kin selection, with Bill Hamilton briefly talking. (This was another aspect that Dawkins was unhappy about; Hamilton's

[185] Horizon, Genes, Roll 1. Undated tape transcription. JMSA Add MS 86765.
[186] Horizon, Genes, Roll 1. Undated tape transcription, p.4f. JMSA Add MS 86765.

inclusion in the episode had been handled awkwardly, he felt: 'it might have been better if he had explained kin selection rather than talked about rotting wood.'[187])

Even though the terms "evolutionary game theory" or "ESS" are not used, the episode's reliance on this body of work is clear. We have seen above, for instance, that BBC staff were corresponding with scientists around the world on the scientific ideas and accuracy of "The Selfish Gene", as part of which Valerius Geist specifically recalled his and Maynard Smith's exchange over the 1973 paper on animal conflict. The fact that Maynard Smith spoke in the first person, as a scientist voicing his own opinions, rather than as a distanced narrator of other people's ideas, created a strong link between the content presented and him as a person. Taken together with the way the episode was advertised (next to the *Daily Mail* advertisement there is the following synopsis in the *Radio Times*: 'Why do animals appear to indulge in self-sacrificing behaviour? Prof John Maynard-Smith [*sic*] says it's sheer selfishness on the part of the genes which make up the animals'),[188] Glyn Jones' confusion that this was Maynard Smith's film is understandable, as is the view that Dawkins' was eclipsed by Maynard Smith. Maynard Smith's 'one man tour de force' in promoting evolutionary game theory to both non-specialist and specialist audiences explains how the idea came to be linked almost exclusively to him.

5.3.2 *Evolution and the Theory of Games* (1982)

Maynard Smith put the final stamp with his name on evolutionary game theory by writing the textbook *Evolution and the Theory of Games*, published in 1982, a decade exactly after he first talked about it in his essay. It was advertised as 'of interest' to a three-fold audience: biologists, mathematicians, and game theorists, with biologists as the main target audience: 'The account is aimed at senior undergraduate and graduate students, teachers and research workers in animal behaviour, population genetics and evolutionary biology. […] the mathematics has been largely confined to appendixes so that the main text may be easily followed by biologists.'[189]

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[187] Dawkins to Jones, 16 December 1976. BBC WAC T63/109/1.

[188] *Radio Times 2767* (1976, 18 November), p.19.

[189] Maynard Smith 1982b, dust jacket; the preface again makes clear that the book is 'addressed primarily to biologists. I have therefore been more concerned to explain and to illustrate how the theory can be applied to biological problems than to present formal mathematical proofs – a task for which I am, in any case, ill equipped' (Maynard Smith 1982b, vii). Prior to publishing his book, Maynard Smith was also

The introduction emphasised that the book is about a method of modelling,[190] and reviewers picked up on the uses for field biologists.[191] (Hamilton also thanked Maynard Smith for 'the copy of your book – an extremely useful work.'[192]) Maynard Smith had been corresponding with experimental biologists and zoologists in the field on how, or if, evolutionary game theory and the evolutionarily stable strategy can apply in practice, and took notes on their papers.[193] He did not necessarily understand all of them, however. A paper by A.W. Ewing and V. Evans on 'Studies on the behaviour of Cyprinodont fish I. The agonistic and sexual behaviour of Aphyosemion biviltatum', published in *Behaviour 46*, 264-278, is accompanied by a handwritten summary of the main points which conclude 'But GOD KNOWS what all this means – I have <u>no</u> <u>idea</u> what the fights are <u>about</u>.'[194] In a letter to E.C. Zeeman, mathematician, he had acknowledged that 'the important thing now is for people to look at animals and see whether they have read my papers.'[195] But overall, one of the most important uses Maynard Smith saw for game theory and ESS was their heuristic value: 'I think it would be a mistake […] to stick too rigidly to the criterion of falsifiability when judging theories in population biology. […] there is a contrast between simple models, which are not testable but which may be of heuristic value, and applications of these models to the real world, when testability is an essential requirement.'[196] This point is echoed in Dawkins' review; he explained that the 'ESS should not be thought of as a

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in correspondence with Ilan Eshel, a statistician who went through some of the proofs of some of the mathematics banned to the appendix. In particular, Maynard Smith wanted to take a look at Eshel's work on dynamics and stability. 'I am no mathematician, so I may get it wrong' (Maynard Smith to Eshel, 3 December 1980. JMSA Add MS 86597A). Eshel assured Maynard Smith that he was 'quite convinced there is no mistake' (Eshel to Maynard Smith, 16 December 1980. JMSA Add MS 86597A). As evolutionary game theory was developed beyond Maynard Smith's original ideas, the mathematics did eventually get too complicated for him (Maynard Smith to Percival, 7 July 1987. JMSA Add MS 86586).

In the book's preface, Maynard Smith also acknowledged the help of his Sussex colleagues, especially Brian and Deborah Charlesworth and Paul Harvey, but also Peter Hammerstein, Jim Bull, Eric Charnov, John Haigh, Susan Riechert and Siewert Rohwer. They had all read parts or all of the book, and Peter Hammerstein – a trained economist who had previously worked with the future Nobel Prize winner Reinhard Selten – had helped with some of the theoretical questions (Maynard Smith 1982b, vii-viii).

190 Maynard Smith 1982b, 1; see also Ridley 1983.

191 Grafen 1983, Dawkins 1983, Ridley 1983.

192 Hamilton to Maynard Smith, note on reprint of his and Marlene Zuk's 1982 paper 'Heritable true fitness and bright birds: a role for parasites?' JMSA Add MS 86840/41.

193 E.g. Caldwell to Maynard Smith 12 October 1979; Riechert to Maynard Smith, 15 May 1980. Both JMSA Add MS 86597A.

194 JMSA Add MS 86597A.

195 Maynard Smith to Zeeman, undated [1978?]. JMSA Add MS 86597A.

196 Maynard Smith 1982b, 9. See Chapter 5 for more on falsifiability and Maynard Smith's attitude towards Karl Popper's philosophy of science, and philosophy of science more generally.

hypothesis about nature, which might be true and might be false […]. Rather, it is a way of thinking, almost a mental discipline, a short cut which, given that we already accept the truth of the neo-Darwinian theory, assists us in avoiding certain kinds of tempting error'[197] (presumably like group selection, which Dawkins once called a 'maddeningly seductive error – the Great Group Selection Fallacy'[198]).

The book itself has the standard textbook setup of simple introductions to the topic, moving to the more complicated cases. These are hinted at early on to highlight the simplifications made in the basic model – it starts with the Hawk-Dove game. Thus one assumption in the simplest model is that two Hawks have a fifty-fifty chance when in contest which each other, whereas Chapter 8 discusses how differences in size and other asymmetries influences conflicts.[199] Similarly, in a contest between two Doves the simplest assumption is that both would benefit from sharing a resource equally. But '[i]f the resource is indivisible, the contestants might waste much time displaying; such contests are analysed in Chapter 3.'[200]

But is it a textbook? Heller's review points out that 'most of the literature cited is not older than five years showing the dynamics of this scientific field.'[201] J.F.C. Kingman wrote in the *New Scientist* that the book is 'both scholarly and speculative, spelling out carefully the assumptions behind the (rather simple) mathematical analysis, but stressing too the many possible biological phenomena that game-theoretic terms can explain.'[202] It is less an introduction for the undergraduate student to a scientific discipline and more an introduction for the researcher to a new way of thinking. 'This is a book that must be read by every serious ethologist/sociobiologist.'[203] That explains its mixture of scientific review and speculation. At the same time, Maynard Smith was in a curious position: as the originator of evolutionary game theory in the form that it took from the early 1970s onwards – Price had passed away in 1975 and exerted no further influence – he was excellently placed to give 'the first full account of the theory, and of the data relevant to

197 Dawkins 1983, 632.
198 Dawkins 2013, 261.
199 Maynard Smith 1982b, 12f.
200 Maynard Smith 1982b, 13.
201 Heller 1983, 265.
202 Kingman 1982, 583.
203 Dawkins 1983, 632.

it.'[204] He had also been constructing the history of evolutionary game theory from the beginning, with his 1976 article in *American Scientist*.

If we turn to Ludwik Fleck for genres of scientific writing, excluding textbooks as not quite fitting, we are left with handbooks and journals. He specifically talked of "handbook science" and "journal science" as constituting "expert science" – as opposed to "popular science".[205] Maynard Smith's book sits somewhere in between those two: handbooks require critical summary of science into an orderly, closed system[206] – speculation has no place in here. Journal science, however, is defined by a difference in opinions, methods, approaches, by contradictive evidence and fragments and the personality of the reports' authors.[207] *Evolution and the Theory of Games* is still strongly linked to Maynard Smith as its author and as founding father of EGT and ESS. But it is not preliminary; except for the later speculations it does present a working method that has been tried and tested over a decade, and not just by Maynard Smith alone.

5.4 Conclusion

As in the previous chapter, Maynard Smith was stimulated to develop an idea after reviewing someone else's manuscript. The collaboration with Price led to a new, influential way of studying animal behaviour. It is impossible to say whether Price, had he been alive after 1975, would have had any further impact on the development of evolutionary game theory, or whether he would have objected to the Hawk-Dove game being known under that name rather than the Hawk-Mouse game. He had abandoned the project before Maynard Smith got involved, having failed to get the computer simulations to work, and a religious conversion was already leading him down very different paths.[208] During his lifetime however, no conflict arose between him and Maynard Smith even though that had been a distinct possibility, especially with Price knowing about Hamilton's feelings towards Maynard Smith. As a factor in the genesis and development of ideas in science this puts the reviewer in a dangerous position when it comes to intellectual property issues. Price never

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204 Heller 1983, 265.
205 Fleck 1935/2017, 148.
206 Fleck 1935/2017, 156.
207 Fleck 1935/2017, 156.
208 See Harman 2010 for the full story of Price's life, also theatrically interpreted by Undercurrent Theatre in "Calculating Kindness" (2016).

published his 'Antlers' paper, leaving Maynard Smith nothing to cite. The solution was to publish the ESS idea first in an essay specially written for a collection, acknowledging Price's influence on the idea. Dawkins, over time – and in light of the later reception of his *Selfish Gene* – revised his own views on science popularisation, concluding that 'science and its popularization could not be clearly separated.'[209] The two work in tandem all throughout the history of evolutionary game theory. Not only is there a parallelism between specialist and non-specialist science, with magazines picking up on the ideas immediately and Dawkins' own book being turned into a *Horizon* episode. Maynard Smith himself dipped in and out of genres and roles, writing for a number of audiences and constructing the history of evolutionary game theory from its beginning.

Maynard Smith's role as a personable narrator with an authoritative voice in "The Selfish Gene" is synonymous with his overall role this decade of games. He was eloquent and omnipresent in the number of publications he put out on the subject, pushing for his ideas – and establishing his authority over Price by turning the Mice back into Doves, and over the discipline by being 'consulting editor for journals and the obvious referee for related papers'.[210] The journal system with its hierarchies and power to establish whether or not ideas are valid and worthy through publication or rejection, gives a certain amount of control to leaders of a field.[211]

> Should one believe Bloggs' result? Does it depend crucially on some parameter? Has Bloggs generalized his result to include the case x=5? Should we really expect to see animals behaving as Bloggs suggests? Has anyone seen this? Maynard Smith will know. He is nearly always right, and always sensible.[212]

At the same time, the system is an 'essential component of […] quality control'[213] and as Alan Grafen, from whom the above quote is taken, pointed out: Maynard Smith 'is nearly always right, and always sensible.'[214] Thus evolutionary game theory became "Maynard Smith's evolutionary game theory" in part through his own stream of specialist and non-specialist publications, his position of authority on the topic making him first point of

209 De Chadarevian 2007, 35.
210 Grafen 1983.
211 Ravetz 1996, 252.
212 Grafen 1983.
213 Ravetz 1996, 252.
214 Grafen 1983.

contact for journal editors, as well as through other scientists' reinforcing the link in their reviews and publications like *The Selfish Gene*. The 'one man tour de force' was supported by the system and colleagues like Alan Grafen, who once wrote to Maynard Smith:

> I hope I've just strangled before birth a book by Rowe and Hubbard intended as an introduction to game theory for biologists. Seen any of it? I didn't think OUP should enter the lists against you and CUP with a weapon so single-edged (on the wrong side).[215]

[215] Grafen to Maynard Smith, 6 April 1987. JMSA Add MS 86576.

PART 3: CONTROVERSIAL SCIENCE

We have now reached the mid- to late stages of John Maynard Smith's career. So far, we have discussed what he is best known for: his science communication to a wide, non-specialist audience, both in writing and on radio and television, his coinage of the term kin selection with the larger implications of group selection and the relationship with Bill Hamilton, and in the previous chapter, evolutionary game theory and evolutionarily stable strategies. But as Joshi has pointed out, '[o]ver his long and very active career, Maynard Smith consistently worked on problems, *often controversial*, that lay at the centre of important debates in evolution.'[1] In the last two chapters, we will therefore turn to Maynard Smith's involvement in what I am calling "controversial science" – as opposed to the previous parts on "popular science" and "professional science". The overlap with previous chapters is obvious: Chapter 3 already dealt with a controversy (a controversy about scientific conduct, however, rather than scientific ideas). This overlapping between themes will continue: Chapter 5 will include moments of popular science as well as professional science, just as the previous parts have included elements of all three areas.

In Chapter 5 we follow Maynard Smith in his dealings with challenges to the theory of evolution at large (put forward by religion and by creationists) and more specifically the neo-Darwinian focus on adaptation (put forward by palaeontologist Stephen Jay Gould). How Maynard Smith dealt with these reveals something about his view of the nature and workings of science, as well as his use of and attitude towards the philosophy of science. Chapter 6 will pick up the theme of evolution, but this time, Maynard Smith found himself on the other side – as someone challenging an orthodox position. In the 1990s, he and several colleagues suggested that human mitochondrial DNA does occasionally replicate, something which was thought impossible and which had implications for evolutionary timelines, in particular in relation to human origins.

[1] Joshi 2004, 107 (emphasis added).

6 Did Darwin get it right?

We know of Maynard Smith's previous involvement in controversies (Chapter 3 and, to a degree, Chapter 4), we know of his emphasis on the fact and facts of evolution by natural selection and his focus on adaptation as the question to answer (Chapter 1), and we know of his use of broadcasting to discuss science (Chapter 2). All of these come back and into focus in this chapter. The title, 'Did Darwin get it right?', is one Maynard Smith used for an essay published in the *London Review of Books* in 1981, then for his second essay collection (first published in 1988 as *Games, Sex and Evolution*), and as a section heading within that collection. The essays collected under that heading are covering the 'latest attempt[s] to dethrone Darwinism as the central theory of biology.'[1] Paul Harvey's review noted: '[t]he supposed threats to neoDarwinism [*sic*] from conspirators who have nothing else in common, and certainly not a constructive approach to science, are dealt with parsimoniously but effectively.'[2] One of these "threats" was Stephen J. Gould and Niles Eldredge's punctuated equilibria theory.[3] The two American palaeontologists first published their views in 1972,[4] and they concerned Maynard Smith from the (late) 1970s to the early 1990s. At the same time, he was actively debating creationists in public events (1979, 1986). These debates happened against the background of Maynard Smith's own interest in the science-religion relationship as well as the rise of creation-science. '[C]ritics of evolution tended to identify themselves as antievolutionists rather than creationists' until the mid-twentieth century;[5] scientific creationism or creation-science is defined in its opposition to evolution.

> Creation-science includes the scientific evidence and related inferences that indicate: (1) Sudden creation of the universe, energy, and life from nothing; (2) The insufficiency of mutation and natural selection in bringing about development of all

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[1] Maynard Smith 1993, 123.
[2] Harvey 1989, 62.
[3] David Sepkoski notes that, especially in his later writings, Gould preferred to call the theory "punctuated equilibrium" whereas Niles Eldredge always used the plural "equilibria" from their original 1972 paper (Sepkoski 2012, 143). I will use 'punctuated equilibria'.
[4] 'Speciation and Punctuated Equilibria: An Alternative to Phyletic Gradualism'. The third draft of the paper has been digitised and is available on the website of the American Museum of Natural History, where Gould worked for most of his career (see http://digitallibrary.amnh.org/handle/2246/6567, accessed 3 July 2018).
[5] Numbers 2013, 476.

> living kinds from a single organism; (3) Changes only within fixed limits of originally created kinds of plants and animals; (4) Separate ancestry for man and apes; (5) Explanation of the earth's geology by catastrophism, including the occurrence of a worldwide flood; and (6) A relatively recent inception of the earth and living kinds.[6]

Creationists like Henry Morris and Duane Gish used punctuated equilibria for their own purposes, bringing in Gould *et al.*'s theory to doubt evolution. Punctuated equilibria and creationism also share a sense of publicity and notoriety that is unusual for controversies around scientific theories and facts. As Kim Sterelny has noted, '[m]ostly these fights are kept more or less in-house, often because the issues are of interest only to the participants.'[7] But questions about evolution at large – rather than perhaps the details – and about the origins of life and human beings spark a more public interest. The topic and the controversy also made for excellent headlines, like 'Survival of the bitchiest as the Darwinian bulldogs go to war'.[8] Gould has blamed the media 'for distorting the state of affairs'[9] but at the same time he did much to popularise his views himself.[10] So both of these challenges to the orthodox neo-Darwinian view of evolution had strong public faces, and the first attack by Gould *et al.* influenced the second by the creationists.

Maynard Smith's interactions with creationism, and the relationship between science and religion more broadly, reveal his views of the nature of science. Bringing in his views on punctuated equilibria, we can extend these views to include more detail on the nature of scientific knowledge, theory, methodology, and evidence. The chapter thus looks at questions that 'have worried [Maynard Smith] ever since [he] was at school. What is the nature of scientific theories, and how do they differ from religious beliefs and political convictions?'[11] He made use of Karl Popper's ideas to formulate and support his own ideas, although he was not uncritical of the philosophy of science. To do so, we will move from the science-external challenges (creationism) to the science-internal challenges (punctuated

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[6] Definition from the 1981 Arkansas law, cited in Numbers 2006, 7.
[7] Sterelny 2001, 3.
[8] MicKle 1998.
[9] Sheldon 2014, 142; see also Gould 2002, 981f.
[10] Sheldon 2014, 140-143.
[11] Maynard Smith 1993b, 2.

equilibria) to neo-Darwinism, from passive engagement (collecting material) to active engagement (debating and publishing) with these challenges on Maynard Smith's part.

6.1 External challenges: creationism

6.1.1 Passive conversations: Jehovah's Witnesses

'One cannot spend a lifetime working on evolutionary theory without becoming aware that most people who do not work in the field, and some who do, have a strong wish to believe that the Darwinian theory is false,' wrote Maynard Smith in 1981.[12] One vocal group disbelieving the theory were – and are – creationists. Maynard Smith had both passive and active conversations with creationism, creationists, and the science-religion relationship. By this I mean that some creationist material he received, he did not comment on (that we know) but still kept in his files, thinking they were of some importance. At other times, Maynard Smith actively engaged with both material and people from a creationist or religious background.

Creationism itself is an ambiguous term that can mean different things to different people. The above definition specifically describes creation-science but the *Oxford English Dictionary*'s more general definition for creationism is much the same.[13] In the Christian context, creationism often includes a literal interpretation of the book of Genesis, such as in Young Earth creationism which believes the Earth was created by God in six days, making it about 6000 years old; other forms allow for the single days to be longer than 24 hours. Maynard Smith engaged with Christian creationists throughout his career. He himself had been raised in the Church of England but decided at as a teenager that he could not believe in religion, for two reasons. First, after coming across Darwin and the theory of evolution, he felt like he had to choose, and he chose science over religion – an 'escape from religion' and 'an enormous relief':

> what had been burdensome was that I didn't feel it allowed me to follow my thought to the end. I would be thinking about something then I'd think no but that's sort of dangerous if I think like that maybe I'll have doubts and then reading

[12] Maynard Smit 1981a, 21. See also Ruse 2005, 2.
[13] 'creationism' (n.d.). *Oxford English Dictionary*. Online version accessed at www.oed.com on 25 October 2018.

> Darwin the doubts just overwhelmed and I thought right I don't have to bother anymore I don't believe it.[14]

Second, like Haldane he went to 'that dreadful school' Eton and part of breaking with this background was to break with Christianity. He admitted that it 'wasn't all that easy' but that he still saw himself as a 'rather militant atheist'.[15] It is against this personal attitude towards religion, in combination with Maynard Smith's neo-Darwinism, that we have to see his interactions with creationism and against the latter only, punctuated equilibria.

As note in Chapter 2, Maynard Smith was a publicly visible scientist who established himself as a public intellectual from the beginning of his career. In 1964/65, he spoke on the science-religion relationship (see below), and his interests in the topic and expertise as an evolutionary biologist were known enough for the Jehovah's Witnesses to repeatedly try to engage with him. The archive holds material sent to Maynard Smith by Witnesses or those with an interest in their ideas, mostly dating to 1967.[16] The material in the folder "Creation" exemplifies the arguments of creationists against the theory of evolution. It includes two issues of the Jehovah's Witnesses' magazine *"Awake!"*, which serves as a news source for Witnesses, 'unfettered by censorship and selfish interest', without political ties or religious fundamentalism but with 'integrity to truth'. It is 'wholesome' and 'instructive', for the whole family, and 'pledges itself to […] to exposing hidden foes and subtle dangers'.[17] At least one of the two issues in the archive was sent directly to Maynard Smith by Witnesses, along with a standard letter sent out by the Brighton North Congregation, typed:

> We have the pleasure of enclosing herewith a copy of "Awake" magazine dealing with the subject of Evolution.
>
> We would appreciate your comments on this, but especially on the article entitled "Is Evolution in Question", to be found on page five.

[14] Maynard Smith and Wright 2001.
[15] Maynard Smith and Erickson 2004. JMSA (uncatalogued).
[16] JMSA Add MS 86614.
[17] Watch Tower Bible & Tract Society of Pennsylvania 1967a, 2.

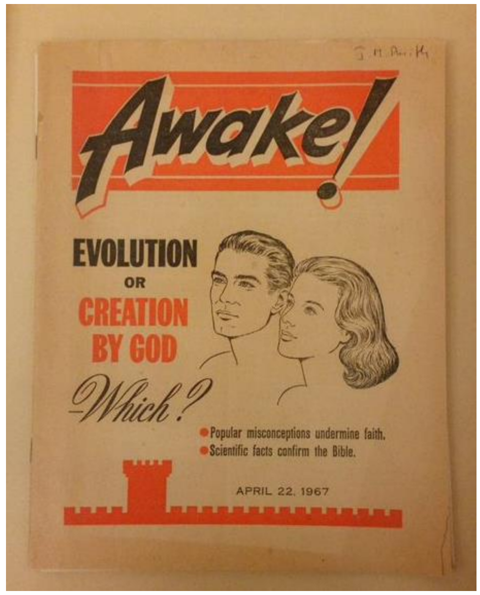

Figure 22. Awake! *magazine, 22 April 1967. (JMSA Add MS 86614)*

(Someone added, in pen: 'P.S. You are a scoundrel.'[18] The handwriting indicates it was not the person who signed the letter.) This specific issue wondered 'Evolution or Creation by God – Which?' and stated on the cover that 'Scientific facts confirm the Bible', making its position clear from the start. The first pages confirm the tenor against evolution, explaining that evolution leads to demoralisation and crime, thus paving the way 'for much agnosticism and atheism'. Because evolution cannot be harmonised with faith or God, it leads to abandonment of God, and teaching evolution to children means they will 'participate in the demoralization rampant today'.[19] In the following, the Bible is presented as 'reasonable' on the topic of the origin of life (in part because it is 'logical and orderly' and because it is 'in harmony with the facts as we find them today': 'Can a dog produce a kitten or an oak seed a palm tree? Of course not.').[20] Evolution, on the other hand, cannot explain life, and scientists cannot make life either. History has no proof for humankind's prolonged existence on earth; scientific dating methods are unreliable and contradictive. Past explanations for evolution, like Lamarck's, were proven wrong – so why believe in Darwin's? Life and organisms are too complex to have arisen through natural selection, and

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[18] Sullivan to "Dear Sir or Madam", undated. JMSA Add MS 86614.
[19] Watch Tower Bible & Tract Society of Pennsylvania 1967a, 3-5.
[20] Watch Tower Bible & Tract Society of Pennsylvania 1967a, 7.

mutations are only ever harmful. In general, the orderliness of creation is opposed to the perceived randomness of evolution by natural selection.

These arguments are very similar to the ones given in another Jehovah's Witnesses' publication from 1967. Mrs Daphne Taylor from Sheffield wrote on 9 October 1967 that '[q]uite a few people in our locality including teachers interested in evolution, have found it (the book) most enlightening.'[21] The book's title was *Did Man Get Here by Evolution or by Creation?* Again, the authors affirm that evolutionary teaching saturates everything, even religion, and then ask what their readers

> personally know of the evidence for or against the belief in evolution? Does it really harmonize with the facts of science? We invite your careful examination of this matter, as it has a direct bearing on your life and your future.

The running argument is one that has famously been used by William Paley in his 1802 book *Natural Theology: or, Evidences of the Existence and Attributes of the Deity.* Nature is too complex for there not to have been an intelligent designer or creator. Paley used the analogy of a watchmaker: suppose you were to find a watch on the heath, and upon examining it and its complexity, would you not suppose there has to have been a watchmaker? Similarly, the Jehovah's Witnesses argue that 'what is made requires a maker'.[22] Liking DNA to 'complex blueprints for future development' (as they also did in the *"Awake!"* issue), they wonder: 'And when we see blueprints responsible for the building of beautiful bridges, buildings and machines, do we ever contend they came into being without an intelligent designer?'[23] What is more, there is not enough evidence for evolution (while all the existing evidence is compatible with the Bible), it is all just a theory based on conjecture and wishful thinking, unsupported by fact, and, really, not proper science at all.

Unfortunately, all of this material is uncommented in the archive. We do not know, for instance, if Maynard Smith read the book or shared his views with Mrs Taylor. Or if he got in touch with the Brighton North Congregation. But his keeping the publications (and signing his name on them) is a strong indicator for his interest in these issues and intent to not just dismiss them. The following will look at three instances in which Maynard Smith

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[21] Taylor to Maynard Smith, 9 October 1967. JMSA Add MS 86839C.
[22] Watch Tower Bible & Tract Society of Pennsylvania 1967a, 36.
[23] Watch Tower Bible & Tract Society of Pennsylvania 1967a, 72.

directly engaged with the relationship between science and religion, including but not limited to creationism. A result of these discussions will be Maynard Smith's views on what constitutes science, scientific theory, scientific knowledge and scientific methodology.

6.1.2 Active conversations: God broadcasts and creationist debates

Chapter 2 discussed Maynard Smith's broadcasting activities in detail, and it is time to return to the category only briefly touched upon then: defending science. Under "God Broadcasts", Maynard Smith filed the transcripts for a series of talks that aired on the Home Service's school programme in January 1965. The actual title of the broadcasts was 'Christianity and the Natural Sciences', part of the Sixth Form series *The Christian Religion and its Philosophy*. The nine episodes were guided by the question "Is there a meeting point?," introduced by Stephen Toulmin. This episode was followed by four episodes with John Maynard Smith and four episodes with the Reverend John Habgood (three consisted of talks, followed by one in which Robert C. Walton, the producer, put questions to them).[24]

date	title	speaker
19-Jan-65	One universe: diverse interpretations	Stephen Toulmin
26-Jan-65	Scientific knowledge and the way to find it	John Maynard Smith
2-Feb-65	The scientific interpretation of the evidence	John Maynard Smith
9-Feb-65	Man and nature	John Maynard Smith
16-Feb-65	Christian knowledge and the way to find it	John Habgood
23-Feb-65	The Christian interpretation of the evidence	John Habgood
2-Mar-65	Nature, man and God	John Habgood
9-Mar-65	Is there a meeting point?	John Habgood, Robert Walton
16-Mar-65	Is there a meeting point?	John Maynard Smith, Robert Walton

Figure 23. 'Christianity and the Natural Sciences' episode overview.

School radio is as old as the BBC. In the early stages, between the 1920s and 1930s, radio for schools was met with positive anticipation by some and scepticism by others. As

[24] Cf. JMSA Add MS 86614 for transcripts of Maynard Smith's talks and BBC WAC TL0 60865 for "The scientist in conversation" transcript.

David Crook has noted in an exploratory study of school radio in the UK, assurances were needed that

> the broadcasts were to supplement, not supplant, teachers, that they should make demands of children, rather than merely "tickling their interest", and that they could contribute to "a curriculum which had a closer connexion with life".[25]

Pupils needed to be engaged and challenged, so they could be turned into thinkers and actors.[26] Maynard Smith entered the field during something of a 'second "golden age"', with a rise from around 3,000 schools listening in at the beginning to a vast majority of schools using radio (an estimated 90% of UK schools) and television broadcasts (80%) aimed at and produced for their pupils.[27] (About ten years previously, 67% of UK schools had been using school broadcasting.[28])

'Christianity and the Natural Sciences' was produced by Robert Walton, head of the BBC's School Broadcasting Department. Walton had previously published on religious broadcasting in the *Expository Times*, a journal of biblical studies, theology and ministry.[29] Religious education was 'given its proper place' and at the time of writing, 1954, there were 'two specifically religious series—a Service for Schools, and a Sixth Form series—*Religion and Philosophy*'. This was an 'intellectual presentation of the Christian religion', aimed at pupils about to leave school and who may be firm in their faith, indifferent, or sceptical. The show brought 'to the microphone distinguished scientists, historians, theologians, and Christian men of action to share their knowledge and experience'.[30] It was broadcast on Tuesdays on the Home Service, 11.40am to 12.00pm. 'Christianity and the Natural Sciences' occupied the same spot in January and February 1965 and followed the same structure. It too was aimed as sixth formers and brought two distinguished scholars together. Maynard Smith was about to start his deanship at Sussex, speaking for the natural sciences. John Stapylton Habgood (1927-2019), who would become archbishop of York, had published a volume in the "Science and Society" series, edited by Eton College's Head of the Science

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25 Crook 2007, 219.
26 Crook 2007, 219.
27 Crook 2007, 223f.
28 Walton 1954, 271.
29 http://journals.sagepub.com/home/ext.
30 Walton 1954, 271.

Department, *Religion and Science* (1964). He was a trained biologist and a sometime research fellow at King's College, Cambridge.[31]

Habgood believed that there is some conflict between science and religion, that we have to live with this, that 'there are no final answers to many of the traditional problems of science and religion, and that we oversimplify our actual experience of life if we ignore one or the other of them, or imagine that the conflict between them is of the kind in which one side or the other must win.'[32] He defined science as asking questions that can be answered, as providing information, and with a strong foundation in mathematics. Religion, on the other hand, can ask questions that may only result in vague but possibly more relevant answers. Maynard Smith, on the other hand, did not think 'there are any problems which are in principle outside the scope of science, problems which scientists cannot study'.[33] In the case of evolution, Habgood reasoned that, to its profit, theology has learnt from science and that admitting this

> is simply to recognise that one of the important ways in which God leads us to the truth is through science; and although theologians claim to be able to say some true and valuable things about God and man, they cannot and should not claim to be able to say everything. There are times when they must discover the meaning of their own doctrines with scientific help.[34]

Science can cause theologians anxiety, but that is not the same as defeat; both science and religion have to realise they are not blueprints for reality. Science can make theologians rethink their ideas, 'and it is no dishonour or disaster when in the light of science old doctrines are understood in new ways.'[35] When this rethinking does not happen, Maynard Smith noted, conflict happens between science and religion. Both science and religion understand themselves as ways of explaining the universe,[36] and any conflicts arise when there are two contradicting explanations for the same phenomenon.[37] Evolutionary theory for him was one such case of contradiction and conflict.

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31 Matthews 1964, vii.
32 Habgood 1964, 10.
33 Maynard Smith 1964, Talk II, p.1. JMSA Add MS 86606.
34 Habgood 1964, 70.
35 Habgood 1964, 71.
36 Maynard Smith, Talk I, 29 December 1964. JMSA Add MS 86614.
37 Maynard Smith, Talk II, 29 December 1964. JMSA Add MS 86614.

This idea of inherent conflict between science and religion, known as the conflict thesis, is widely discredited in scholarly circles. Those studying the relationship between science and religion have pointed out, like John Hedley Brooke, that the

> fundamental weakness of the conflict thesis is its tendency to portray science and religion as hypostatized forces, as entities in themselves. They should rather be seen as complex social activities involving different expressions of human concern, the same individuals often participating in both.[38]

This idea of complexity often gets lost in Maynard Smith's dealings with religion, part of which is due to the fact that most of these were with extremist religious views and in the form of debates. Maynard Smith was less contrarian in the "God broadcasts", allowing that religion may have poetic value. What he focused on was drawing a distinction between science and religion as two attempts to explain the universe with the main difference being their methodology. Earlier in 1964, the year in which the broadcasts were recorded, he brought up Karl Popper's philosophy of science in a book review on the origin of scientific ideas. Popper, he wrote,

> is a philosopher rather than a psychologist, so that he is not primarily concerned with where ideas come from, except to show that theories cannot be deduced logically from observations; his main thesis is that an idea only belongs to science if it could be falsified by observation.[39]

Maynard Smith did not mention Popper in his God broadcasts, but the concept of falsification guided his explanations of how science works. In science, one starts with a problem or puzzle that needs addressing. A hypothesis is formulated that is tested through experiment, observation, and fact-gathering. This turns into a scientific theory making sense of all the results and which is informative (i.e. tells us something about the problem it addresses) and able to predict things. 'If a scientific theory predicts that X won't happen, then if somebody does and experiment and show [*sic*] that X does happen, then you can reject the scientific theory, you can test it.'[40] This testing is the crucial difference to faith and religion.

[38] Brooke 2014, 56.
[39] Maynard Smith 1964b, 881.
[40] Maynard Smith, Talk I, 29 December 1964. JMSA Add MS 86614.

Postulating the Popperian influence on Maynard Smith is further possible by remembering Peter Medawar's influence on him. Not only is the example for the scientific process described – problem, hypothesis, experiment, theory – Medawar's work on skin grafting in cattle and in mice. Medawar had taught Maynard Smith 'the importance of clarity and rigour' and that ultimately,

> scientific issues […] have to be settled by observation or experiment. If there is no observation or experiment that can settle a scientific question, it's not a scientific question. I mean, leave it to the philosophers and let them waste time on it. Ultimately, there has to be a scientific... there has to be an experimental or observational way of doing it.[41]

Medawar was a strong proponent and populariser of Popper's ideas,[42] and may have discussed them with Maynard Smith. They were both still at UCL when Popper's *Logic of Scientific Discovery* was translated into English in 1959,[43] and Maynard Smith accepted its views on what a scientific theory is.[44] Maynard Smith was also occasionally in touch with Popper who had sent him an offprint of his 1963 paper 'Science: problems, aims, responsibilities'.[45] But he never whole-heartedly accepted all of Popper's philosophy, as is evident in his review of Popper's *The Open Universe*: on a first reading of *Logic*, he disagreed with Popper's 'propensity theory of probability', though upon rereading it two decades later, he 'found [him]self accepting it like an old friend'.[46] He disagreed with views presented in *The Open Universe* too, partly because he was a biologist and because he felt that 'Popper is sometimes too ready to treat as insoluble problems I would like to see solved', examples being consciousness and the origin of life.[47] Another source of disagreement between them were Popper's views on evolution. The archive contains a manuscript written and sent by the molecular biologist and 1962 Nobel Laureate Max Perutz. Perutz was reacting to Popper giving the first Medawar Lecture at the Royal Society on 12 June 1986 with a piece

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41 Maynard Smith and Dawkins 1997, https://www.webofstories.com/play/john.maynard.smith/22.
42 Calver 2013.
43 Medawar left in 1962 (Mitchison 1990, 283).
44 Maynard Smith 1965a, 51.
45 Popper, K.R. (1963). Science: problems, aims, responsibilities. *Federation Proceedings 22*(4), 961-972. JMSA Add MS 86840/79.
46 Maynard Smith 1983b, 247.
47 Maynard Smith 1983b, 249. Popper enjoyed 'this very charming piece': 'Your Review-Chapter "27 Popper's World" is the most pleasant piece about myself I have ever read (according to my miserable memory: I am in my 92nd year). Thank you very, very much.' Popper to Maynard Smith, 7 December 1993. JMSA Add MS 86604.

entitled 'Popper's new interpretation of Darwinism'. He wrote to Maynard Smith, 'I am so glad that you liked my article – I thought I could not let Popper get away with all that nonsense.'[48] ('All that nonsense' was Popper's suggestion to split Darwinism into an active and a passive form. The 'main sources of nature's creativity are not Darwin's blind chance and natural selection but the problem-solving of all organisms and, in a later evolutionary stage, the curiosity, preferences, and anxieties of individuals.[49])

It is unclear how deeply Maynard Smith engaged with Popper's philosophy, and he was generally wary of letting philosophy influence science. But he had 'great respect' for him and considered him as 'a genuine contributor to our understanding of what we're doing.'[50] What he took from Popper's work were his justifications for accepting a scientific theory and for considering a theory as scientific in the first place.

> What we can demand of a theory is that it should be possible to deduce from it by logic certain consequences which we can test. In particular, a theory should exclude certain classes of events […]. A theory which excludes certain events can be falsified, if it is accepted that event which it excludes in fact happen. The wider the range of events which a theory excludes, the more opportunities there are to falsify it, and the more informative the theory is.[51]

These views were published in a 1965 book based on a conference where experts in biochemistry, biology, neurophysiology and psychology met with officers of the Modern Churchman's Union and discussed views of science and religion.[52] Maynard Smith explained Popper's concept of falsifiability in more detail than in his allusions to it in the God broadcasts. He again used Popper – without explicit mention of or reference to him – in an essay on the 'status of neo-Darwinism', in which he defined evolution as having the following properties: multiplication, heredity, and variation.[53] The way to refute neo-Darwinism, to falsify it along Popperian lines, would be to demonstrate either that its assumptions made in relation to and because of the properties mentioned 'are not in fact

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48 Max Perutz to John Maynard Smith, 29 July 1986. JMSA Add MS 86840/78.
49 Niemann 2014, 2. Popper's views on evolutionary biology changed throughout his life, cf. Stamos 1996.
50 Maynard Smith and Dawkins 1997, https://www.webofstories.com/play/john.maynard.smith/99.
51 Maynard Smith 1965a, 51.
52 Whitehouse 1967, 351.
53 Maynard Smith 1969b, 83.

true of all organisms' or that 'patterns of evolution may occur which are inexplicable on the neo-Darwinist assumptions' (Lamarckian patterns being an example).[54]

Maynard Smith felt it was important that people understood how science works and how it differs from religion and he used Popperian philosophy of science to highlight the differences. He was not dogmatically refusing religion as having no value at all but pointed out that science was the better way of explaining the world. This diplomatic view becomes less so when Maynard Smith moved from general discussions of science and religion to direct challenges to the scientific worldview – and his field of evolutionary science – by creationists. In the introduction to the 1972 collection containing the essay on the status of neo-Darwinism he explained the book's purpose as a means of 'taking stock' of evolutionary biology.[55] Like physicists at the end of the nineteenth century, population geneticists now thought that 'the fundamentals are known, and all that remains is to work out the details.' The question arising is whether this is actually right, considering that 'there appears to be a widespread conviction that there is something rotten in the state of evolutionary theory' – although he added 'that this conviction, although widespread, is confined to those who do not work in the field of population genetics.'[56] Maynard Smith differentiated between specialists and non-specialists' views on the theory of evolution and detected a reluctance on the part of the latter to accept natural selection as the process bringing about humans. (That reluctance is very apparent in the criticisms voiced in creationist publications like those of the Jehovah's Witnesses discussed above.) 'Certainly the odd enthusiasm for Teilhard de Chardin points to this explanation.'[57]

Teilhard de Chardin was a French Jesuit theologian and palaeontologist who mixed science and religion in a 1955 publication (translated into English in 1959).[58] *The Phenomenon of Man* had a favourable introduction by Julian Huxley who wrote:

> Père Teilhard de Chardin […] has effected a threefold synthesis—of the material and physical world with the wold of mind and spirit; of the past with the future; and of variety with unity, the many with the one.[59]

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[54] Maynard Smith 1969b, 86.
[55] Maynard Smith 1972, 1.
[56] Maynard Smith 1972, 1.
[57] Maynard Smith 1972, 1.
[58] Ruse 2009, 35.
[59] Huxley 1958b, 11.

Medawar, on the other hand, gave it a scathing review ('the greater part of it […] is nonsense […] and its author can be excused of dishonesty only on the grounds that before deceiving others he has taken great pains to deceive himself'),[60] and Maynard Smith was not fond of it either. He discussed Teilhard on BBC One in 1966,[61] in 1972 still noted an 'odd enthusiasm' for him,[62] and in 1981 commented in a review of Gould's *The Panda's Thumb* that he 'learnt a lot about the Piltdown forgery, and was delighted to find that [his] long-felt suspicion that Teilhard de Chardin had something to do with it is not entirely without support.'[63] Maynard Smith worried that work like de Chardin's was a sign of people turning to evolutionary biology looking for guidance to morality and ethics. In a *New Scientist* article on C.H. Waddington, he wrote about the dilemma between the scientific worldview that was increasingly the basis for 'the way we make our living' and the fact that (in the West at least) our moral and belief system is based on Christianity. 'Many of our present problems stem from the irreconcilable differences between these two methods of thought,' he continued, and there were two ways of dealing with the dilemma. One can, as Jacques Monod had in his *Chance and Necessity*, accept the dualism: 'The scientific world picture carries no moral message, and ascribes no role or purpose to man. Man needs beliefs and values, but cannot derive them from science.' Or one can follow Waddington's approach as outlined in *The Ethical Animal* and 'attempt to rebuild a single coherent picture of the world, which includes science, ethics and aesthetics.'[64] Maynard Smith was inclined to agree with Monod. As Ullica Segerstråle has noted, Maynard Smith (and Richard Dawkins, Bernard Davis as well as E.O. Wilson 'in his objectivist mode') strongly favoured a fact-value distinction. She refers to them as the "objectivist school", regarding 'evolutionary biology as a regular descriptive and explanatory science, just like other sciences. Members of this group point out we need to keep science separate from ideology, usually warning about the Lysenko case.'[65]

Against this backdrop of scientists like de Chardin or Waddington looking for holistic explanations and science-religion syntheses, Maynard Smith started debating creationists. In

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60 Medawar 1961, 99.
61 Viewpoint, "Teilhard Discussed". *Radio Times 2207* (24 February 1966), 42.
62 Maynard Smith 1972, 1.
63 Maynard Smith 1981b, 94.
64 Maynard Smith 1976c, 120.
65 Segerstråle 2000, 376.

the 1970s and 1980s, the evolution-creation issue was continually discussed in debates which started in the US and then found their way abroad.[66] Duane Gish, one of the most publicly known creationists, debated the palaeontologist E.G. Halstead at Reading, the zoologist Professor J. Alexander at Leeds, and John Maynard Smith at Sussex in 1979.[67] These debates were funded in a variety of ways, through ticket sales or with the help of organisations like the Campus Crusade for Christ,[68] which also organised the Sussex debate.[69] Gish was a trained biochemist who resigned from a pharmacological company in 1971 to devote all his time on 'the study of the scientific evidence related to the question of creation versus evolution theory'. He was associate director of the Institute for Creation Research in San Diego and published and talked widely on 'scientific evidence against evolution and on other Bible-science subjects.'[70] In the late 1970s, he was on a lecture tour through Britain, with scheduled appearances at ten universities, amongst which those mentioned above. As Stephen Sizer of the University of Sussex's Campus Crusade for Christ branch wrote to Maynard Smith, Gish was to give four lectures at Sussex on: Creation, Evolution and the Laws of Science; Creation, Evolution and the Origin of Life; Creation, Evolution and the Fossil Record; and Creation, Evolution and the Origin of Man. Sizer informed Maynard Smith that Gish 'has participated in over 50 debates in the United States, and would like the opportunity of meeting you. The title he has suggested is, "The Theory of Evolution is Superior to the Theory of Special Creation as an explanation for the Scientific Evidence related to Origins."'[71] Maynard Smith agreed, and a date was set for 14 February.

[66] Numbers 2006, chapter 16.
[67] Lubenow 1983, chapter 33. Although the initials do not match, Lubenow may be referring to Beverly Halstead (Sarjeant 2008) and Robert McNeill Alexander (Biewener and Wilson 2016).
[68] Lubenow 1983, esp. chapter 1.
[69] Sizer to Maynard Smith, 15 January [1979]. JMSA Add MS 86614.
[70] Resume. JMSA Add MS 86614. See Numbers 2006, 247ff for Gish's entry into organized creationism.
[71] Sizer to Maynard Smith, 15 January [1979]. JMSA Add MS 86614.

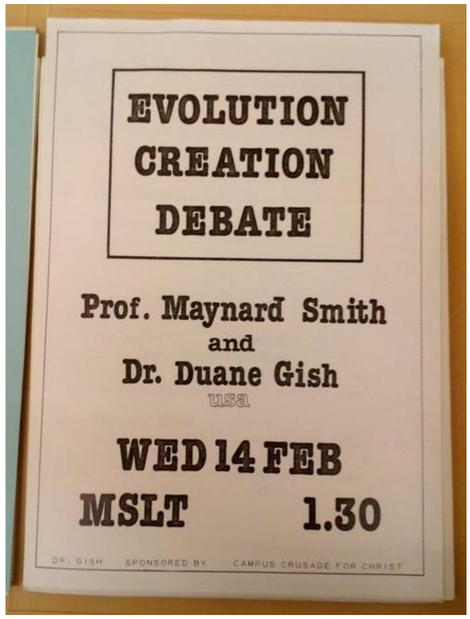

Figure 24. Poster for the debate between Duane Gish and John Maynard Smith. (JMSA Add MS 86614)

No recording or transcript of the debate exists in Maynard Smith's archive, but we know that he used a publication of Gish's to prepare himself. In "CREATION, EVOLUTION, AND PUBLIC EDUCATION" Gish argued that

> modern formulations of evolutionary mechanisms are vacuous and are contradictory to well-established natural laws, and, in contrast to commonly accepted views, the fossil record actually contradicts the predictions based on evolution theory. On the other hand, the major features of the fossil record conform admirably to predictions based on a creation model. When all of the scientific evidence is considered, creation provides a model for explaining origins that is superior to the evolution model.[72]

The gaps in the fossil record were contradictory to the story of gradual evolution and change from one species in another. What the fossil record did show, according to Gish, is the distinct nature of each species, set out in the Bible. Evolution had never been witnessed, could not be subjected to experimental methods, and was therefore not a proper scientific theory. Gish concluded that belief in evolution was as intrinsically religious as belief in creation, that creation was a better explanation for nature and that it should therefore be taught in schools. Out of this preparatory reading, Maynard Smith drew three main

[72] Gish, "CREATION, EVOLUTION, AND PUBLIC EDUCATION". JMSA Add MS 86614.

arguments for him to deal with during the debate: the fossil record, the scientific nature of evolution, and that of creation.[73]

Maynard Smith's notes are prompts that allow an approximation of his argument. Regarding the fossil record he made two points. On the issue of finding intermediate forms, something to show one species changing into another, he pointed to Darwin's difficulties when writing the *Origin of Species*. Only few fossils had been discovered, and Darwin developed his theory without having seen any intermediate forms. Even though many more fossils have been found since then, there were still gaps in the record. As Maynard Smith pointed out, this is only to be expected. For something to be fossilised, conserved and found, many conditions need to be met. But a lot can still be inferred from the existing fossil record, such as that we see a move from simpler to more complex organisms. Maynard Smith also considered referring to Gould in this instance. 'S.J. Gould – has recently emphasized this point at the <u>species</u> level,' the notes read, but the point was crossed out.[74] 'This point' referred to the lack of intermediaries; a rough drawing of an evolutionary tree accompanies the note. Perhaps considering the use creationists made of Gould and punctuated equilibria (see below) stopped Maynard Smith from using Gould. Instead he may have used an argument from his *Theory of Evolution*, of which the 1975 (third) edition (the passage is unchanged from the first edition) reads:

> Now if it is true that decisive evolutionary advances would be expected to take place by rapid evolution in single species (or at most groups of related species) confined to a particular part of the world, it follows that the number of individuals representing any particular structural stage is very small when compared to the number of individuals at a given stage in a larger group of animals evolving more slowly. Consequently, transitional forms are less likely to be found as fossils. It is, in fact, the case that major groups often appear suddenly in the fossil record, and although it is usually possible to identify the group from which they have originated, intermediates are rare; sometimes, as in the case of *Archaeopteryx*, one is lucky. Strictly, the rareness of such intermediates is a confirmation of the view that the origin of major groups occurs rapidly in a limited population, rather than a deduction from it.[75]

To Gish's argument that evolutionary theory is not scientific because it cannot be tested, Maynard Smith replied that science did not claim to provide certainty. His notes

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[73] Maynard Smith, "Deal with 3 Things". JMSA Add MS 86614.
[74] Maynard Smith, "Deal with 3 Things". JMSA Add MS 86614.
[75] Maynard Smith 1993a, 307; compare Maynard Smith 1958, 260.

read, 'roughly, Popper. "FALSIFIABLE" / in this sense, Evolution Theory manifestly falsifiable.'[76] He then used the same argumentation to demonstrate that creation is not scientific:

> BUT – cannot be refuted – GOSSE "one enormous and unnecessary lie...
> What force is "cannot be refuted"?? 9AM??
> The Essential Difference[77]

This references Philip Gosse's book *Omphalos: An Attempt to Untie the Geological Knot* (1857). Gosse attempted to explain why geological and other signs imply the Earth's history is longer than the 6,000 years suggested by the Bible. Gosse rejected the idea of Earth's antiquity but needed to explain why it appeared old. He proposed two "'laws" – all organic nature moves in a perpetual circle, and creation is interruption into the circle – and conclude[d] syllogistically that every created organism must possess all those physical attributes characterizing the position in the circle at which its creation occurred'.[78] The book was a failure, and more cynical interpretations summarised it as God having created "one enormous and unnecessary lie". The repetition of quotation marks in Maynard Smith's notes hints at incredulity at some of the creationist arguments and stories, such as Bishop Ussher's attempt to calculate the exact day and time of creation.[79]

There are two published summaries of the Sussex debate, by Marvin Lubenow and the University of Sussex. Lubenow is a Baptist pastor and member of the Creation Research Society. He helped organise and was present at many of Gish and Morris' debates and wrote a book on them, "*From Fish to Gish"* (1983). (He has also written a book on the fossil record, *Bones of Contention: The Bible and the Human Fossils*, to demonstrate that the fossil record proves Special Creation.)[80] Lubenow's summary brings in Maynard Smith's Penguin on *The Theory of Evolution*.

> Gish held aloft a copy of Maynard Smith's book, *The Theory of Evolution*, with a picture of an evolutionary tree on the cover. He emphasized that this evolutionary tree, to be a legitimate scientific theory, must be a continuum from the roots to the

[76] Maynard Smith, "Deal with 3 Things". JMSA Add MS 86614.
[77] Maynard Smith, "Deal with 3 Things". JMSA Add MS 86614.
[78] Ross 1977, 93. See also Roizen 1982.
[79] He concluded it was created in 4004 BC, based on Biblical genealogies. See Theodossiou 2004 on Christian chronologies. Both Ussher and Gosse's attempts have made it into Terry Pratchett and Neil Gaiman's opening of their novel *Good Omens* (1990).
[80] Lubenow 1983, iii-iv.

> ends of the branches without a single gap anywhere. Gish then went on to demonstrate that the only part of the tree that does exist is the tips of the branches—the tiny twigs that represent present-day life.
>
> Gish first declared that a tree must have a seed. He likened this seed to the first single-celled organism in the evolution of life. He then demonstrated that a naturalistic origin of life was simply out of the question based on known principles of kinetics and thermodynamics.[81]

Lubenow then complained that Maynard Smith used humour and sarcasm rather than facts when dealing with Gish and his arguments.[82] Gish refused Maynard Smith's Popperian explanations of what it means for a theory to be scientific.

> Gish […] claimed that neither evolution nor creation were refutable scientific theories—although both have elements of scientific data in them. Smith then protested saying that he had given certain criteria whereby evolution could be falsified. If the deeper rocks (allegedly older rocks) had more species in them belonging to existing genera than the more recent rocks have, Smith stated, evolution would be falsified.
>
> Smith: "Would you not accept that as a falsification of evolution?"
>
> Gish: "No, and I don't believe you will either, because on that basis I can falsify your theory."[83]

On the other hand stands the Sussex University *Bulletin's* note, which sided with Maynard Smith. It pointed out that Gish used stock lecture notes for his statement and failed to answer Maynard Smith's question on what kind of creationist beliefs he had. The contrast of memories and comments is remarkable. In *The Neck of the Giraffe: Where Darwin Went Wrong* (1982), Francis Hitching argued that the event 'wasn't so much a debate as a statement of two irreconcilable points of view.' He described Maynard Smith as 'doughty' and 'theatrical', while Gish 'made a confident, knowledgeable speech about the fossil record'.

> No vote was taken, though undoubtedly the great majority were on Maynard Smith's side. But in England, students by and large are no longer Christians, except in name. 'A tragedy,' Duane Gish said sadly to me afterwards.[84]

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[81] Lubenow 1983, 211f.
[82] Lubenow 1983, 213.
[83] Lubenow 1983, 213f. Throughout the brief account of the debate, Lubenow refers to Maynard Smith as Maynard Smith, Smith and Dr. Smith (he did not have a PhD).
[84] Hitching 1982, 125f. While Lubenow had given Maynard Smith the title Dr, Hitching equally wrongly indexed him as "Smith, Sir John Maynard" (p.287).

In comments on an internet forum discussing a 2014 debate between Ken Ham and Bill Nye (and whether or not Nye should debate Ham in the first place, if all the debate will do is fund the Creation Museum with the $25 entrance fee, and if Nye will be able to withstand the "Gish Gallop"), howiekornstein wrote:

> It doesn't take expertise in Biology to argue against the idiocy of creationism, only good debating skills. The specific talent needed is an ability to deal a fatal blow to a high-steam gish gallop. The most skilled debater in doing a hatchet job on a creationist gish gallop (IMHO) was John Maynard Smith.[85]

He was echoed in another post by colnago80 who wrote that 'it is possible to debate creationists if one is well prepared. […] John Maynard Smith successfully debated Duane Gish. The bottom line is preparation to combat the Gish gallop.'[86] Colnago80 also pointed out, in a post after the debate, that the 'late John Maynard Smith […] pummelled' Gish.[87] (On a different forum, colnago80 has described Maynard Smith as dismembering Gish: 'Gish was considered a great debater until he made the mistake of debating John Maynard Smith'.[88])

Maynard Smith is on record for one more debate. In 1986, Oxford University's debate club, Oxford Union, invited speakers for a Huxley Memorial Debate to debate the motion "That the doctrine of creation is more valid than the theory of evolution".[89] The main speakers for the motion were Professor Arthur Wilder-Smith (chemist) and Edgar Andrews (physicist); against spoke Richard Dawkins and Maynard Smith. On both sides of the house there were further shorter speeches by members of the union. The archive contains no record of any preparation on Maynard Smith's side, although Dawkins sent him a letter quoting from Andrews' book *From Nothing to Nature*, adding 'What is the total number of

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[85] howiekornstein, 3 January 2014, https://whyevolutionistrue.wordpress.com/2014/01/03/this-may-not-end-well/#comment-672796. The "Gish gallop" is now the more or less official name for a debating technique: it is a way of arguing one's cause 'by hurling as many different half-truths and no-truths into a very short space of time so that their opponent cannot hope to combat each point in real time.' (Holder 2012).
[86] colnago80, 3 January 2014, https://whyevolutionistrue.wordpress.com/2014/01/03/this-may-not-end-well/#comment-672649.
[87] colnago80, 5 February 2014, https://whyevolutionistrue.wordpress.com/2014/02/05/who-won-the-big-evolutioncreation-debate/#comment-716147.
[88] colnago80, 2 November 2014, http://americanloons.blogspot.com/2011/02/149-duane-gish.html?showComment=1414968706730#c6629932962759198274.
[89] Wilson to Maynard Smith, 29 July 1985. JMSA Add MS 86614.

errors in this short passage?'[90] (That was Dawkins' strategy for the debate: taking apart Edwards' book, for which he was criticised by Wilder-Smith.) Maynard Smith took brief notes during the debate, however, starting with writing down 'The most bogus ideas'.[91]

The debate was recorded and is currently available on YouTube,[92] yet given the sound quality, the vote is unclear. The most quoted number of ayes are 115 or 150, opposing 198 noes. Popper made no appearance in this debate, but Maynard Smith repeated his point made in the God broadcasts: one very important difference between science and religion lies in their explanatory power. In 1965 he had explained that both are attempts to understand the world. In 1986 he charged creation scientists with not contributing anything to this understanding. Reflecting on his own scientific career, Maynard Smith concluded that in the previous decades evolutionary biologists had come closer to solving problems like the evolution of ageing, of sex, or of conventional behaviour. They had done so by working within a scientific framework. Creationists, on the other hand, had mainly gone through scientific literature looking for contradictions.

> I believe that what this evening you have to decide, in deciding between the validity of the doctrine of creation or the theory of evolution is, which of these methods of approach have added most to our understanding of the natural world during recent years. If you believe that, as I do, that evolutionary biologists – even if they've not solved all their problems – have really added to our knowledge and to our understanding of the world, whereas creation scientists have added virtually nothing to our understanding of the world, then you will oppose the motion.[93]

Let me summarise by citing Maynard Smith's three objections against the religious worldview. 'They are of three kinds, to factual claims, to methods, and to concepts of intervention.'[94] The first related to claims such as resurrection, the third to the idea of 'interventionist God fiddling with the machine'.[95] The second one reiterates the above arguments Maynard Smith brought against creationists in particular and religion more in

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[90] Dawkins to Maynard Smith, 10 February 1986. JMSA Add MS 86614.
[91] Maynard Smith, notes on the back of "Giving some account...". JMSA Add MS 86614.
[92] 'Huxley Memorial Debate' (1986).
[93] 'Huxley Memorial Debate' (1986), Prof John Maynard Smith. https://www.youtube.com/watch?v=Nmk3m04vDtA.
[94] Maynard Smith 1965, 61.
[95] Maynard Smith 1965, 62f.

general: the theological method of gaining (absolute) truth and certainty without readiness to adapt or discard theories contradicts his conviction that the scientific method is the better and more powerful way of gaining knowledge of the world. Religion is likened to poetry – it can only give us knowledge in a poetical sense.

6.2 Internal challenges: Stephen Jay Gould

6.2.1 Punctuated equilibria – revolutionising evolution?

As has been noted above, one argument that creationists liked to make is that evolutionists cannot agree among themselves and that their theory is therefore just a theory and not science.[96] They also highlighted any disagreements to undermine the authority of experts. One of their favourite examples was palaeontologist and evolutionist Stephen Jay Gould and his theory of punctuated equilibria.[97] Francis Hitching for example described Gould and his colleague Niles Eldredge as 'neo-catastrophists' whose views cast doubt on the gradualist neo-Darwinian orthodoxy.[98] Similarly, Lubenow wrote:

> The newer 'punctuated equilibrium' model which does not require transitional forms and which deemphasizes the role of natural selection is a tacit admission that the fossil record has failed evolution and that natural selection is not an adequate mechanism.[99]

In an earlier part of the book, he referred to the fossil record as the 'crack in the evolutionary wall', saying that '[i]t was only a matter of time before something had to give. Something has given—evolutionary theory. Instead of having a theory that required transitional forms, they now have a theory that does not need them.'[100] As Myrna Perez Sheldon has argued, the revisions to neo-Darwinism suggested by Gould and colleagues 'closely resembled creationist criticism that paleontological data could not definitely prove evolution.'[101] In light of this, Robert Wright has dubbed Gould an 'accidental creationist': 'if

[96] See for instance the section 'Modern theory' in Chapter 2 of *Did Man Get Here by Evolution or by Creation?* (1967).
[97] Numbers 2006, 369.
[98] Hitching 1982, 165.
[99] Lubenow 1983, 218.
[100] Lubenow 1983, 55.
[101] Sheldon 2014, 139.

you really pay attention to what he is saying, and accept it, you might start to wonder how evolution could have created anything as intricate as a human being.'[102]

Chapter 1 demonstrated that Maynard Smith's view of evolution was strongly neo-Darwinian and that for him, adaptation was the one problem evolutionary biology needed to explain. The same goes for Richard Dawkins.[103] Maynard Smith was convinced, as he wrote in a letter to Richard Lewontin, 'that people in love with nature usually become adaptationists.'[104] Gould, an American, considered adaptation to be a 'British hang-up'.[105] Together with Eldredge, he developed the theory of punctuated equilibria to explain evolution.[106] These are internal challenges to Maynard Smith's neo-Darwinian and adaptationist understanding of evolution which inadvertently bolstered up the external challenges by creationists. To those Maynard Smith could reply by taking an idea from the philosophy of science to demonstrate the differences in method between science and religion. The latter he originally welcomed as additional perspectives to be discussed, if not necessarily agreed with. After all, science, according to the picture Maynard Smith painted in response to the creationists, lives on testing theories and, if necessary, changing theories and assumptions. With time, however, he grew increasingly critical of Gould's ideas.

The challenges did not come from Gould alone.[107] Eldredge, with whom Gould was to present a first set of criticisms to the neo-Darwinian orthodoxy (and in particular the idea of gradual evolutionary change), had published the ideas they developed already in 1971, but 'that first paper sank without a trace.'[108] Their joint paper of the following year made more of an impression, although it 'hardly arrived to a major crashing of symbols' either.[109] Eldredge and Gould argued that

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[102] Wright 1999, 56.
[103] Sterelny 2001, 59.
[104] Maynard Smith to Lewontin, 24 May 1989. JMSA Add MS 86582.
[105] Cited in Kohn 2004, 14. Cf. Brockman 1995. See Gould 2002, 252f on the English tradition of adaptation.
[106] '(also called "punk eek" and, by critics of Gould and Eldredge, "evolution by jerks")' (Horgan 1995, 26).
[107] For Gould's account of punctuated equilibria and its history, see Gould 2002, chapter 9.
[108] Eldredge cited in Sepkoski 2012, 157.
[109] Ruse has traced the controversy through citations, and the 'smallness of figures' for 1970-74 suggests that '[p]unctuated equilibria is under way, but this is not yet really the stuff of controversy' (2000, 233).

> [t]he history of life is more adequately represented by a picture of "punctuated equilibria" than by the notion of phyletic gradualism. The history of evolution is not one of stately unfolding, but a story of homeostatic equilibria, disturbed only "rarely" (i.e. rather often in the fulness [*sic*] of time) by rapid and episodic events of speciation.[110]

They looked at the lack of intermediates in the fossil record and argued that these gaps were not just the result of an imperfect record. Rather, 'this appearance of evolutionary stasis reflects reality. Most species come into existence relatively rapidly, having acquired their distinctive characteristics, and do not significantly change thereafter.'[111] Starting from their palaeontologist backgrounds, they developed the argument over the next few years in three phases.[112] According to Michael Ruse, the 1972 paper marked the first phase, intended as a 'fairly straightforward extension of orthodox Darwinism.'[113] The second phase – 'the peak'[114] – was marked by Gould's 1980 paper, 'Is a new and general theory of evolution emerging?':

> Gould assured us that the synthetic theory of evolution is effectively dead. Basically, I see a major deemphasis of the importance of organic adaptation, with a consequent downplaying of the role of natural selection. Gould certainly was also starting to toy with the idea of macromutations of some sort (perhaps due to chromosomal rearrangements), with species' changes occurring in one or a couple of generations.[115]

The last phase – the one in which, Ruse said, they still were at the time of his writing in 1989 and which is the last for his citation analysis of 2000 (the years 1985-1990) – toned down some of the more extreme views on macroevolution (such as the support of Richard Goldschmidt's ideas) without fully retreating on Gould's part. The view of evolution now was of a hierarchical nature, with individual selection at a lower level and species selection at a higher level.[116] More recently, Sepkoski has argued that Ruse's model is influenced by Ernst Mayr's reading of the punctuated equilibria theory and that 'brute chance was *always* a central component of the theory. If it was not mentioned as explicitly in the 1972 paper as

110 Eldredge and Gould 1972, Third Draft, 1f.
111 Sterelny 2001, 74f.
112 Ruse 1989, 2012.
113 Ruse 1989, 119f.
114 Ruse 2000, 237.
115 Ruse 1989, 121.
116 Ruse 1989, 122f.

it was in later publications, it was highly visible in many of Gould's significant publications throughout the early and mid-1970s.'[117]

The criticisms presented by Gould were thus not only of the gradualist view of evolution, but – for instance by bringing in mass extinctions as another factor in evolutionary history – also of the view that macroevolution is microevolution on a larger scale and of the adaptationist argument:

> the level of adaptation of a species is irrelevant. For adaptation is adaptation to a specific environment. Mass extinctions are caused by events which disrupt those environments catastrophically. They suddenly change the rules of the game. Since these changes are sudden and severe, selection is powerless to adapt organisms to their changed circumstances.[118]

The critique of adaptationism and its forefront position in the neo-Darwinian theory of evolution was made explicit in another joint paper of Gould's, this time presented with Richard Lewontin. They spoke at a symposium on 'The evolution of adaptation by natural selection' – organised by John Maynard Smith for the Royal Society.[119] Now mostly known as the Spandrels paper (the full title is 'The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme'), Maynard Smith remembered it in 1991 as 'much the most influential paper' read at the meeting.[120] Gould and Lewontin criticised the focus on adaptation and natural selection as the main if not only focus of Anglo-American contemporary evolutionary biology. They pointed out that in continental Europe organisms were more often analysed as integrated wholes rather than being broken up into adaptive traits and wished to re-introduce a more pluralistic approach to the study of evolutionary change. Neo-Darwinism's view of Darwin as a strict selectionist was wrong, they claimed, and their alternative pluralism much more in line with 'the master'.[121] Maynard Smith reflected that Gould and Lewontin did not want to 'deny the effectiveness of natural selection in adapting organisms to their way of life' but instead wanted to emphasise that this is not the only way of explaining evolutionary change.[122] Over the years, however,

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[117] Sepkoski 2012, 184 (emphasis in original).
[118] Sterelny 2001, 70.
[119] Maynard Smith 1991.
[120] Maynard Smith 1991. Dawkins calls it 'the most overrated paper in my field, if not in all of biology' (2015, 341).
[121] Gould and Lewontin 1979.
[122] Maynard Smith 1991.

Gould wrote increasingly against the "adaptationist programme" that he saw, suggesting that in the 1940s and 50s, neo-Darwinism "hardened" into a more and more adaptation-focused theory from originally more pluralistic accounts.[123]

By now, '[a]lmost everything about punctuated equilibria has become mythologized to some degree'.[124] Maynard Smith's engagement was more with these punctuationist than the Panglossian criticisms of neo-Darwinism's adaptationist focus – Pangloss' theorem refers to Voltaire's Dr Pangloss, who proclaimed that we live in the best possible world and everything has its reason (the nose is for holding up glasses etc.).

6.2.2 Welcome to the high table?

These discussions are much more internal than the ones on the creationist challenges to neo-Darwinism – at least at the beginning. What started with critiques, replies and articles in scientific journals and books moved onto more public platforms, from Gould's non-specialist science writings like his column in the *Natural History* magazine to exchanges in the *New York Review of Books.* Maynard Smith's way of dealing with the views proposed by Gould and colleagues was three-fold, making use of scientific, philosophical, and historical approaches and explanations. These overlap, but generally speaking the most strictly scientific engagements are confined to the pages of *Nature* and other professional publications whereas the philosophical and historical musings appear in book reviews and columns. Correspondence with fellow scientists has a more informal character of discussion, in which for instance ideas that are later published are first put forward in writing. We also see a development from openness to increasingly critical statements; moreover, in some of these writings, a common theme to the two challenges discussed here becomes obvious: there was a general confusion about what evolutionary theory and biology are and how much they can really tell us about the natural world. Creationists had their take on it, but there were difficulties in talking to non-specialists within the scientific community as well. This confusion was therefore not so much a science/non-science divide as a biology/non-biology one.

> There are a lot of things we do not know about evolution, but they are not the things that non-biologists think we do not know. If I admit to a non-biological

[123] Gould 1983; see also Ruse 2009, 389.
[124] Sepkoski 2012, 143.

> colleague that evolution theory is inadequate, he is likely to assume at once that Darwinism is about to be replaced by Lamarckism and natural selection by the inheritance of acquired characters. In fact, nothing seems to me less likely. In common with almost everyone working in the field, I am an unrepentant neo-Darwinist.[125]

Writing in 1977, Maynard Smith continued his chapter for the *Encyclopaedia of Ignorance* on the limitations of evolutionary theory by briefly explaining each and outlining current views. Popper reappears to stress the fact that neo-Darwinism is a hypothesis rather than fact and that 'observations may one day oblige me to abandon it'. Maynard Smith was not expecting this to happen because 'everything that has happened during my working life as a biologist, and in particular the development of molecular biology, has strengthened rather than weakened the neo-Darwinian position.'[126]

Darwin got it right then. Did he? This chapter's titular essay was first published in the *London Review of Books* (*LRB*) in 1981 and introduced a number of ideas and themes that Maynard Smith would repeat in later writings on punctuationist challenges to neo-Darwinism.[127] The first is that Gould and colleagues are making two claims: a minimum and a maximum one. The minimum claim is empirical, stating that the fossil record is not imperfect in showing periods of no change (stasis) interrupted by moments of change (punctuation) – on the contrary, that is how evolutionary change works. The maximum claim, derived from this, decouples macroevolution from microevolution, taking natural selection out of the equation as the driver for large scale evolutionary change.[128] Maynard Smith agreed to the possibility of accepting the first claim but 'without being driven to accent the second' as well.[129] He cited P.G. Williamson's study on molluscs found in Lake Turkana, Africa, as a good example of stasis and punctuation. But, he went on to say, the punctuationists' maximum claim did not follow; the evolutionary changes and phases of punctuation and stasis in the Turkana molluscs could be explained by natural selection

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125 Maynard Smith 1977, 236.
126 Maynard Smith 1977, 236.
127 The essay was republished at least twice: in Maynard Smith's own collection and in Michael Ruse's edited volume *But is it Science? The Philosophical Question in the Creation/Evolution Controversy* (1988, Prometheus Books).
128 Maynard Smith 1981d, 148f.
129 Maynard Smith 1981d, 149.

acting within populations. There were no Goldschmidtian 'hopeful monsters' – although Maynard Smith did have a soft spot for them and in his *Theory of Evolution* pointed out that

> it is possible that single mutations with phenotypic effects large enough decisively to alter the selection pressures acting on their carriers have played a part in the origin of new groups, particularly because the capacity of animals to regulate during development means that even quite large changes in phenotype may be adaptive in certain circumstances.[130]

There also were no other factors present in the Turkana case that would or could outweigh natural selection. 'Williamson's study suggests an easy resolution of the debate,' Maynard Smith then suggested:

> Both sides are right, and the disagreement is purely semantic. A change taking 50,000 years is sudden to a palaeontologist but gradual to a population geneticist. My own guess is that there is not much more to the argument than that. However, the debate shows no signs of going away.[131]

Switching explanatory modes, he then brought in history to prove that the minimal claim made by punctuationists is not new: G.G. Simpson, one of the founding fathers of neo-Darwinism and a palaeontologist himself, had shown that evolutionary rates vary and are not uniform, as the criticism against gradualism suggested.[132] Going even further back in time, Maynard Smith explored Darwin and the reasons for his belief in gradual change, concluding that he completely agreed with Darwin's 'emphasis on detailed adaptation as the phenomenon to be explained, and his conviction that to achieve such adaptation requires large numbers of selective events.'[133] There was thus nothing in the punctuationist criticisms and claims presented so far that made Maynard Smith abandon his neo-Darwinism; these ideas would 'prove to be a ripple rather than a revolution in the history of ideas about evolution.'[134]

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130 Maynard Smith 1958, 283f.
131 Maynard Smith 1981d, 151.
132 Maynard Smith 1981d, 151. See also Sepkoski 2012, 175-180 on the immediate reception of the Eldredge and Gould paper which, though overall positive, included 'several reviewers also express[ing] concern—and even mild offense—that Eldredge and Gould were claiming as a "new" theory an idea that had long been recognized in biology and even paleontology.'
133 Maynard Smith 1981d, 153. The discussion of Darwin in fact starts on p.152 and continues until p.156.
134 Maynard Smith 1981d, 156. Segerstråle adds other critics with similar views to Maynard Smith (2000, 126).

Maynard Smith's faith in neo-Darwinism would not waver over the next two decades, nor would his arguments first presented in this essay change much. But he kept an open mind towards unorthodox or controversial ideas and was not afraid of introducing them directly to a wider audience in the midst of these discussions around (neo-)Darwinism. The collection *Evolution Now. A Century after Darwin* (1982) (co-edited with the editorial staff of *Nature*[135]) presented scientific papers on current controversies to non-specialists. The book was an attempt to invite readers into these "in-house" debates by giving them direct access to the sources, scientific papers previously confined to professional journals where they remained largely inaccessible for anyone outside academia. Thus rather than reading secondary commentaries in the popular press, non-specialists were invited to go to the source material and to form their own opinion.

The papers were, however, all accompanied by an introduction written by Maynard Smith. While these primarily served as an explanation for the relation between the topic and controversy to Darwin's original ideas and as guidance towards the technical details and jargon, Maynard Smith added that '[f]inally, I have allowed myself the indulgence of expressing my own opinion on some of the more controversial issues.'[136] That is, even though he was about to welcome palaeontologists and their views to "the high table" two years later (see below), he did not necessarily agree with them – as we have already seen in the *LRB* essay – and was keen not to let the criticisms stand completely uncommented. But he did always welcome (scientific) discussion, as James Crow noted in his introduction to a 2000 Festschrift for Maynard Smith: 'One of the articles is a book review in which the author takes strong exception to one of JMS's ideas about the evolution of language. I am sure that John loves it and is eagerly looking forward to an argument.'[137]

Chapter 5, "Evolution – sudden or gradual?" is of particular interest to the discussions Maynard Smith was engaged in in the 1980s and 1990s. While his own copy does not show much use generally, there is one crack in the spine that will inevitably lead the reader to the introduction to this section. In fact, those pages have become loose. Maynard Smith wrote that the 'attack' on the gradualist interpretation of evolution could be read to 'imply an

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135 Maynard Smith 1982a, 6.
136 Maynard Smith 1982a, 5.
137 Crow 2000, 2.

attack on Darwinism itself'.[138] He therefore became historical, turning to the question of what the connection is between Darwin/ism and gradualism. 'Both for Darwin and for neo-Darwinists,' he concluded,

> it is central that the adaptation of organisms to their ways of life is, in the main, brought about by the natural selection of numerous genetic differences between the members of populations. However, it has never been part of the theory that evolution proceeds at a constant rate.[139]

The same tactic was used by Eldredge and Gould in their paper of 1972. They quoted the first edition of *The Origin of Species* in order to show the difficulties Darwin saw in the imperfect fossil record and to define his view of speciation which 'entailed the same expectation as phyletic evolution: a long and insensibly graded chain of intermediate forms. Our modern texts have not abandoned this view, although modern biology has.' Eldredge and Gould continued to say that the framework palaeontology drew based on Darwin's views from 1859 resulted in what they called "phyletic gradualism" and which they wanted to adjust to include non-gradual change as well.[140] In 1979, Gould and Lewontin would again utilise Darwin to strengthen their claims: the later Darwin had moved away from an exclusive focus on natural selection as the means of evolutionary change; he had been a pluralist himself and so should twentieth-century evolutionists be.[141] (This paper, now probably more famous than the 1972 one, is not included in the edited collection.) So Maynard Smith too drew on Darwin's authority, quoting him (without reference to which edition he used) on rates of change in species:

> Although each species must have passed through numerous transitional stages, it is probable that the periods during which each underwent modification, though many and long as measured by years, have been short in comparison with the periods during which each remained in an unchanged condition.[142]

The articles making up the section on evolution in *Evolution Now* are led by Gould's provocative 'Is a new and general theory of evolution emerging?'; the remaining articles are by Russell Lande, P.G. Williamson (two), J.S. Jones, with a joint paper by Peter T. Boag and Peter R. Grant. Gould's article caused controversy around his ideas and started attracting

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[138] Maynard Smith 1982a, 125.
[139] Maynard Smith 1982a, 126.
[140] Eldredge and Gould 1972, Third Draft, 6f.
[141] Gould and Lewontin 1979, 155f.
[142] Darwin quoted in Maynard Smith 1982, 126.

negative criticisms to them. Maynard Smith's answer to Gould's question in his introduction was that no, neo-Darwinism stands. Once more he pointed out that punctuationists have made two claims, and that of those only the minor one about observable stasis and interruptions to these in the fossil record holds. Their major claim however, that macroevolution 'can be "decoupled" from the processes occurring within populations that are studied in existing species by ecologists and population geneticists' (microevolution) was still not convincing.[143] This claim had also been discussed at a conference in Chicago in 1980, reported on for *Nature* by Maynard Smith (where again he made the same distinction between a minimum and a maximum claim).[144] He acknowledged that he was a geneticist, not a palaeontologist (and thus an outsider), and not quite convinced by the palaeontological suggestions put forward by Eldredge, Gould, and Steven Stanley, the main proponents of punctuated equilibria present at the conference. With such an interdisciplinary attendance as in Chicago, 'much misunderstanding, confusion and even indignation' also had to have been expected. And yet, 'despite my reservations,' he concluded that he 'found the meeting immensely stimulating. It can only be good for evolutionary biology that people from such different disciplines should meet, talk and, occasionally, listen.'[145]

This positive attitude towards interdisciplinarity and the discussion generated by palaeontologists moving into evolutionary biology stayed with Maynard Smith. Over a decade after Eldredge and Gould had introduced their ideas, and half a decade after Gould and Lewontin's paper, he wrote a short piece that most 'signaled paleobiology's entry to the mainstream of evolutionary biology'.[146] Palaeobiology describes the synthesis of palaeontology and biology emerging in the 1970s, with Gould, Eldredge, Stanley, and David Raup as its best-known proponents.[147] As Sepkoski has argued, this piece, published in *Nature* in 1984 and called 'Palaeontology at the high table', 'acknowledged a correction, not

143 Maynard Smith 1982, 126.
144 Maynard Smith 1981c; see also Rensberger 1980 and Sepkoski 2012, 363ff.
145 Maynard Smith 1981c, 14. Gould remembered this meeting for another reason: creationism (2002, 981). The press became aware of it and 'grossly misread the […] meeting as a sign of deep trouble in evolutionary sciences (rather than the fruitful product of a time of unusual interest and theoretical reassessment for a factual basis that no one doubted) and therefore as an indication that creationism might actually represent a genuine alternative' (982).
146 Sepkoski 2014, 134.
147 Sepkoski 2009. Sepkoski points out that, programmatically speaking, Gould and Eldredge were not the driving forces behind palaeobiology, Thomas Schopf was (see also Sepkoski 2012).

a replacement, in the disciplinary organization of evolutionary biology'.[148] Reacting to Gould's Tanner lectures, delivered at Cambridge on 30 April and 1 May 1984, Maynard Smith took 'the opportunity to assess the current contribution of palaeontology to evolutionary theory.'[149] Casting himself as, again, an outsider to palaeontology and an 'old-fashioned proponent of the modern synthesis',[150] he briefly ran through the main arguments and pointed out agreements and disagreements that he personally had with the theory and that were more generally applicable to geneticists and palaeontologists. Famously, Maynard Smith concluded: 'The palaeontologists have too long been missing from the high table. Welcome back.'[151] The paper and this statement could be – and was by many – read as an acknowledgement that palaeontology was positively contributing to evolutionary biology, though some regarded it with suspicion as to its sincerity and even felt it was patronising.[152] It fits however with Maynard Smith's previous comments on punctuated equilibria theory as a welcome stimulation for discussion, as well as with his general (critical) openness to unorthodox ideas.

Gould himself felt vindicated by the column. In a letter to Maynard Smith he admitted that the negative, and often venomous and small-minded, commentary he was receiving was 'deeply discouraging'. But, he continued,

> then I meet the people whose minds I most respect and who combine that extraordinary intellectual power with a wonderful absence of pettiness -- and who seem willing to judge issues on their intellectual merits and not to indulge in useless speculation about motives. I know that we disagree about many things, but that is not important (or rather, the intellectual issues are vitally important, but a search for understanding transcends the actual answers). I am just so pleased that you take the issues at face value, that you acknowledge them as a different view of life with some coherence and reasonable testability, whatever the eventual outcome. I ask for no more than this recognition as a member of a group of paleontologists who are excited, even thrilled, by a set of intellectual issues about the nature of life. Thank you so much for understanding so deeply what we are trying to say, for characterizing its issues so well (far better, I think, than I can do myself), and above all for taking us seriously. […]

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148 Sepkoski 2009, 180.
149 Maynard Smith 1984, 401.
150 Maynard Smith 1984, 402.
151 Maynard Smith 1984, 402.
152 Sepkoski 2014, 134.

> John, I guess all I am really trying to say is that you are a splendid man and that I am glad I know you.[153]

The relationship did not stay this friendly. Segerstråle has suggested 'that Maynard Smith, as Gould's anti-adaptationist program progressed, simply *continued* disliking it, and *continued* saying so' rather than turning his back because of a grudge he developed against Gould after the Spandrels paper (as Gould suggested).[154] She was writing about a 1993 exchange between Maynard Smith and Gould which took place in the *New York Review of Books* (*NYRB*), and there are indeed critical voices by Maynard Smith before 1993. We can go back to 1981 for a first sign that Maynard Smith was taking note of Gould's radicalism. Replying to a letter in the *LRB* by Anthony Hallam, he noted that 'the disagreements between us, although important, are certainly not of a kind to suggest that he is supporting a new paradigm, incommensurable with neo-Darwinism, as suggested by Stephen Gould.'[155] Kuhnian language reappears in a more critical piece published in *Nature* in 1987. Reviewing an article by P.R. Sheldon under the title 'Darwinism stays unpunctured', Maynard Smith concluded that Sheldon's study showed the uselessness of species selection as an explanation for morphological evolution – and that 'there never was much sense in the idea anyway.' That the punctuationists' major claim did not hold for Maynard Smith is not new but he came to criticise the minor claim as well:

> Geneticists have tended to explain such stasis by normalizing selection for an unchanging optimum, and palaeontologists by developmental constraints: no doubt we shall continue to argue about their relative importance. *But my own view, which will not be universally shared, is that we can forget about new paradigms and the death of neodarwinism* [*sic*].[156]

Eldredge and Gould replied by suggesting that Maynard Smith did neither understand Sheldon's study properly nor the theory of punctuated equilibria. His definition of species selection was not theirs, for instance – '[o]f course it makes no sense – stated this way'. There were other misrepresentations such as Maynard Smith's insistence that palaeontologists ignore normalising selection in favour of developmental constraints. They concluded that they were 'all darwinians [*sic*]' but that palaeontologists like themselves

153 Gould to Maynard Smith, 14 June 1984. JMSA Add MS 86604. Gould again thanked Maynard Smith for his way of dealing with him and his ideas in 1989.
154 Segerstråle 2000, 112 (emphasis in original).
155 Maynard Smith 1981e.
156 Maynard Smith 1987, 516 (emphasis added).

sought 'a deeper understanding' of the evolutionary theory and processes 'than that already achieved'.[157] (Gould insisted throughout his career to be strictly Darwinian.[158]) Maynard Smith replied that he was 'delighted that Eldredge and Gould have abandoned species selection as a significant cause of morphological evolution, but they really must not pretend they never said otherwise.'[159] He cited Gould's 1980 article:

> Macroevolutionary trends do not arise from the gradual adaptive transformation of populations, but usually from a higher-order selection operating on groups of species, while the individual species themselves generally do not change.[160]

Maynard Smith concluded that he still welcomed palaeontological input into evolutionary biology, but that it had to be recognised that none of the suggestions made so far marked the breakdown of neo-Darwinism. 'It seems,' he finished with a nod to his 1984 article, 'that Eldredge and Gould now recognize this. Welcome back!'[161]

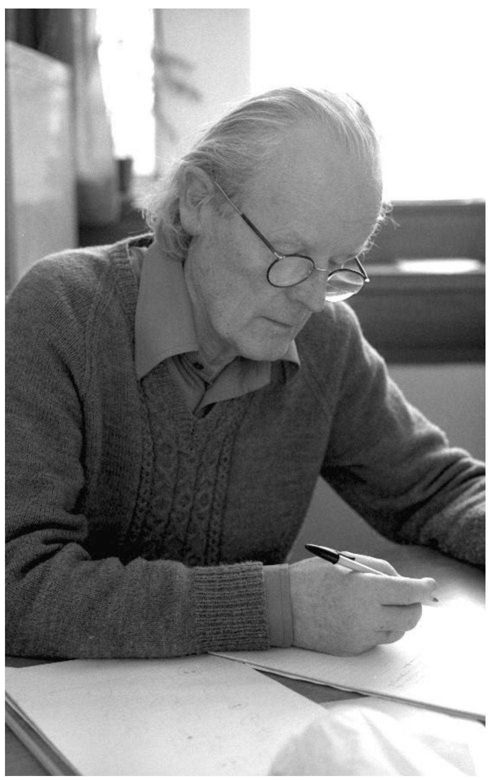

Figure 25. John Maynard Smith, ca. 1984. © University of Sussex.

[157] Eldredge and Gould 1988, 212.
[158] Sheldon 2014, 139.
[159] Maynard Smith 1988b, 311.
[160] Gould 1980 cited in Maynard Smith 1988, 311.
[161] Maynard Smith 1988b, 312.

Gould and Eldredge were not leaving the last word to Maynard Smith. Again, they suggested Maynard Smith misunderstood their theory, as illustrated by the quotations he had chosen. Those were advocating 'species selection as a cause of palaeontological "trends" and Maynard Smith has equated trends with complex adaptations. Not so,' they wrote.[162] They refused to be 'welcomed back' to Maynard Smith's orthodoxy and accused him of being stuck in the past with his limited view of the Darwinian theory:

> Maynard Smith ends by welcoming us back to his conceptual edifice. But while he was out crusading for his castle, the building was growing. The darwinian [*sic*] ground floor is as vibrant as ever, but a wonderful basement has been added for gene and cell-lineage level selection – and a lovely attic for the level of species. The view from the top is puzzling, but endlessly fascinating.[163]

There is no reply by Maynard Smith. But this public, scientific discussion in the pages of *Nature* was connected to background correspondence. Philip Gingerich, a vocal opponent of punctuated equilibria,[164] wrote to Maynard Smith after the original publication of his comment on Sheldon's study. His letter does not suggest any disagreement with Maynard Smith's representation of either Sheldon or Eldredge and Gould's work. In fact, he was pleased about it, though he suggested, 'respectfully', that Maynard Smith

> might want to expand your circle of acquaintances among paleontologists. Just because Eldredge and Gould 'distrust' the evolutionary mechanisms of population geneticists is no reason to caricature the whole paleontological profession. Many paleontologists (like me) have been saying from the beginning, as Sheldon does again, that punctuation is not a universal pattern.[165]

Gingerich pointed out that interdisciplinary and synthesising work between palaeontology and genetics is necessary, and that Maynard Smith could – and should – use his status in evolutionary biology to bridge any differences rather than antagonise palaeontologists by 'writing [them] off as simple-minded punctuationists.' While these exchanges took place, Maynard Smith was also in the process of writing a textbook on evolutionary genetics for advanced undergraduates. On his treatment of macroevolution Maynard Smith sought the expertise from Richard Fortey, a palaeontologist. Maynard Smith admitted that it 'is always worrying to write something one is not an expert on, but it has to be done when writing a

162 Gould and Eldredge 1988, 19.
163 Gould and Eldredge 1988, 19.
164 Sepkoski 2012, 201; see also Ruse 2000, 234.
165 Gingerich to Maynard Smith, 2 February 1988. JMSA Add MS 86756.

text book. I am relieved I did not get it too badly wrong.'[166] Fortey mentioned that he had 'taken a passing interest in the problem of the debate between gradualists and punctuationalists' and felt that Maynard Smith's views were 'just fine'.

> It might be worth pointing out that the examples of supposed gradualistic change tend to be from those groups which have a good and continuous fossil record, such as planktonic foraminifera, ammonites and graptolites. Since Eldredge's analysis of Phacops (not Phacopus by the way) there has been something of a sea change among palaeontologists, many of whom have abandoned the 'gradualistic' paradigm and instead appear to observe nothing but punctuational change. My own belief is that a conviction in the reality of one process or the other influences the way the observations are made, and the interpretations are made. Particularly when the fossil record is sparse it is easy to 'see' punctuational change. In the case of the debate about fossil Man, for example, there appear to be equally passionate protagonists on both sides, and this depends on the conceptual stance of the worker involved.[167]

At the same time, Tim Halliday from the Open University's Biology department wrote to Maynard Smith in 1988 asking him to be a course assessor; they were restructuring their dated course on evolution. Regarding the punctuated equilibria debate, Halliday argued that

> [t]he dust has rather settled on this debate now: the palaeontologists' 'punctuations' no longer pose a threat to neo-Darwinian models, with the mutual confusion of timescales being resolved. Interest has shifted to purported 'stasis' and/or 'gradual change' as a palaeontological pattern of interest; but even here, higher resolution sampling has begun to show up a much more fluctuating record, again consistent with neo-Darwinian thinking.[168]

The dust had not settled quite as much as Halliday suggested, and in the 1990s the debate moved into the pages of the *NYRB*.[169] As shown by Sheldon and Ruse, Gould had very effectively used his non-specialist writing and history of science to support palaeobiology, punctuated equilibria, and his other critiques of neo-Darwinism and adaptationism.[170] Gould particularly drew on Darwin, as we have briefly seen above, and so did Maynard Smith in some of his responses. Maynard Smith turned to history of science again when he changed publication styles. 'Dinosaur dilemmas', an essay review covering two books on

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166 Maynard Smith to Fortey, 14 January 1987 [1988]. JMSA Add MS 86575.
167 Fortey to Maynard Smith, 7 January 1988. JMSA Add MS 86575.
168 Halliday to Maynard Smith, 4 October 1988. JMSA Add MS 86577.
169 This move into non-specialist literature is not covered by Ruse's 2000 citation analysis which focused on specialist literature and ended in 1990.
170 Sheldon 2014, Ruse 2013.

dinosaurs, turned into a reflection on the 1979 Gould and Lewontin paper as well as the English fondness for adaptationism. 'The effect of the Gould–Lewontin paper has been considerable,' Maynard Smith wrote, 'and on the whole welcome.' But

> I doubt if many people have stopped trying to tell adaptive stories. Certainly I have not done so myself. […] As we have sought for adaptive explanations, however, we have done so with an occasional glance over our shoulders to see if Gould or Lewontin were watching.

For example, alternative explanations to adaptationism were considered more than before and methods of comparing different species to test hypotheses used more. How much of these changes were due to the Gould and Lewontin paper, Maynard Smith could not say for sure, but he quoted Paul Harvey – apologising for revealing this – as saying 'after he completed a paper on allometry, "That'll get Lewontin."' From personal experience he knew that Gould, Lewontin and himself rarely disagreed about cases and more about what they researched, and that he himself – like many if not most English evolutionists – chose to seek explanations for adaptations more than anything else. He had come to reflect on why that might be so, and found two historical reasons: English people's 'escape from natural theology, and their continued love of natural history.'

The first of these, Maynard Smith argued, related to the fact that in the eighteenth century, scientists were looking to prove God's existence by finding evidence of his work in the designed complexity of nature – the most famous example being William Paley's watchmaker analogy. Darwin liberated science from this view by inventing natural selection, Dawkins' blind watchmaker.[171] This argument might look naive, Maynard Smith continued, because there are 'Christians who accept natural selection and evolutionists who have never been Christians, and there are reasons other than the argument from design for believing in God.'

> Yet the path that starts with the argument from design goes on to see that the main problem for any theory of evolution is to explain adaptation, and concludes by seeing natural selection as the major cause of evolutionary change, is a common one. It accurately describes my own intellectual development as a boy, and I think it is widespread among evolutionary biologists: in England and America, at least, it is surprising how many of them are lapsed Christians.[172]

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[171] Dawkins 1986.
[172] Maynard Smith 1991.

The other historical – and contemporary – reason why the English prefer adaptationist explanations is their love for natural history, an aspect of biology that needed to be taken seriously and as more than fact gathering.[173] Naturalists, Maynard Smith argued, were adaptationists because 'if one watches an animal doing something, it is hard not to identify with it, and hence to ascribe a purpose to its behavior. [...] Of course, there is a simpler reason why naturalists tend to be adaptationists: it is an approach that usually works.'[174] He himself had been a bird watcher and bug collector as a child and still was a keen naturalist – and he was a strict adaptationist. Gould, however, had been fascinated by dinosaurs and fossils all his life, and that, Maynard Smith suggested, might explain the differences between them: 'he fell in love with fossils which, being dead, do not really reveal what they were up to.'[175]

This quote comes from private correspondence about two years prior to the essay review. Maynard Smith had first tested out this historical explanation of the differences between himself and Gould as well as Lewontin (who had just reviewed Maynard Smith's *Evolutionary Genetics,* stating that its 'organization reflects Maynard Smith's commitment to natural selection as the real stuff of evolution'[176]). 'Why are the British so obstinately selectionist, whereas (at least until recently) Americans tend to be obsessed by accidents?' There were, he told Lewontin, nationally and historically – as well as philosophically – different entrance points to the study of evolution. Again, England had its 'intelligent natural history'. America, in contrast, had 'agrarian roots', France was intellectually hampered by its focus on Paris and his Japanese students and colleagues 'were all refugees from theoretical physics, who didn't know a daisy from a dandelion, so no wonder they became neutralists. But there must be a philosophical background that I know nothing about.'[177] He wished philosophers of biology would pay more attention to natural history to shed some light on issues like these. Lewontin replied that he was 'both amused and in complete agreement' with Maynard Smith. He not only agreed with the hypothesis on the origins of these differences but also that '[a] more general approach to the relationship between social background, ethnicity, etc. and scientific interest really is in order. For

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173 Maynard Smith 1982c.
174 Maynard Smith 1991.
175 Maynard Smith to Lewontin, 24 May 1989. JMSA Add MS 86582.
176 Lewontin 1989, 107.
177 Maynard Smith to Lewontin, 24 May 1989. JMSA Add MS 86582.

example, if one looks simply at different sub-fields in the U.S., one sees big ethnic differences.'[178] (Gould, too, had linked scientific outlooks in evolutionary biology to national backgrounds: adaptationism was 'the British hang-up', the 'hard-line view […] which has been so characteristic of English natural history since Darwin'.[179]) Despite his own attempts at some form of history of science, Maynard Smith told an editor at OUP that same year that he had a '(rather superficial) acquaintance with the sociological approach to the history of science, which, in common with many other scientists, I find unconvincing. These guys seem to throw away the baby but keep the bath water.'[180]

Maynard Smith was not too far off with his musings about intellectual upbringing. Philosophers and sociologists have written about the differences between the "Gouldians" and "Dawkinsians", also called "ultra-Darwinians". Kim Sterelny notes that they 'are representatives of different intellectual and national traditions in evolutionary biology.'[181] He traced the disagreements back to Gould and Dawkins' disciplinary upbringing and early mentors – ethology under Niko Tinbergen in the latter's case and palaeontology under George Gaylord Simpson in the former's. As a result, they have different views not only on the need to explain adaptation and the power of selection but also on what science is:

> Dawkins is a whole-hearted son of the Enlightenment. We should embrace the scientific description of ourselves and our world, for it is true (or the nearest approach to truth of which we are capable), beautiful and complete. It leaves nothing out. Gould, on the contrary, does not think that science is complete. The humanities, history and even religion offer insight into the realm of value – of how we ought to live – independent of any possible scientific discovery.[182]

Ruse similarly writes that punctuated equilibria theory 'stands in this American tradition' which, as a consequence of being influenced by Herbert Spencer more than Charles Darwin, has been less focused on adaptationism from the beginning.[183]

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178 Lewontin to Maynard Smith, 13 June 1989. JMSA Add MS 86760.
179 Gould in Brockman 1995, chapter 2.
180 Maynard Smith to Maidment, 8 September 1989. JMSA Add MS 86585.
181 Sterelny 2001, 6.
182 Sterelny 2001, 13.
183 Ruse 2000, 243.

6.3 Conclusion

The relationship between John Maynard Smith and Stephen Jay Gould was one of respect but one that over time deteriorated as Gould's critique on neo-Darwinism continued and intensified. It got to the point that Maynard Smith, who had previously praised Gould's ability to write well for both non-specialist and specialist audiences,[184] felt this was a problem:

> Because of the excellence of his essays, he has come to be seen by nonbiologists as the preeminent evolutionary theorist. In contrast, the evolutionary biologists with whom I have discussed his work tend to see him as a man whose ideas are so confused as to be hardly worth bothering with, but as one who should not be publicly criticized because he is at least on our side against the creationists. All this would not matter, were it not that he is giving nonbiologists a largely false picture of the state of evolutionary theory.[185]

He published this in a review of philosopher Daniel Dennett's book *Darwin's Dangerous Idea*, which criticised Gould and his anti-adaptationist programme and advocated a neo-Darwinian approach to evolution.[186] Dennett was very grateful for the review because it was public support for his Gould criticism: 'I've been getting lots of <u>private</u> letters of support from eminent biologists, thanking me for daring to challenge Gould's public image as the great authority on evolution, but until you came out in print, they were apparently reluctant to express this view in public.' He was hoping that this would change now and told Maynard Smith that the review had already 'provoked some surprised discussion on the Internet'.[187]

The timing of Maynard Smith's engagements with these two challenges to neo-Darwinism is telling. Religion was an overall concern that was expressed early on in relation

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184 Maynard Smith 1992b.
185 Maynard Smith 1995b.
186 Dennett 1995.
187 Dennett to Maynard Smith, 11 December 1995. JMSA Add MS 86760. Trivers (2015) characterised Gould as

> something of an intellectual fraud because he had a talent for coining terms that promised more than they could deliver, while claiming exactly the opposite. One example was the notion of 'punctuated equilibria'—which simply asserted that rates of (morphological) evolution were not constant, but varied over time, often with periods of long stasis interspersed with periods of rapid change. All of this was well known from the time of Darwin.

Even Gould's collaborator Lewontin struggled with Gould's 'desire to be considered a very original and great evolutionary theorist' which would lead him to exaggeration and caricature (Lewontin and Wilson 2015).

to how science works. It fitted well within Maynard Smith's role on radio and TV, that is, of explaining, defending, advertising, and discussing science. But the late 1970s and 1980s saw a rise in creationism that, contrary to common perception, was not limited to the United States (Gould once referred to creationism as a 'local, indigenous American bizarrity',[188] and Lewontin felt it could 'only be understood as part of the history of southern and southwestern American populism'[189]).[190] At the same time, Gould was increasingly popularising his critique of neo-Darwinism. Thus these two decades became crucial for the specific challenges presented by creationism and Gould: after evolutionary biology had gained professional status and established itself in academia and the public, it had also gained professional authority as 'science' rather than a gentleman's hobby. With that the public perhaps paid more attention to what was said by the new experts, who – as Ruse wrote – were making sure the professionalisation process was not undermined by keeping their more metaphysical thoughts on, for instance, the role of progress outside of their professional publications.[191] At the same time, America saw the rise of creationism, and creationists picked up on any scientific voices dissenting with the standard theory. In Britain and elsewhere, the ideas of Teilhard de Chardin were popular, synthesising evolution and purpose and thus offering something other than an impersonal evolution. On a different level Gould, who had become a public face through his non-specialist writings in the late 1970s and in the 1980s, also offered alternatives to the neo-Darwinian perspective that had dominated the outward-facing unified image of evolutionary biology.

Maynard Smith engaged with both Gould's and creationist claims at the same time, occasionally explicitly linking them. Both his non-specialist and specialist writings are concentrated in the late 1970s and the 1980s, with additional interactions in the case of Gould in the 1990s. That is, even though creationists had been engaging with him since the late 1960s, and even though Gould and Eldredge first published their critiques in the early 1970s, he did not become active until both challenges were starting to make a wider impression, being discussed in lecture halls on Gish's tour or in the newspapers. Simultaneously, the sociobiology controversy was raging, featuring similar contestants on

188 Gould 1986 cited in Numbers 2006, 399.
189 Lewontin 1983.
190 See for instance Numbers 2006, 2011; Krasnodebski 2014; Zimmermann 2011.
191 Ruse 1999.

both sides: Gould and Lewontin *versus* Trivers and Wilson, for instance. Maynard Smith occupied the position of the mediator. He 'was in the interesting position of being able to empathize both with Wilson and with the critics, especially Lewontin.' He was also making 'a clear analytical distinction between science and moral/political concerns.'[192] Not too dissimilarly, he engaged with the science of Gould's challenges to neo-Darwinism. As Lewontin recalled, Maynard Smith had a 'sensibly skeptical view of science and its claims, which is best encapsulated in the famous dictum of his teacher, J. B. S. Haldane, who said that a scientific idea ought to be interesting even if it is not true.'[193] The main tenet of his responses is that they were scientifically stimulating – by highlighting the puzzle of stasis, for instance – and may in fact have strengthened the neo-Darwinian case by making their work more focused in addressing possibly anti- or non-adaptationist explanatory possibilities. He also acknowledged that 'Darwinism is not all that we need to know' – but he was afraid that

> when people argue that Darwinism is not enough, it is not the absence of a theory of development, or of ecology, that they are worried about. Often, I suspect that they are hankering after some kind of Lamarckian inheritance of acquired characters, or some Teilhardian inner urge towards the omega point. If so, they would be better to stick with Darwin.[194]

But overall, Gould's ideas did not revolutionise the field. Natural selection and adaptation still provided the core of Darwinian theory for Maynard Smith and he was determined to continue teaching this view. Thus he told John Campbell, neurobiologist at UCLA with whom he corresponded on Sheldon's trilobite study and whether it demonstrated punctuationism, that he had met his daughter who would be 'attending a 3rd-year course I run on population genetics. I hope to turn her into a good neo-Darwinist!'[195] After publishing his textbook *Evolutionary Genetics* in 1989, he replied to Lewontin's review by saying he would attempt to 'smuggle a few copies into Cambridge so your students can read the book despite you.'[196]

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[192] Segerstråle 2000, 241.
[193] Lewontin 2004, 979.
[194] Maynard Smith to Appignanesi, 17 October 1984, attached draft 'Structuralism vs selection – is Darwinism enough?' JMSA Add MS 86579.
[195] Maynard Smith to Campbell, 12 January 1988. JMSA Add MS 86604.
[196] Maynard Smith to Lewontin, 24 May 1989. JMSA Add MS 86582.

Neither did creationism pose a serious threat to neo-Darwinism. It was not even a stimulation for scientific discussion, considering that for Maynard Smith it was not science and therefore could not be compared. There may be a role for religion as a form of poetry, yet scientific communication is the one that will lead to knowledge; thinking of knowledge as one and of science and religion as two ways of talking about it is unhelpful and damaging. Referring back to Teilhard de Chardin and Bernard Shaw, he wrote that '*Back to Methuselah* and *The Phenomenon of Man* alike illustrate what nonsense intelligent men, agnostic or Christian, can write when they confuse science and poetry.'[197]

Towards the end of his book *The Evolution-Creation Struggle,* charting the history and positions of the current debates, Michael Ruse asked two questions: do evolutionists promote an either/or view towards religion, i.e. that one must 'choose between God or Darwin'?[198] And do they promote evolution 'as a guide to and justification for morality'?[199] The answer to the first question is that for Maynard Smith personally, it *was* a choice. Science offered the better explanation for the world, its origins and its developments. There was a 'good dose of scientism' in Maynard Smith's worldview, 'in the sense of belief in the Progressive nature of science': scientific knowledge advances, improving our understanding of the world.[200] In addition we have his regard for Karl Popper's philosophy of science, although it needs to be noted that Maynard Smith's overall view and use of the history and philosophy of science (HPS) was ambiguous. He loved reading and arguing about it, but he did 'not believe one should allow oneself to be influenced by it, when actually thinking about science.'[201] Maynard Smith mostly used HPS as a means to advance arguments about (the validity of) science, in particular Popper's notion of falsifiability. Although using Kuhnian terminology at least once in the above described debates, he was unconvinced by his philosophy.[202] This ambiguity towards the philosophy *of* science stemmed from a mistrust of philosophy (more accurately, ideology) *in* science (as discussed in Chapter 2, his

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197 Maynard Smith 1965b, 64.
198 Ruse, op. cit., p. 203.
199 Ibid., p. 207.
200 Michael Ruse, *Monad to Man. The Concept of Progress in Evolutionary Biology* (Cambridge, Mass., 2009), p. 478.
201 Maynard Smith and Dawkins 1997, https://www.webofstories.com/play/john.maynard.smith/99.
202 Cf. conclusion of Chapter 6.

favourite example being Lysenkoism) as well as from feeling misunderstood by philosophers (from which he excluded Dennett).[203]

Maynard Smith too remained ambiguous about religion until old age, saying three years before his death:

> I think there are two views you can have about religion. You can be tolerant of it and say, I don't believe in this but I don't mind if other people do, or you can say, I not only don't believe in it but I think it is dangerous and damaging for other people to believe in it and they should be persuaded that they are mistaken. I fluctuate between the two. I am tolerant because religious institutions facilitate some very important work that would not get done otherwise, but then I look around and see what an incredible amount of damage religion is doing.[204]

[203] Maynard Smith 1995b.
[204] Maynard Smith 2001.

7 'The last nail in Eve's coffin'? The possibility of recombination in human mitochondrial DNA

7.1 Questioning the orthodoxy

In the previous chapter, John Maynard Smith has tackled large questions about evolution, defending not only its existence against creationism but also defending his neo-Darwinian perspective against suggestions by Gould. In both of these cases Maynard Smith was on the orthodox side of the debate, defending a majority view. He was not afraid of being on the other, non-orthodox side of a debate, and would 'cause a flurry of indignation by suggesting that there may be recombination in human mitochondrial DNA' towards the end of his scientific career:[1] in March 1999, Maynard Smith had published a paper co-authored with Adam Eyre-Walker and Noel Smith, claiming that mitochondrial DNA (mtDNA) might recombine.[2] The general consensus was that this is impossible because mtDNA is inherited strictly clonally and maternally, the same copy of mtDNA being transferred only from mothers – so with one set of mtDNA, how should recombination happen? The months and years following the original 1999 articles – Eyre-Walker *et al.*'s paper had appeared back to back with another article that also claimed to have proof for mtDNA recombination[3] – both showed and questioned several implicit and explicit assumptions on what good data and good methodology in genetics and human evolution are. The dismissing of mtDNA recombination was strengthened when it turned out that Eyre-Walker and colleagues had used possibly erroneous data,[4] and Hagelberg and colleagues' (the authors of the second paper) analysis and conclusions were based on an error in their data.[5] For the majority of scientists, there could be nothing to the claims put forward by the two 1999 papers since they were based on errors. Maynard Smith and his team, as well as Erika Hagelberg, however, thought differently. Instead of binning the idea of mtDNA recombination, they

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[1] Spratt 2004, 299.
[2] Eyre-Walker *et al.* 1999a.
[3] Hagelberg *et al.* 1999.
[4] Macaulay *et al.* 1999; Eyre-Walker *et al.* 1999b.
[5] Hagelberg *et al.* 2000.

wrote follow-up articles, correcting their mistakes, using different data and claiming 'that there is still evidence of recombination.'[6]

This chapter tells the story of Maynard Smith's role in this controversy around human mitochondrial DNA. Part of why the suggestion of recombination caused a larger controversy (one that spilled over into the press as well) lies in its implications for several theories on when and where the most recent common ancestor (MRCA) of humans lived. To understand these implications, the chapter begins by filling in the historical background: what is the importance of mitochondrial DNA for studies of human evolution? Mitochondrial Eve, as the posited MRCA immediately became known, was first described in 1987, a decade before our debate, and these studies were continuously and widely discussed within and beyond science. I will show how Maynard Smith was aware of this work and, rather by accident, ended up working on related questions, proposing his controversial idea with colleagues in 1999. Tracing the development of the controversy through private and public reactions in science and beyond, closure appears to have been achieved soon after in the early 2000s.

Even though Maynard Smith's direct involvement officially ended with the publications of replies to early criticisms, we will follow the controversy beyond that point and in fact beyond his death in 2004. Firstly, we need to differentiate between the issue of recombination in human and in animal mitochondrial DNA. After the controversy of 1999 which focused on human mtDNA (which was dismissed), Maynard Smith worked on a piece with Noel Smith on recombination in animal mtDNA in the early 2000s[7] – a possibility now acknowledged in several instances. Co-authored with Lindell Bromham, Adam Eyre-Walker and again Noel Smith, he also published a research focus article on 'mitochondrial Steve', commenting on a report which had found paternal mtDNA in a human male.[8] Secondly, even though Maynard Smith's working life has ended, going beyond 2004 will enable us to see that the life of the recombination question has not: scientific controversies can take on the appearance of being dead and buried, and yet occasionally rise back to the surface; the idea of closure is not as straightforward as it looks.

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[6] Eyre-Walker *et al.* 1999b, 2041.
[7] Maynard Smith and Smith 2002.
[8] Bromham *et al.* 2003.

7.2 The history of mitochondria, mitochondrial DNA and mitochondrial EVE

Let us take a closer look at mitochondrial DNA to better understand why the suggestion of recombination would cause such a stir. Mitochondria are also known as the 'powerhouses of the cell' in higher organisms because they handle a cell's energy production. They contain their own DNA, which in mammals 'makes up less than 1% of the total cellular DNA.'[9] The consolidation of our understanding of mitochondria, their origins, and mtDNA is indebted to work done in the 1970s and 1980s by Lynn Margulis.[10]

Margulis – a Darwinist but, as she highlighted, not a neo-Darwinist: 'I've been critical of mathematical neo-Darwinism for years; it never made much sense to me'[11] – was writing as Lynn Sagan when she published 'On the origin of mitosing cells' in the *Journal of Theoretical Biology* in 1967. She argued that

> mitochondria, the (9+2) basal bodies of the flagella, and the photosynthetic plastids can all be considered to have derived from free-living cells, and the eukaryotic cell is the result of the evolution of ancient symbioses.[12]

Although endosymbiosis as an idea was not new when Margulis wrote, her views were not taken up immediately nor unchallenged. On the one hand, there have been challenges to her originality, in parallel to the development of Hamilton's inclusive fitness idea discussed in Chapter 3:

> Margulis' critics were wrong. It is true that the idea of endosymbiosis had been developed and advocated by others long before she did, but the schemes they presented were largely speculations with little if any empirical evidence. Her proposal was not a mere recapitulation of past ideas, but a coherent narrative of the role of endosymbiosis in the origin of eukaryotes, which she developed further than ever before.[13]

Similar to Hamilton, there had been a pre-history of the idea, but Antonio Lazcano and Juli Peretó, from whose historical appraisal of Margulis' paper half a century later the above is taken, point out that it was only her contribution that developed it into something usable.

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[9] 'mitochondrial DNA' 2016.
[10] Smith 2016, 49. That mitochondria contain DNA was published by Nass and Nass in 1963.
[11] Margulis 1995; see also Laczano and Peretó 2017, 84.
[12] Sagan 1967, 226.
[13] Lazcano and Peretó 2017, 82.

However, the endosymbiotic theory was not accepted as readily as Hamilton's ideas; it was considered unorthodox. 'If by 1967 polite biological society was not yet ready to embrace the centrality of endosymbiosis to eukaryotic evolution, after Margulis's paper serious biologists could no longer afford to ignore it.'[14] Today, the central thesis is accepted by many, if not most, scientists – how accepted depends on whom you ask.[15] Maynard Smith was sceptical. In 1987, he wrote to Alan Grafen about a review of Margulis and Sagan – likely 'Order amidst animalcules: the Protoctista kingdom and its undulipodiated cells' (1985) – saying that '[t]he review is ill-tempered, but it does suggest that they are as inaccurate in their treatment of protists as I already knew they were on prokaryotes and higher eukaryotes.'[16] (In the second edition of his textbook *Evolutionary Genetics* he did however cite Margulis on the origins of the eukaryotic cell and on the role of symbiosis in evolution.[17])

Human and mouse mtDNA were fully sequenced by 1981 (mtDNA is much smaller than nuclear DNA; the sequencing of the human nuclear genome was not declared completed until 2003). The inheritance pattern of mtDNA was another point of interest, and by 1999 – when Maynard Smith and others started publishing about recombination as a possible pattern – the consensus had emerged that mtDNA was inherited clonally and maternally: in mitochondria, DNA is passed on, without change, from mothers only to their offspring and no copy of paternal mtDNA is passed on. In contrast, nuclear DNA is inherited from both parents, both of which pass on half of their genetic make-up which recombines when reproductive cells are formed – that is, the genes are re-arranged, and offspring ends up with a combination of characteristics different from that of their parents.

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14 Lane 2017, 58.

15 E.g. Cornish-Bowden 2017, Michod 2005; for a refutation of the endosymbiotic theory, see for example Harish and Kurland 2017. Dawkins (1995) wrote: 'I greatly admire Lynn Margulis's sheer courage and stamina in sticking by the endosymbiosis theory, and carrying it through from being an unorthodoxy to an orthodoxy. I'm referring to the theory that the eukaryotic cell is a symbiotic union of primitive prokaryotic cells. This is one of the great achievements of twentieth-century evolutionary biology, and I greatly admire her for it.'

16 Maynard Smith to Grafen, 2 February 1987. JMSA Add MS 86576. Margulis (1995) said of Maynard Smith and others that they 'come out of the zoological tradition, which suggests to me that, in the words of our colleague Simon Robson, they deal with a data set some three billion years out of date.' What is more, they are missing out on 'four out of the five kingdoms of life. Animals are only one of these kingdoms. They miss bacteria, protoctista, fungi, and plants. They take a small and interesting chapter in the book of evolution and extrapolate it into the entire encyclopedia of life. Skewed and limited in their perspective, they are not wrong so much as grossly uninformed.'

17 Maynard Smith 1998, 318.

This assumption underpinned the birth of mitochondrial Eve. Eve is an idea – though not a name – going back to the 1987 *Nature* paper 'Mitochondrial DNA and human evolution' by Rebecca L. Cann, Mark Stoneking and Allan C. Wilson. Cann and Stoneking had both taken their doctoral degree with Wilson as their supervisor, with Cann having graduated in 1982 and Stoneking (whose PhD was a continuation of Cann's) in 1986. Wilson's biochemistry lab transitioned from working primarily on 'proteins and immunology to restriction enzyme analysis, recombinant DNA work and DNA sequencing' in 1978 and interest in mitochondria grew.[18] (Wilson is also well-known for early work on the relation between humans and chimpanzees.[19])

Cann, Stoneking and Wilson premise their paper on the clonal uniparental inheritance of mtDNA. Nuclear DNA, they wrote, was less useful in studying human genetic history because 'nuclear genes are inherited from both parents and mix in every generation. This mixing obscures the history of individuals and allows recombination to occur.'[20] Their research therefore focused on the examination of mtDNA, derived from the placentas of 147 people of five geographic populations (African, Asian, Caucasian, aboriginal Australian, aboriginal New Guinean). The focus on mtDNA was combined with the idea of the molecular clock. Molecular clocks, first championed by Émile Zuckerkandl and Linus Pauling, are based on the neutral theory of molecular evolution, proposed by Motoo Kimura in the 1960s.[21] In DNA, non-adaptive, or neutral changes, occur at a fairly constant rate and can therefore be used to estimate the time that has elapsed since the divergence of species.[22] Wilson was a pioneer in establishing the use of molecular clocks[23] and based on the combination of mtDNA studies with molecular clocks, he, Cann and Stoneking concluded that '[a]ll these mitochondrial DNAs stem from one woman who is postulated to

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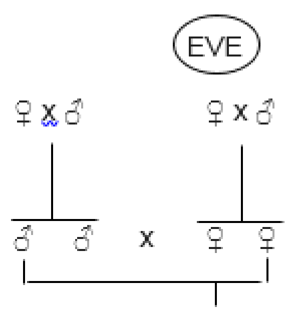
18 Cann 2014, 467.
19 King, M.C. and Wilson, A.C. (1975). Evolution at two levels in humans and chimpanzees. *Science 188*(4184), 107-116.
20 Cann *et al.* 1987, 31.
21 The idea of non-adaptive changes goes counter to the neo-Darwinian view with its strong focus on adaptation. Nevertheless, Maynard Smith was essential to Kimura writing *The Neutral Theory of Molecular Evolution* and Cambridge University Press publishing it (Maynard Smith and Dawkins 1997, https://www.webofstories.com/play/john.maynard.smith/86).
22 'molecular clock' 2016.
23 Cann 2014, 457.

have lived about 200,000 years ago, probably in Africa.'[24] (Therefore some people also talk of "African Eve".)

Maynard Smith had both a copy of the Cann, Stoneking and Wilson paper in revised draft form (as of 16 July 1986) and a copy of the published version.[25] While both are without annotations, the folder includes separate, handwritten notes headed similarly to the article's title: 'Molecular Data & Human Evolution'. (Maynard Smith was aware of Wilson's work at least since 1975; he had both an uncorrected proof of King and Wilson's paper 'Evolution at two levels in humans and chimpanzees' and cited Wilson and colleagues in a 1975 paper.[26]) In his notes, Maynard Smith recapitulated why mtDNA is useful for the study of human evolution: 'easy to get hold of/ 16,500 bp (in mammals)/ Maternal inheritance' (bp = base pairs, a small number compared to the 6 billion base pairs of nuclear DNA per cell[27]). Next to the question, 'Why uniparental inheritance important?', he drew an image indicating sex and recombination.[28] Maynard Smith then broke down Cann and colleagues' paper, concluding that mitochondrial Eve was 'One Woman? NO!', again visualising it. How many Eves had there been? His calculations lead him to a population of 10,000:

> ? How Many?
> The Larger the population, The Longer to a common ancestor.
> Knowing, say, 200,000 years ≡ 10,000 generations.
> Population V. approx = 10,000[29]



[24] Cann *et al.* 1987, 31.
[25] JMSA Add MS 86840/120.
[26] see JMSA Add MS 86840/120 for the proofs; Maynard Smith, J. (1975). Molecular evolution and the age of man. *Nature 253*, 497-498.
[27] Annunziato 2008, 26.
[28] Molecular Data & Human Evolution [1988?]. JMSA Add MS 86840/120.
[29] Cann, Stoneking & Wilson Nature 325 (1987) [1988?]. JMSA Add MS 86840/120.

Lastly, Maynard Smith wondered, 'Was "EVE" in AFRICA???', but did not spell out his conclusion on that topic. Nonetheless, his notes show that he was following the development with interest and tried to clarify the research for himself. His putting Eve in quotation marks also illustrates scepticism, one that links well to the implications of that name. In fact, 'Eve' was not chosen by any one of the original research team but first appears in Jim Wainscoat's commentary on the article: 'A paper by R. L. Cann, M. Stoneking and A. C. Wilson on page 31 in this issue reports that Eve was alive, well and probably living in Africa around 200,000 years ago.'[30] From there, it took on a life of its own; it was repeated, for instance, in the *Science* research news article 'The unmasking of mitochondrial Eve' by Roger Lewin[31] and in the following year in the magazine *Newsweek* cover which headlined with 'The Search for Adam & Eve'.[32] Wilson did not like the term, understandable given the biblical connotations and the fact that creationists picked up on it readily. As Linda Maxson, whom Maynard Smith contacted in his quest to gather material for Wilson's memoir (Wilson had died suddenly of leukaemia in 1991, aged 56)[33] and who had worked in Wilson's lab, wrote:

> Much of what Allen [*sic*] did created 'a stir' of excitement and always seemed to raise some consternation – from his earliest work on humans and chimps to his latest work using PCR to address questions of the origin of humans and 'mitochondrial Eve'; a name he always disliked.[34]

The name Wilson preferred was 'lucky mother', 'to emphasize that there had to be such a person, but it was pure chance who it would be.'[35]

In 1991, the year of Wilson's premature death, the proposal of mitochondrial Eve was still being debated. Tracing Eve as the MRCA of all anatomically modern humans to Africa meant a refutation of the multiregional model of human origins which was – and to various

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30 Wainscoat 1987, 13.

31 Lewin 1987.

32 Tierney, J. (1988). The search for Adam & Eve. Scientists explore a controversial theory about man's origins. *Newsweek 111*, 46-52.

33 Maynard Smith had been collecting a file on Allan Wilson because he had originally agreed to write a memoir of Wilson for the Royal Society.[33] Much material – photocopies of newspaper articles on the "Eve" research and following accolades, but also obituaries, many in draft form by, among others, Rebecca Cann and Gunther Stent – had been forwarded from the University of Berkeley (Kelley Thomas to Maynard Smith, 15 July 1992. JMSA Add MS 86725). Ultimately however, the published biographical memoir (2014) was written by Cann.

34 Maxson to Maynard Smith, 22 September 1992. JMSA Add MS 86725.

35 Lake to Friends, Relatives and Family of Allan Wilson, 24 July 1991. JMSA Add MS 86725.

degrees still is – held next to the 'Out of Africa' model. The discovery of Eve meant that we humans are all descendent from one common ancestor, rather than the result of different groups of humans evolving in different regions. (At least one problem was that, until the 1980s, human evolutionary history had been the prerogative of anthropology and palaeontology before molecular biology and population genetics started to take a closer interest too. As Venla Oikkonen wrote in her analysis of mitochondrial Eve, mtDNA was part of yet another controversy 'between paleontology and population genetics over what should count as evidence in the study of human evolution.'[36])

7.3 The history of the recombination challenge

But how did Maynard Smith get interested in mitochondrial DNA and recombination in the first place? We know he took an interest in the research of Wilson and his team since at least the 1970s, and engaged directly with the paper that postulated the MRCA of modern humans as having lived in Africa approximately 200,000 years ago. But taking an interest does not necessitate starting research in the same area. In fact, Maynard Smith never intended to start working on mitochondrial DNA and its properties; his involvement rather came about by accident.

Towards the end of his career he had turned to working on bacteria. Bacterial genetics had been a field in which his wife Sheila, a trained mathematician who had worked as an engineer and a human geneticist before moving into bacterial genetics, had been active until her retirement of the University of Sussex.[37] Her laboratory was in the same corridor as that

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[36] Oikkonen 2015, 752.

[37] Charlesworth 2004, 1105. Maynard Smith on his wife's work: 'she's not an engineer – I'm not allowed to say she's a mathematician, because she's – actually, it's quite true, she's not a mathematician, but she took her first degree in mathematics. And if you took a degree in mathematics and it was wartime, you were employed as an engineer. And she sort of picked up the engineering on the way. And then she had a biggish break for producing kids, you know. Then, when, you know, the youngest was old enough to go to nursery to be looked after and so on, she wanted to get back into some sort of work and actually worked in human genetics, at University College, which was nice because... I mean, she wasn't working directly for Haldane but she was working for Haldane's colleague, Lionel Penrose, and we were all in the same department, so that was a good relationship. And then, when we came down here, there's no medical school, and there was no way she could go on being a human geneticist. You can't be a human geneticist without a medical school because you can't let blood out of people, even, you know, unless you've got a medical colleague. And I had this colleague, Neville Simons, who was working on bacterial genetics, and so Sheila decided to become a bacterial geneticist. If you can add and subtract, you can do anything in science, I believe' (Maynard Smith and Dawkins 1997, https://www.webofstories.com/play/john.maynard.smith/80).

of Brian Spratt, an expert in bacterial populations and evolutionary biology. Spratt 'came frequently into contact with John as he waited for Sheila to finish work. Sometimes, he would wander into [Spratt's] laboratory to see what was going on.'[38] Their collaboration, starting in 1988 when Spratt asked Maynard Smith to look at some data and to say whether he agreed with the interpretation, would last over ten years.[39] 'For the past two years,' Maynard Smith wrote to Roger Milkman, whom he had met during his time in Chicago, 'I have been getting increasingly interested in bacterial evolution – mainly because my colleague, Brian Spratt, has been collecting fascinating data on the evolution of penicillin resistance in *Pneumococcus* and *Neisseria*.'[40] Spratt recalls that Maynard Smith, '[a]lthough very aware of the importance of sequence data to evolutionary biology,' had probably never 'really looked at DNA sequences before, but he soon became fascinated by them, and was never happier than when he received a new set of interesting sequences to puzzle over.'[41] This newly acquired knowledge of working with DNA sequences would become vital for the work on mitochondrial DNA in the late 1990s. Interest in recombination is already visible in the work on bacteria. The work Maynard Smith did with Spratt and other bacterial population geneticists led to the 1993 paper, 'How clonal are bacteria?'[42] – a title that would be echoed in the 1999 'How clonal are human mitochondria?'[43] This 1993 paper showed that there was 'much more exchange of genetic information among bacterial cells in nature than was formerly believed.'[44] Indeed, the belief that there were only low rates of recombination in bacterial pathogen populations had become somewhat of a dogma by the late 1980s.[45] Thus 'Maynard Smith first discovered potential evidence of recombination in mitochondria during his work on recombination in bacteria.'[46]

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[38] Spratt 2004, 297.
[39] Spratt 2004, 297.
[40] Maynard Smith to Milkman, 6 December 1990. JMSA Add MS 86751.
[41] Spratt 2004, 298.
[42] Maynard Smith, J., Smith, N.H., O'Rourke, M. and Spratt, B.G. (1993). How clonal are bacteria? *Proceedings of the National Academy of Sciences of the United States of America 90*(10), 4384-4388.
[43] Eyre-Walker, A., Smith, N.H. and Maynard Smith, J. (1999a). How clonal are human mitochondria? *Proceedings of the Royal Society of London B 266*(1418), 477-483.
[44] Charlesworth 2004, 1109.
[45] Spratt 2004, 298.
[46] Eyre-Walker 2000, 1573.

Bacteria, clonality, and linkage disequilibrium are a constant theme in his research notes throughout 1990s.[47] Undated notes in a folder generally containing work from the early to the mid-1990s are titled, 'How to measure clonal structure', describing a method based on 'multi-locus electrophoresis of bacterial populations'. (Electrophoresis is a way of separating molecules by size, used frequently in DNA analysis.) Maynard Smith concluded that 'there seems to be no generally accepted measure of "clonality" – i.e. the departure from random assortment.'[48] Linkage disequilibrium (LD) is a possibility, used by others, and Maynard Smith drew up computer programs to test several assumptions, simulating whether LD could be used as an indicator for clonality. Linkage disequilibrium is opposed to linkage equilibrium (the 'complete random assortment from what genes you have at different loci'[49]) and 'means simply a nonrandom association of alleles at two or more loci'. The concept is important in evolutionary biology and human genetics because

> throughout the genome [it] reflects the population history, the breeding system and the pattern of geographic subdivision, whereas LD in each genomic region reflects the history of natural selection, gene conversion, mutation and other forces that cause gene-frequency evolution. How these factors affect LD between a particular pair of loci or in a genomic region depends on local recombination rates. The population genetics theory of LD is well developed and is being widely used to provide insight into evolutionary history and as the basis for mapping genes in humans and in other species.[50]

LD can be measured through an 'index of association' or I_A, as Maynard Smith suggested in the 'How clonal are bacteria' joint paper with Noel H. Smith, Maria O'Rourke and Brian G. Spratt.[51] That method was tried by several researchers from around the world, who unfortunately had trouble with it. Jacqui Shykoff and Erika Bucheli, for instance, wrote:

> We have a problem. We are pondering the intricacies of linkage analysis and degree of clonality. We are struggling with your paper from 1993. Long ago […] you told me that if one does not understand something that someone else is explaining, one

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[47] E.g. JMSA Add MS 86722: Clonality (1992-96) or JMSA Add MS 86751: How Clonal? [bacteria] (1990-94).
[48] 'How to measure clonal structure', undated. JMSA Add MS 86722.
[49] Maynard Smith and Dawkins 1997, https://www.webofstories.com/play/john.maynard.smith/73.
[50] Slatkin 2008, 477.
[51] Maynard Smith *et al.* 1993; see also JMSA Add MS 86724.

> should consider this the responsibility of the one doing the explaining. This is a challenge.[52]

Maynard Smith replied, wondering where the error may be: it could be his program, or the formula, but he could not find the error so offered a third option: 'iii) There is a glitch in the universe. This seems to me increasingly likely.'[53] He ultimately wrote to Mark Feldman from whose work he and his colleagues had taken their starting point, asking for clarification on his end and mentioning that the suggested measure was 'becoming a popular way of measuring the effects of recombination in bacteria',[54] but by 1995 Feldman had not yet got back to Maynard Smith.[55]

These troubles notwithstanding, Maynard Smith and his colleagues produced 'pioneering work' with bacteria.[56] And this work is not so far away from Maynard Smith's previous research interests as it might appear; Maynard Smith had worked on sex and recombination and their role in evolution earlier in his career. The 'problem of discerning the evolutionary advantages of sexual recombination' had been with Maynard Smith from early on.[57] At least from the 1970s onward, recombination came up again and again in his work, both in papers and less specialist works such as *The Problems of Biology* (1986). The shift from bacteria to mitochondrial DNA took place thanks to work with Noel Smith, who had been one co-author on the 'How clonal are bacteria?' paper.[58] Since 1996, Maynard Smith and Smith had been working on a way to detect recombination from gene trees, as part of which they designed the homoplasy test.[59] The homoplasy test

> determines if there is a statistically significant excess of homoplasies in the phylogenetic tree derived from the data set, compared to an estimate of the number of homoplasies expected by repeated mutation in the absence of recombination. An excess of homologies is considered a hallmark of recombination.[60]

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52 Shykoff and Bucheli to Maynard Smith, 7 September 1994. For other inquiries on the method, see Lan to Maynard Smith, 26 August 1994, Lomholt to Maynard Smith, 10 November 1994, or Maynard Smith to Haubold, 2 August 1995. JMSA Add MS 86724.
53 Maynard Smith to Shykoff and Bucheli, 28 September 1994. JMSA Add MS 86724.
54 Maynard Smith to Feldman, 19 October 1994. JMSA Add MS 86724.
55 Maynard Smith to Haubold, 2 August 1995. JMSA Add MS 86724.
56 Michod 2005, 4.
57 Karlin 2005, 3.
58 Eyre-Walker 2000, 1573.
59 Maynard Smith and Smith 1998.
60 Maynard Smith and Smith 1998, 590.

In other words, a homoplasy is a repeated event, a character that is present in a set of species, but not in their common ancestor, that is, the character – for instance, powered flight – has evolved independently.[61] Homoplasies are usually caused by mutation or recombination in the DNA, and can be

> as simple as single DNA monomer changes […], or as complex as the independent reorganization of multiple systems with numerous genes and body parts to converge on a solution (as in the case for powered flight in birds and bats). In both cases, however, we can determine that they arose as independent events on separate lineages because these features do not fit onto the species tree as unique events.[62]

Let us look at an example for a DNA sequence homoplasy, since that will feature largely in the controversy. A DNA sequence homoplasy might be the following: suppose you have three species A, B, and C, with the DNA sequences TGATCC, TCATCC, and TCATCC respectively. Assuming additional information that A and B are closer related than B and C, and that additional data strongly suggests that the sequence in the common ancestor is TTATCC, the need arises to explain the changes in the second position of the sequences of A, B, and C. For the outlined information, the most parsimonious tree (basically, the simplest one with the given data – cf. Occam's razor[63]) would look as follows:

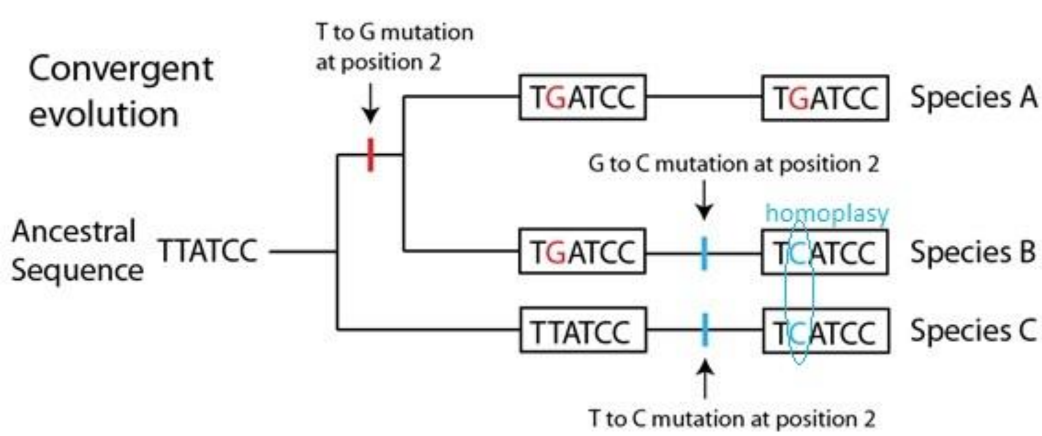

Figure 26. Homoplasies

[61] In contrast, a homology would be a character shared by a set of species which is present in those species' common ancestor (Ridley n.d., 'Homoplasies').
[62] Venema 2013.
[63] See for instance Maynard Smith 1998, 300.

The C's at the second position in species B and C are homoplasies, because they evolved independently and were not present in the common ancestor. In this example the homoplasies were caused by mutations: first, the T at position 2 of the ancestral sequence mutates into a G on the branch with Species A and B. Then, another mutation occurs at position 2 of both the sequences of the more recent ancestors of Species B and C. The G of Species B and the T of Species C both mutate into a C. Consequently, we now have a shared characteristic – C – that was not present in the two species' common ancestor.

If we now return to the homoplasy test developed by John Maynard Smith and Noel Smith, we better understand what the test actually does. A dataset would be sequences of DNA – or, in our case study, mtDNA – which are compared with regard to their number of homoplasies. In the above example, the homoplasies were caused by mutation, and mutation rates can be estimated. Thus, a number of homoplasies occurring in the absence of recombination can be estimated too and then be compared to the actual number:

> The test tries to determine if there is a statistically significant excess of homoplasies […] derived from the dataset, compared to an estimate of the number of homoplasies expected by mutation in the absence of recombination. An excess of homoplasies is likely to have been brought about by recombination. The test requires at least six sequences containing at least ten 'informative sites' (sites at which the rarer of two alternative bases is present at least twice). A 'homoplasy ratio' is calculated which should range from zero, for a clonal population, to one, for a population under free recombination.[64]

In acknowledgement of the digital age, the test was shared on Maynard Smith's website which was, however, prefaced by, 'Please note – I cannot be contacted here.'[65] The website contained a readme.txt file explaining the purpose and method of the test (apologising for its having been written in the language QBASIC: 'sorry!'). The accompanying paper was published later that year in *Molecular Biology and Evolution.*

To be sure their test worked, Maynard Smith and Smith wanted to do a negative control and 'check [their] method on something that did not recombine.'[66] The decision fell onto human mitochondrial DNA. After all, the clonality of mtDNA was a well-known and

[64] Jolley 2000. 'Homoplasy Test'. Retrieved 19 January 2017 from https://pubmlst.org/software/analysis/start/manual/homoplasy_test.shtml.
[65] John Maynard Smith's Home Page, 30 April 1998. JMSA Add MS 86717.
[66] Eyre-Walker 2000, 1573.

widely established fact. In fact, looking at Maynard Smith's own textbook on *Evolutionary Genetics*, the second edition of which had just been published, we read on mitochondrial DNA: 'To a population geneticist, its most interesting characteristic is that it is maternally inherited'![67] But as an undated draft manuscript titled 'The problem' revealed, first doubts were being sown in the mid to late 1990s: in the sub-section 'Comment on Data', Maynard Smith noted:

> ii) The observed data differ qualitatively in the way we expect: Neisseria is known to have a lot of recombination: E. coli is thought to have some: Mitochondria are thought to have none at all. It would be an important discovery if it could be shown that there is recombination in mitochondria. BUT this is not what we were looking for: we were looking for a 'control'![68]

7.4 The controversy around the mtDNA and mtEVE question

The wider scientific world became aware of Maynard Smith and his colleagues' research – he had drawn in Noel Smith, co-author of the homoplasy test paper, and Adam Eyre-Walker – with the publication of 'How clonal are human mitochondria?' in March 1999. They had concluded that 'it seems possible that there is recombination between mitochondrial lineages and that the inheritance of mitochondria is not clonal.'[69] In the same journal, *Proceedings of the Royal Society of London B*, Erika Hagelberg and colleagues published the results of an empirical study conducted with mtDNA sequences from island Melanesia and suggest that '[a]lthough at odds with current dogma on mtDNA inheritance, paternal contribution and genetic recombination are possible explanations for the phenomenon observed in Nguna.'[70]

What are the implications of these suggestions? They were pointed out by the authors themselves: by questioning the clonality of human mtDNA, they questioned analyses and conclusions made premised on this assumption. In particular, assumptions about the origin of anatomically modern humans and the age and existence of our MRCA, mitochondrial Eve, are challenged. '[R]ecombination,' said Hagelberg and colleagues, 'would perturb

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[67] Maynard Smith 1998, 151.
[68] 'The Problem', undated. JMSA Add MS 86724.
[69] Eyre-Walker *et al.* 1999a, 477.
[70] Hagelberg *et al.* 1999, 490.

estimates of the time of divergence of mtDNA types, raising questions about the suggested time and mode of recent human evolution.'[71] Eyre-Walker and colleagues concluded much the same:

> Mitochondrial DNA has been used extensively in the study of human evolution. In many of these analyses the clonality of mitochondria has been either explicitly or implicitly assumed […]. It is clear that many of these conclusions will have to be treated with caution or reassessed. It certainly seems dangerous to assume that mitochondria are clonal when there is evidence against and no evidence in favour of such a conjecture.[72]

On a different level, 'the occurrence of recombination would cast doubts on the labelling of some mtDNA control region nucleotide positions as mutation hotspots.'[73]

It is worth returning to the assumption that mtDNA is inherited clonally and looking at it more closely. In a set of typewritten notes titled 'What can mtDNA tell us, and does recombination matter?' (undated), John Maynard Smith briefly tackled two main questions: the origin of *Homo sapiens* and the migration of human populations.[74] He first set out the necessary conditions for speaking of a "'time of origin", T': T only existed if changes in a population occurred within a limited period of time, with the descendants of that population being reproductively isolated from other hominins.[75] Any gradual changes or interbreeding (which would result in recombination) would mean there is no specific time of origin.[76] Next Maynard Smith brought in mitochondrial Eve. He pointed out that for Eve to have existed, the defining characteristics of *Homo sapiens* not only needed to have arrived in a short period of time but also in a small (bottleneck) population of, 'say, 10,000'.[77] (10,000 is the same number he had come up for the original population in his

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[71] Hagelberg *et al.* 1999, 490.
[72] Eyre-Walker *et al.* 1999a, 482.
[73] Hagelberg *et al.* 1999, 490.
[74] Maynard Smith, undated. JMSA Add MS 86697A.
[75] Hominids in the original; the terminology in anthropology has changed in light of a reclassification of hominoids (humans and all apes): 'the term *hominid*, which has been used for decades to refer to our specific evolutionary lineage, has a quite different meaning in the revised classification; now it refers to *all* great apes and humans together.' *Hominin*, in contrast, is now exclusively referring to 'us', the bipedal hominoids (Jurmain *et al.* 2013, 200).
[76] Maynard Smith, undated. JMSA Add MS 86697A. In parenthesis, Maynard Smith remarked: 'The assumption that there is an event to date is a relict of religious/typological thinking'.
[77] Maynard Smith, undated. JMSA Add MS 86697A. He added: 'If the changes occurred in a large population, then Eve could have been an ape, or a tree shrew.'

notes on Cann *et al*.'s paper from the late 1980s; see above.) At this point recombination and mtDNA become relevant:

> If mitochondria recombine, so that Eve never existed, we can still ask the "date of human origin", *T*, provided such an event ever happened. Mitochondrial (or other DNA) data are useful only because they help us date the bottleneck.[78]

Without negating the utility of mtDNA analyses in studies of the human evolution, Maynard Smith called attention to what exactly we can learn from them while being conscious of not having a definite answer on the issue of recombination. He did, however, seriously doubt the existence of mitochondrial Eve and surely would not have, had he lived, congratulated her on her thirtieth birthday in 2017. Indeed, he was ready to bury her at twelve: 'I'm back from "holiday", and have got your draft,' he wrote to Philip Awadalla on 30 July 1999. 'I'm delighted with it – it really is the last nail in Eve's coffin, I think.'[79]

A first hint of how the papers were going to be picked up by the scientific community is visible in the developments following their initial submission to *Nature*. The journal not only took its time reaching a decision – with Eyre-Walker and colleagues' paper going through revision twice – but ultimately rejected them both on the basis of highly unfavourable reviews. A letter Maynard Smith sent to *Nature*'s manuscript assistant shows he was increasingly annoyed by the journal and one of the referees, who was requesting additional information on the method used. (This was already the second round of review; Maynard Smith had got the first rejection of the paper on 17 March 1998.[80]) Enclosing a copy of a paper explaining and describing the statistical method used, Maynard Smith could not

> resist adding that I am getting a bit fed up both with Nature and your referee. The referee could have found our method paper by looking in his library, and it would take him about twenty minutes to type the data in Table 1 into his computer if he

78 Maynard Smith, undated. JMSA Add MS 86697A.
79 Maynard Smith to Awadalla, 30 July 1999. JMSA Add MS 86697B. There are at least two other people who will not have congratulated Eve on her 30th birthday: Brad Harrub and Bert Thompson wished to bury her aged sixteen (Harrub and Thompson 2003).
80 Howlett to Maynard Smith, 17 March 1998. JMSA Add MS 86697B.

> really feels a need to reanalyse them. Could it be that he is reluctant to accept our conclusions?[81]

As it turned out, he was, and so was the second referee. The paper of Maynard Smith and his colleagues had in fact been in the review process for so long that he added,

> Nature has had, for some months now, two papers, completely independent, claiming that human mitochondria recombine, using different data, and different methods of analysis. It is really time you publish them.[82]

This second paper had been sent to *Nature* by Erika Hagelberg, having been encouraged by Maynard Smith to do so. The referees' comments on both 'How clonal are human mitochondria?' and 'Evidence for mitochondrial DNA recombination in a human population' point to a certain feeling of uncomfortableness, visible in the 'substantive concerns'[83] and '[serious] criticisms'[84] directed towards the conclusions. Ultimately, both papers were rejected by *Nature* in 1998.[85]

On 7 March 1999, another journal (the *Proceedings of the Royal Society*) finally published the two papers. Comments and reactions followed almost immediately. The news sections of two of the most prestigious academic journals, *Science* and *Nature,* picked up on the studies. *Science* had already published a special issue on 'new work on the biology of mitochondria [which] suggests that their evolution may be more complicated than researchers had suspected' on 5 March.[86] In her overview, Evelyn Strauss dealt, among other issues, with the 'riddles of recombination'. She quoted both Adam Eyre-Walker and Erika Hagelberg on their research. *Nature* declared that 'Fathers can be influential too' on 18 March 1999.[87] On 11 March, the *Guardian* published a small piece titled 'A little bit of Adam'. The teaser quote was naturally drawing on the more sensational implication of the research – 'Our view of our relationship to the Neanderthals may be revised' – but in general it gave a good

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[81] Maynard Smith to Hodges, 8 July 1998. JMSA Add MS 86697B.
[82] Maynard Smith to Hodges, 8 July 1998. JMSA Add MS 86697B.
[83] Howlett to Maynard Smith, 17 March 1998. JMSA Add MS 86697B.
[84] Howlett to Hagelberg, 29 July 1998. JMSA Add MS 86697B.
[85] Howlett to Maynard Smith, 29 July 1998, and Howlett to Hagelberg, 29 July 1998. JMSA Add MS 86697B.
[86] Strauss 1999, 1435.
[87] Lawrence 1999.

summary of the research done.[88] Similarly, the *New Scientist* published a note on 13 March. Like the *Guardian*, they did not open with the question of recombination but with the implications for human evolution: 'Mitochondrial Eve, from whom all women are descended, is twice as old as we thought.'[89]

These translations from specialist to non-specialist science reflect wider interest in the topic, although perhaps less so for the details. The *Guardian* publication is the strongest indicator for this; the *New Scientist* is a popular science magazine one would expect to report on new and interesting scientific developments. *Science* and *Nature,* of course, are academic journals in their own right. Their picking up of the story highlights the newsworthiness of the research within science itself. Some of these stories already hinted at the controversy to follow. The *New Scientist* quoted evolutionary geneticist Laurence Hurst as saying, 'These papers are going to create some waves'.[90]

These waves were more visible by May of 1999. Most of the initial back and forth took place backstage before the actors made their arguments public by publishing. On 4 May, Vincent Macaulay wrote a letter to Maynard Smith. He pointed out a likely problem in the data and sent the draft of a short response to 'How clonal are human mitochondria?' which he had written with Martin Richards and Bryan Sykes. Sykes remembers this letter as the result of an 'emergency meeting' called because of the tremendous implications Maynard Smith's paper had for Sykes' research: 'Something had to be done.'[91] Macaulay had checked the sequence data from the paper; '[i]ncredibly, a lot of them were wrong' and 'it was obvious that the force of the theoretical argument for recombination was seriously diluted. We wrote at once to Maynard Smith […].'[92] The letter is very cordial; Macaulay and his colleagues would not only 'be very interested to hear your comments' but also, 'if you like it, wonder whether you, and Drs Eyre-Walker and Smith, would like to be co-authors?'[93] Maynard Smith replied promptly, agreeing on the problematic nature of the data: 'I believe

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[88] Jones 1999 in JMSA Add MS 86697A.
[89] Day 1999.
[90] Day 1999.
[91] Sykes 2001, 162.
[92] Sykes 2001, 163.
[93] Macaulay to Maynard Smith, 4 May 1999. JMSA Add MS 86697B.

that Adam has told you that we already realized that the MZ data are suspect. Luckily for us, additional sequences have since been published.'[94] He and his colleagues were in fact in the process of analysing this new set of data to check their claims. This, he informed Macaulay, would take a few weeks so it might be best to publish two separate papers, both in *Proceedings*.

> Yours could be very much as it stands (I like the title!), although we would show you our MS so that you could make any changes that you wanted. Ours would say 1) that we agree with what your say, and 2) that additional data support our original claim for recombination. How does that strike you?

Maynard Smith concluded by mentioning that he was also looking at other ways to test for recombination in mitochondrial DNA. In the hope of finding a way to avoid errors, or being misled by errors in data, he and his colleagues were seeing how useful an analysis of linkage disequilibrium is. This research – a cooperation between Philip Awadalla (then a PhD student at Edinburgh), Adam Eyre-Walker (Maynard Smith's post-doc with a grant of the Royal Society) and John Maynard Smith himself – was to enter the controversy in December 1999.[95]

The title that Maynard Smith so liked claimed 'Mitochondrial DNA recombination—no need to panic'. By then, the suggestion of recombination had not generated much heat – publicly, that is. The referees' reports referred to earlier had, of course, already put quite some criticisms forward. Macaulay and colleagues submitted their draft to *Proceedings* in June, followed by a submission of the reply by Eyre-Walker and colleagues. Around the same time, end of June, a letter appeared in *Science*. Taking Strauss's overview as a starting point, Peter Arctander briefly summarised Eyre-Walker and colleagues' paper and took offense at the following:

> The high number of homoplasies claimed by the authors might well be an artifact of the analysis applied.[96] An answer to the important question of mitochondrial

[94] Maynard Smith to Macaulay, 6 May 1999. JMSA Add MS 86697B. The problematic data set was a series of mtDNA sequences published by Marzuki and colleagues in 1991. Eyre-Walker, Smith and Maynard Smith had copied one position wrongly from this set for their own analyses; in addition, 'there are several peculiarities in the sequences from the Marzuki *et al.* (1991) data set […]. It seems likely that these sites have been mis-sequenced' (Eyre-Walker *et al.* 1999b, 2041; cf. Macaulay *et al.* 1999, 2037).
[95] Awadalla *et al.* 1999.
[96] A 'fundamental principle of their tree construction algorithm is that hypothetical ancestral types at nodes of the tree are all extinct. There is no reason to believe that this is a valid assumption for populations in general, and specifically in the case of humans' (Arctander 1999, 2091).

> recombination is likely to stem from the application of more appropriate analytical tools to the now very large database of human mitochondrial sequences.[97]

In August, Andrew Merriweather and Frederika Kaestle agreed 'that these are improbable suggestions.' They had gone even further and done some estimations of their own, which in their view support that there is 'little evidence for recombination.'[98]

So the first researchers began to publicly voice their doubts about the possibility of recombination. Meanwhile Maynard Smith was working on strengthening the case against strict clonality. The work with Awadalla and Eyre-Walker was coming along nicely; they had found the 'last nail in Eve's coffin.'[99] Their paper was published in December 1999. (Even before they had replied to Macaulay and colleagues' criticisms and assurance that there is 'no reason to panic' by saying that there are, in fact, 'reasons to panic.'[100]) It used the analysis of linkage disequilibrium in human and chimpanzee mitochondrial DNA to support recombination. Since they found that LD is declining as a function of the distance between the sites in humans and chimpanzees, genetic recombination seems to be taking place. Mitochondrial DNA, therefore, undergoes genetic recombination. One suggested pathway for this to happen is paternal leakage: an amount of paternal mtDNA can enter and briefly survive in an egg, making recombination possible. A second pathway is possible recombination with copies of mtDNA sequences in the nuclear genome.[101] The question of pathways is one to return in later papers by Eyre-Walker, one of which is co-authored by Awadalla, with paternal leakage being the most likely.[102]

By 2000, the controversy had taken off and we have two levels to consider. First, it turned out that Hagelberg and colleagues had misaligned their sequences by ten nucleotides (in order to compare the sequences of the various test groups, they need to be aligned against a reference sequence in order to spot changes; see Figures 27 and 28) and they needed to correct their findings. Figure 27 shows the original alignment of sequences in the

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97 Arctander 1999, 2090.
98 Merriweather and Kaestle 1999, 837.
99 Maynard Smith to Awadalla, 30 July 1999. JMSA Add MS 86697B.
100 Macaulay *et al.* 1999; Eyre-Walker *et al.* 1999b.
101 Awadalla *et al.* 1999.
102 Eyre-Walker 2000; Eyre-Walker and Awadalla 2001.

1999 paper; Figure 28 shows the corrected alignment from 2000, each highlighting the position that seemed to show clear evidence for recombination.

> The previously described C to T substitution at position 16 076 corresponds to a T to C substitution at 16 086. The individuals thought to carry the rare mutation at 16 076 are in fact identical to the reference sequence at this position.[103]

The evidence had thus been an artefact of erroneous data and could no longer be used as such.[104] To Hagelberg's irritation, her work was subsequently reduced to the mistake and hardly anyone seemed to take into consideration that not all phenomena could be explained by the misalignment and thus the possibility of recombination was not off the table.[105] She published an opinion piece to that effect in 2003, pointing out that 'some of the anomalies have no satisfactory explanation.'[106]

	mtDNA position																												
	41	76	83	129	140	148	176	182	183	189	217	223	241	245	247	261	263	265	266	270	294	311	318	342	343	355	357	362	
	reference sequence																												
	A	C	T	G	T	C	C	A	A	T	T	C	A	C	A	C	T	A	C	C	C	T	A	T	A	C	T	T	*n*
haplogroup I		**T**						C	C	C	C				G	T													3
haplogroup II				A		T						T																C	17
	G			A		T						T																C	2
				A		T						T														T		C	4
		T		A	C	T						T																C	2
		T				T						T									T		T					C	1
		T	C	A		T							G				C	C				C		C	G				1
haplogroup III		**T**					T												T	T							C		8
		T					T												T								C		1
		T					T							T					T								C		1
other		**T**							C	C		T									T								1

Figure 27. Hagelberg et al. *1999, 488.*

103 Hagelberg *et al.* 2000, 1595f.
104 Hagelberg *et al.* 2000; see also Hagelberg to Maynard Smith, 8 February 2000. JMSA Add MS 86699.
105 Hagelberg to Maynard Smith, 8 February 2000. JMSA Add MS 86699.
106 Hagelberg 2003, 84.

	mtDNA position (minus 16 000)																														
	51	86	93	129	140	144	148	176	182	183	189	217	223	241	245	247	261	263	265	266	270	291	294	311	318	342	343	355	357	362	422	*n*
reference sequence	A	T	T	G	T	C	C	C	A	A	T	T	C	A	C	A	C	T	A	C	C	C	C	T	A	T	A	C	T	T	T	—
haplogroup I	.	.	.	.	.	.	.	.	C	C	C	C	.	.	.	G	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3
haplogroup II	.	C	.	A	.	.	T	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	17
	.	C	.	A	.	.	T	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	C	.	4
	G	C	.	A	.	.	T	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	2
	.	.	.	A	C	.	T	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	2
	.	.	.	.	.	.	T	.	.	.	.	.	T	.	.	.	.	.	.	.	.	T	.	.	T	.	.	.	.	C	.	1
	.	.	C	A	.	T	T	.	.	.	.	.	.	G	.	.	.	C	C	.	.	.	.	C	.	C	G	.	.	.	.	1
haplogroup III	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	T	T	.	.	.	.	.	.	.	C	.	C	8
	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	C	.	C	1
	.	.	.	.	.	.	.	T	.	.	.	.	.	.	T	.	.	.	.	T	.	.	.	.	.	.	.	.	C	.	C	1
other	.	.	.	.	.	.	.	.	.	C	C	.	T	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	1

Figure 28. Hagelberg et al. *2000, 1595.*

Second, turning to Maynard Smith *et al.*'s work, *Science* had published several criticisms directed towards recombination in general, but with a response by Awadalla, Eyre-Walker and Maynard Smith, under the title 'Questioning evidence for recombination in human mitochondrial DNA.'[107] Prior to the publication in June, drafts of the single pieces had been circulated backstage. Taking these and the replies and comments on them, as well as the published versions together, we can roughly group the criticisms into two categories. The first of those takes up issues of methodology: choice of data, errors in data and/or analysis of data, choice of analytical tools, and consistency/replicability of tests.[108] Criticisms in this category, at least at first glance, should be possible to address without there being much room for discussion. The second category, on the other hand, is less straightforward, covering criticisms relating to interpretation: interpretation of the significance of results, detached from how they were come by. In a controversy both types of criticism are equally difficult to resolve. To use the terminology developed by Harry Collins, we are confronted with the interpretative flexibility of scientific findings: 'scientific findings are open to more than one interpretation.'[109] As a result experiments, by themselves, are not able to decide a controversy. The approach to scientific controversies Philip Kitcher calls the rationalist approach, proposing that 'scientific controversies are ultimately settled by experimentation,

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[107] Kivisild, T., Villems, R., Jorde, L.D., Bamshad, M., Kumar, S., Hedrick, P., … Maynard Smith, J. (2000). Questioning evidence for recombination in human mitochondrial DNA. *Science 288*(5473), 1931.
[108] Kivisild *et al.* 2000; JMSA Add MS 86699.
[109] Pinch and Bijker 1989, 27.

evidence and the exercise of reason',[110] thus does not work in this context: once the definitions of not only test results but also the tests themselves are called into question and discussed, you need a criterion 'independent of the output of the experiment itself' to decide.[111]

But what is it that Maynard Smith himself and other proponents of recombination were putting out to defend recombination? They point, for instance, to circular argumentation in the criticisms.

> In essence there is an error in the logic in their argument: they implicitly assume that recombination does not occur in estimating their tree, so they cannot use the tree to argue that there is no recombination, as they do. The most obvious property of the tree is the number of homoplasies it contains; homoplasies can only be produced by recombination or multiple mutation.[112]

They also kept pointing to the need to consider recombination – a need which their opponents simply did not see due to their interpretation of the situation.[113] After the publication of a 2002 paper that reported paternal leakage in a human male, they returned to the controversy and introduced 'Mitochondrial Steve' in 2003.[114] While they agreed that the case study did not definitively prove recombination, they reiterated their conviction that the *possibility* needed to be seriously taken into consideration: 'Now that we know that paternal inheritance of mitochondria can occur in humans, we should to look for it wherever comparison of parent and offspring mtDNA is possible.'[115]

Maynard Smith and Smith also turned to animal mitochondrial DNA and whether recombination might be possible there with work done between 2001 and 2002. In 2001, Emmanuel Ladoukakis and Eleftherios Zouros had published a paper in *Molecular Biology and Evolution* claiming animal mtDNA showed signs of recombination, using Eyre-Walker *et al.* and Awadalla *et al.*[116] (The animals in question were *Gammarus* [crustaceans]*, Rana* [frogs] and *Apodemus* [rodents].) Maynard Smith and Smith wrote a reply, re-analysing the paper.

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110 Kitcher 2000, 21.
111 Collins and Pinch 2004, 98; compare 'experimenter's regress'.
112 Reply to Kumar *et al.* (undated draft). JMSA Add MS 86699.
113 Eyre-Walker *et al.* 1999a and 1999b; Awadalla *et al.* 1999; Eyre-Walker 2000; Eyre-Walker and Awadalla 2001; Hagelberg 2003.
114 Bromham *et al.* 2003.
115 Bromham *et al.* 2003, 4.
116 Ladoukakis, E.D. and Zouros, E. (2001). Recombination in animal mitochondrial DNA: evidence from published sequences. *Molecular Biology and Evolution 18*(11), 2127-2131.

The reviewers' reports had opposing views on their success, and only reviewer 2 recommended publication. The difference is due to the two reviewers' understanding of what constitutes significant results, in this case, results significantly different from the original paper. Both agreed with Maynard Smith and Smith that Ladoukakis and Zouros' analysis was criticisable, but reviewer 1 faulted them for re-analysing the data using a modified simulation:

> The repetition of the original analysis is however not quite the same analysis. S&S [*sic*] arrive at slightly different conclusions. However, this does not justify a publication in MBE, at least in my opinion. It is well known, that different tests applied to the same data set provide various answers.

Furthermore, they argued, 'the present manuscript does not lead to a more insightful interpretation of the data and does not give any guidelines how the uninitiated reader should interpret the controversial results.'[117] Reviewer 1 was worried that, by only insignificantly differing from the original analysis – due to a different simulation used – and by not offering sufficient re-interpretation, publishing Maynard Smith and Smith's reply to Ladoukakis and Zouros could reify 'the controversial results'.

Reviewer 2, on the other hand, considered the difference between the original and the re-analysis to be 'different', 'notably not being able to find unambiguous evidence for recombination in two of the three groups analysed. For this reason the note should be published.'[118] The emphasis on the fact that Maynard Smith and Smith could not confirm recombination in all the mtDNA re-analysed seems to be more significant to reviewer 2 than the fact that they adjusted the simulation. In fact, they wrote that 'MS&S provide a more objective and more easily defendable method'!

Maynard Smith and Smith met the criticisms of reviewer 2 in their revision; they were 'uncertain how to meet Referee 1's criticism' but attached an explanation of their objections to Ladoukakis and Zouros' statistics and were published in 2002.[119] Since then, several more research papers have appeared with supporting evidence that, at least in animals, mitochondrial DNA does recombine.

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117 Reviewer 1, attached to Tautz to Smith, 1 July 2002. JMSA Add MS 86624.
118 Reviewer 2, attached to Tautz to Smith, 1 July 2002. JMSA Add MS 86624.
119 Maynard Smith, J. and Smith, N.H. (2002). Recombination in animal mitochondrial DNA. *Molecular Biology and Evolution 19*(12), 2330-2332.

Support for recombination also came from a somewhat surprising corner. 'The Demise of mitochondrial Eve' is a paper published with the creationist Apologetics Press in 2003. Apologetics Press and anyone actively participating in their work assign to a list of ten 'principles of truth'. The first of these agrees that 'Faith in God and the Bible must be based on evidence, and not blindly accepted (Thessalonians 5:21; Acts 17:11; 1 John 4:1; John 8:32).' But poignantly, the fourth principle states that '[t]he entire material Universe was specially created by this almighty God (who exists and can be known by man) in six days of approximately 24-hours each, as revealed in Genesis 1 and Exodus 20:11.'[120] Indeed, Apologetics Press 'has waged a quarter-century battle against atheism and the theory of evolution'.[121] Until 2005, one of the authors of the 'Demise' article, Bert Thompson (PhD in microbiology), had been director of Apologetics Press.[122] The other author, Brad Harrub (PhD in anatomy and neurobiology), gives weekend seminars on 'Christian evidence' and has co-authored several books examining evidence for Christianity or the truth of human origins.[123] Maynard Smith would surely have had his thoughts on how much support he wanted from creationists. Harrub and Thompson used the research by Maynard Smith and his colleagues to dismantle the idea of a common human ancestor originating in Africa. They quoted Awadalla and colleagues' 1999 paper on linkage disequilibrium, concluding that

> rather than merely 'reconsidering' their theory and attempting to revamp it accordingly, evolutionists need to admit, honestly and forthrightly, that 'mitochondrial Eve,' as it turns out, has existed only in their minds, not in the facts of the real world. Science works by analyzing the data and forming hypotheses based on those data. Science is not supposed to massage the data until they fit a certain preconceived hypothesis. All of the conclusions that have been drawn from research on mitochondrial Eve via the molecular clock must now be discarded as unreliable. A funeral and interment are in order for mitochondrial Eve.[124]

120 'About Apologetics Press' 2016.
121 Ross 2005.
122 Ross 2005.
123 Harrub n.d. 'Welcome'.
124 Harrub and Thompson 2003.

With Eve and the molecular clock out of the way, evolutionists have lost one important argument in their ongoing debate with creationist accounts of human origins – if we follow Harrub and Thompson's reasoning through, that is.

Creationists have also drawn opposite conclusions from the adjustments to the data and time scales undertaken by scientists. Though not citing the Maynard Smith research,[125] Carl Wieland, founder of the *Creation* magazine, wrote in 2005, two years after Harrub and Thompson, that 'Creationists have enthusiastically welcomed the "mitochondrial Eve" hypothesis (i.e. that all modern humans can be traced back to one woman) because it clearly supports biblical history and contradicts evolutionary scenarios.'[126] His point of view (one he first proposed in 1998[127]) is that the uncertainty around the exact date of mitochondrial Eve means that there is no proof that she was *not* the same woman as biblical Eve. (We may remember from the previous chapter that creationists like to point to the uncertainty of scientific dating methods like radiocarbon dating to show that the Earth is not as old as science claims – here, Wieland does the same with Eve.)

It should be clear, however, that neither proponents nor opponents at the heart of the recombination controversy seemed to have had any religious agendas; for them, the debate was firmly situated within science. But this case highlights that as humans, we get rather involved when it comes to stories of our origins. As Maynard Smith has pointed out once when asked about evolution and religion: 'The basic point is this.'

> Every society and every group of people that we've ever known has some kind of myth about origins and where they came from. This is usually seen as part of their religion, like the story of Genesis. The object of this myth is to place man in the cosmos and in society and say why he's valuable and how God minds about him, and so on. Darwinism is also a story about origins – it says where man comes from – but is has a totally different function. It's not actually intended to tell you that man is particularly marvellous or that God loves him or anything like that. It's just to tell you what happened. So these two things are bound to come into conflict.[128]

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125 Although he does cite Marvin Lubenow, whom you may remember from the previous chapter on the 1979 creationist debate between Maynard Smith and Gish at Sussex. In 1998, Lubenow wrote in the *Technical Journal*, now rebranded as the *Journal of Creation*, about human and Neanderthal mtDNA. He too pointed to difficulties with the molecular clock as a dating method and listed several biases, including that the "Out of Africa" model is more politically correct, in part, he said, because the sudden replacement of Neanderthals by modern humans favoured punctuated equilibria.

126 Wieland 2005, 57.

127 Wieland, C. (1998). A shrinking date for 'Eve'. *Technical Journal* (now *Journal of Creation*) *12*(1), 1-3.

128 Maynard Smith 1988a, 133.

7.5 The long view

It remains to be asked what has become of the controversy. Scientific controversies can last for a long time – a persistence that again problematises the rationalist approach towards them.[129] Has the controversy around mtDNA recombination achieved closure? That is, has there been any solution to the debate? Today, the textbook view is that mitochondrial DNA is inherited clonally and transmitted maternally.[130] Anthropology textbooks agree that the first modern *Homo sapiens* originated in Africa some 200,000 years ago, the place and time originally suggested by Cann and colleagues.[131] However, mitochondrial Eve is curiously absent from the vocabulary of, for instance, the authors of *Essentials of Physical Anthropology*. Yet Grupe and colleagues do talk about mitochondrial Eve ('*Ur-Eva'* in German) in their summary of how anatomically modern humans originated. Interestingly, while they do point to some criticisms of the conclusions and implications following from Cann *et al.* 1987, stating that the discussion is still ongoing, they do not specifically refer to the controversy around the clonality of mtDNA; that stays an unchallenged and uncritical assumption within the book.[132] Similarly, Jurmain and colleagues do not doubt the maternal inheritance,[133] but they do point to some limitations of mtDNA data and their possible unreliability:

> MtDNA data, however, are somewhat limited because mtDNA is a fairly small segment of DNA, and it is transmitted between generations as a single unit; genetically it acts like a single gene. Indeed, in just the last few years, comparisons of Neandertal and early modern mtDNA led to some significant misinterpretations. Clearly, data from the vastly larger nuclear genome are far more informative.[134]

Hagelberg's suggestion of 2003, that there might have been interbreeding between *Homo sapiens* and *Homo neanderthalensis* (the view against hybridisation between the two had at least partly been resting on mtDNA data[135]) is now confirmed '[w]ithout a doubt' in the view of (some) physical anthropologists.[136]

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129 Kitcher 2000, 24f.
130 Grupe *et al.* 2005, 157; Bandelt *et al.* 2006, 19f; Jurmain *et al.* 2013, 84.
131 Grupe *et al.* 2005, 157f; Jurmain *et al.* 2013, 283.
132 Grupe *et al.* 2005, 157f.
133 Jurmain *et al.* 2013, 84.
134 Jurmain *et al.* 2013, 286.
135 Hagelberg 2003, 88f.
136 Jurmain *et al.* 2013, 286.

Another interesting case is the 2015 paper 'Ancestral DNA – an incontestable source of data for archaeology' by Neculai Bolohan, Mitică Ciorpac, Florica Măţău, and Dragoș Lucian Gorgan. They cite both Eyre-Walker *et al.* 1999 and Awadalla *et al.* 1999 to say that 'little to no genetic recombination occurs on the mitochondrial chromosome', from which they follow that 'all genes are inherited as if they were a single unit. Because only maternal DNA is present, mtDNA can be considered haploid for mitochondrial genes.'[137] A bit further on in the article they point out, however, that '[f]or archaeological purposes, mtDNA *is considered to be* inherited solely from one's mother.'[138] This suggests that they consciously choose to consider mtDNA to be clonal in order to simplify studies of human ancestry. In the conclusion, this view is confirmed by the authors first pointing to 'a general lack of recombination, which means that offspring *usually* will have (barring mutation) exactly the same mitochondrial genome as the mother' and then decidedly saying 'mtDNA *is* haploid and unilaterally inherited'.[139]

Todd Disotell, in his chapter 'Phylogenetic relationships of hominids: biomolecular approach' (*Handbook of Paleoanthropology*, second edition (2015), edited by Winfried Henke and Ian Tattersall), summarises that Eyre-Walker *et al.*'s suggestion of possible nonmaternal inheritance 'has been amply countered by further analyses', citing Macaulay *et al.* 1999.[140] (Disotell cites the 1999 Eyre-Walker *et al.* paper wrongly, removing Maynard Smith both from his in-text citation and the bibliography.[141])

The waves caused by John Maynard Smith and others – and predicted by Laurence Hurst in the *New Scientist* – thus appear to have run ashore without leaving much of trace. Several of the controversy's principal participants have moved on to different areas of research, or at least do not publish on recombination in mtDNA anymore. But others, like, Adam Eyre-Walker, now professor at Sussex University, still profess an 'an interest in whether mitochondria recombine.'[142] In 2004 he co-authored two papers appearing side by side in

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[137] Bolohan *et al.* 2015, 164.
[138] Bolohan *et al.* 2015, 166 (emphasis added).
[139] Bolohan *et al.* 2015, 176 (emphasis added).
[140] Disotell 2015, 2024.
[141] Disotell 2015, 2024 and 2036.
[142] Eyre-Walker n.d.

Heredity: the first concluded that while '[t]he overall significance of these findings is hard to quantify because of nonindependence, […] our results suggest a lack of evidence for recombination in human mtDNA.'[143] The second was in response to two papers reporting paternal leakage in a human: 'The challenge for the future will be to determine how frequent paternal leakage and recombination are in humans, and how frequent these processes are in other species.'[144] This instance captures the current situation: does human mtDNA recombine? Yes, no, maybe – depending on your perspective. Looking at some people of the opposing side, we find Vincent Macaulay is still working on prehistoric human demography and what mtDNA variation can tell us in that context. Hans-Jürgen Bandelt, on the other hand, has not recently published on mtDNA, and for Bryan Sykes the whole affair seems to have been over after Hagelberg and colleagues' 2000 correction. 'Mitochondria had survived the recombination scare,' he wrote in 2001.[145]

On the other hand, a decade after the controversy, an invited review in *Molecular Ecology* concluded that 'mitochondrial DNA is not always clonal, far from neutrally evolving and certainly not clock-like.' As such, its 'relevance as a witness of recent species and population history' was questionable, according to the authors.[146] The article's focus was molecular diversity in animals rather than human origins but the authors briefly review the three 1999 articles (Eyre-Walker *et al.*, Hagelberg *et al.* and Awadalla *et al.*) as well as the debates that followed. As such, the authors Galtier, Nabholz, Glémin and Hurst highlight that the three articles suggesting recombination in human mtDNA spawned research in animal mtDNA, for instance primates, a mussel, fish, a butterfly, a lizard and scorpions.[147] 'Ironically enough,' they then highlight that 'we now know that the three human studies which motivated this fruitful search for mtDNA recombination were actually questionable.'[148] That notwithstanding they still believe that these three and the animal studies show that recombination is, if not a fact, at least a possibility, even if it is difficult to assess.

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143 Piganeau and Eyre-Walker 2004, 282.
144 Ladoukakis and Eyre-Walker 2004, 321.
145 Sykes 2001, 168.
146 Galtier *et al.* 2009, 4541.
147 Galtier *et al.* 2009, 4542.
148 Galtier *et al.* 2009, 4543.

Here Galtier *et al.* refer to a paper of the same year by Daniel White and Neil Gemmell who asked, 'Can indirect tests detect a known recombination event in human mtDNA?'[149] The question is of major importance, considering that one of the criticisms put towards Maynard Smith and his colleagues was methodological. White and Gemmell distinguish between direct and indirect means to detect mtDNA recombination in humans, with the former being 'absent or scarce' and the latter including the methods employed by Maynard Smith and colleagues in 1999.[150] They refer to the often ambiguous evidence gathered through indirect means, but point out that in animals, recombination *has* been detected: this raises 'the possibility that the lack of evidence for recombination in human mtDNA is not due to an absence of recombination per se, but rather the ineffectiveness of current tests to detect it.'[151] In their research, they used several indirect methods (including Awadalla *et al.* 1999 and Maynard Smith and Smith 1999, but also an earlier method suggested by Maynard Smith in 1992[152]) on the one dataset of human mtDNA in which recombination had been directly detected. One conclusion White and Gemmell draw is that the utility and accuracy of the different methods analysed is dependent on the datasets, for instance, if they are real or simulated: tests run on simulated sequences are more likely to show recombination than those run on real sequences.[153] In other words, even though recombination was known to have occurred in the dataset used, no recombination was detected using the indirect methods. Thus they suggest that

> one reason for the apparent lack of indirect evidence of recombination in human mtDNA may derive from an inability of many of the contemporary tests being used to detect naturally occurring recombination in human mtDNA.[154]

These suggestions and results were taken up and extended by White and Gemmell with their colleague David Bryant in 2013. This time, they asked, 'How good are indirect tests at detecting recombination in human mtDNA?' Again, they ran several tests, this time on simulated sequences, and they concluded that all methods performed poorly. They then 'strongly recommend further development of indirect tests of recombination […]. At the

149 White and Gemmell 2009.
150 White and Gemmell 2009, 1435.
151 White and Gemmell 2009, 1435.
152 The 'maximum chi-squared method', see Maynard Smith 1992c.
153 White and Gemmell 2009, 1436.
154 White and Gemmell 2009, 1436.

very least, we suggest that simulations be run to explore the limitations of tests as part of empirical investigations.'[155] So while the scientific community appears content in considering human mtDNA clonal, the authors assert that the implications if this were *not* the case are too great to ignore the possibility of recombination.[156]

This case of mtDNA recombination, and in particular its 'closure', resembles the controversy surrounding the chemical transfer of memory:

> [M]emory transfer is an exemplary case of controversial science. We no longer believe in memory transfer but this is because we are tired of it, because more interesting problems came along, and because the principal investigators lost their credibility. Memory transfer was never quite disproved; it just ceased to occupy the scientific imagination.[157]

Similarly, the research community at large has turned away from researching the possibility of recombination in mtDNA. The field might have lost its appeal to some – but the controversy is not quite over yet. It is true that the majority of articles – at least those in direct relation to the original debate of 1999/2000 – seemed to have been published before 2004. And yet as the above shows, a consensus was never quite reached: a small number of researchers keep suggesting that recombination is a possibility even though it may not be able to detect it with current research tools. They insist that given the implications of recombining human mtDNA for past studies on, for instance, human evolution, we would be ignoring this possibility at our own peril.

This last point returns us to the idea of 'experimenter's regress': when recombination is not detected by tests and experiments that might only show us that the tests and experiments are not able to detect recombination. How do we know if we have designed a

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155 White, Bryant and Gemmell 2013, 1102.

156 Interestingly, in a *Genetics* paper citing Eyre-Walker *et al.* 1999, Miguel Arenas and David Posada highlight that '[n]early every published study incorporating ancestral sequence reconstruction assumes no recombination, despite the fact that recombination is widespread on the nuclear genome of many eukaryotes, and in particular in RNA viruses and some bacteria' (2010, 1138). While Eyre-Walker *et al.* and Hagelberg *et al.* problematised studies reliant on mtDNA sequences and assumptions of clonality based on the possibility of non-clonality and recombination, Arenas and Posada pointed out that even though recombination is a known and widespread phenomenon in nuclear DNA, it is often ignored in the reconstruction of ancestral sequences, biasing the outcomes and assumptions that can be drawn on most recent common ancestors.

157 Collins and Pinch 2004, 25.

test that can show recombination? When it shows recombination. How do we know that we have shown recombination? When we have designed a test that can show recombination… This problem of circularity happens in one of the criticisms of recombination. As Maynard Smith noted in reply to Kumar *et al.*: 'In essence there is an error in the logic in their argument: they implicitly assume that recombination does not occur in estimating their tree, so they cannot use the tree to argue that there is no recombination, as they do.'[158] But if they were to reorganise their tree assuming recombination, a criticism might be that their tree only shows the possibility of recombination because recombination was assumed. What is necessary to break this circle is a 'criterion […] independent of the output of the experiment itself.'[159]

Depending on one's point of view, the mtDNA debate both achieved and did not achieve closure. 'Closure' implies that the controversy disappears, and a consensus emerges.[160] Yet while textbooks may proclaim maternal inheritance and some of the key figures have moved on to other subjects, every now and then, another article surfaces and argues in favour of recombination in mitochondrial DNA. The can of worms first opened by Eyre-Walker and his colleagues in 1999 has in fact just now, almost exactly twenty years later, been reopened. A large, international research group based in the US, China and Taiwan has published an article in the December issue of *PNAS,* the *Proceedings of the National Academy of Sciences of the United States* demonstrating 'Biparental inheritance of mitochondrial DNA in humans'.[161] The authors agree that, generally speaking, human mtDNA is inherited clonally and maternally. However, their research showed 'rare exceptions': in three unrelated families, paternal inheritance had been detected.[162] In the paper's discussion section, they highlight that these results were unequivocal; they

> clearly demonstrate biparental transmission of mtDNA in humans, counter to the central dogma of mitochondrial inheritance. This test has been confirmed in three separate lineages with multiple generations and by two other laboratories.[163]

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158 Maynard Smith. JMSA Add MS 86699.
159 Collins and Pinch 2004, 98.
160 Pinch 2015, 283.
161 Luo *et al.* 2018.
162 Luo *et al.* 2018, 13039.
163 Luo *et al.* 2018, 13041; on the following page, they use 'unequivocally demonstrated'.

'One is forced to wonder,' they continue, 'how many [...] instances of individuals with biparental mtDNA inheritance have been dismissed as technical errors'.[164] The authors further suggest possible mechanisms for the biparental inheritance of mtDNA observed.

Article usage: November 2018 to March 2019

	Abstract	Full	Pdf
Nov 2018	83925	14300	4523
Dec 2018	55318	9595	3607
Total 2018	**139243**	**23895**	**8130**
Jan 2019	18682	4440	1676
Feb 2019	6311	2093	711
Mar 2019	2764	850	274
Total 2019	**27757**	**7383**	**2661**
Total	**167000**	**31278**	**10791**

Figure 29. Luo et al. *2018, article usage November 2018 to March 2019.*

As of 20 March 2019, the article has been viewed over 31,000 times (in full; the abstract has been viewed 167,000) and downloaded nearly 11,000 times (Figure 30).[165] It has been followed by a commentary[166] and a letter[167] (and the authors' reply to the letter[168]) in *PNAS*. Like the original two 1999 articles by Eyre-Walker *et al.* and Hagelberg *et al.,* Luo *et al.'s* research was quickly picked up by *Nature*[169] and *Science*[170]. And, again like the brief coverage of the 1999 controversy but on a much larger scale, the 2018 case is also being reported on outside of the strictly professional circles and popularised: *The Scientist*[171], *New Scientist*[172],

164 Luo *et al.* 2018, 13042.
165 https://www-pnas-org.ezproxy.library.ubc.ca/content/115/51/13039/tab-article-info accessed 20 March 2019.
166 Vissing 2019.
167 Lutz-Bonengel and Parson 2019.
168 Luo *et al.* 2019.
169 McWilliams and Suomalainen 2019.
170 Leslie 2018.
171 Azvolinsky 2018.
172 Le Page 2018.

Discover[173], PBS's science series *NOVA*[174], the *Smithsonian*,[175] and *ars technica*[176] are among the (online) science news outlets that have picked up the story.

Concerning this parallel case to our core controversy from 1999, it is early days and hard to tell how much of an impact the study will have. It should also be pointed out that the focus in terms of consequences is drawn differently: Luo *et al.* are more concerned with therapy of pathogenic mitochondrial DNA rather than large-scale evolutionary events. (mtEVE makes no appearance.) So far, the letter by Lutz-Bonengel and Parson negates Luo and colleagues' results. 'While this line of argument may be a theoretical, albeit highly unlikely, explanation for their findings, their conclusion that it provides evidence for paternal inheritance of mtDNA is not supported by the data.'[177] They go even further, saying that the experiments are 'by no means sufficient to even suggest' biparental inheritance of human mtDNA.[178] Lutz-Bonengel and Parson suggest that the paternal mtDNA found by Luo *et al.* originated in nuclear DNA, to which the authors reply that they 'appreciate these concerns' – meaning those suggested alternative origins – but then point out that they, in their paper, did not in fact propose any origins: 'our paper merely documents the unusual transmission of apparently full-length paternal mtDNA sequences to offspring.'[179] Luo and colleagues summarise their method again, point out that they followed 'standard protocols' and conclude that Lutz-Bonengel and Parson's suggestion in fact cannot explain the origin of the discovered paternal mtDNA.

7.6 Conclusion

In lecture notes dating from around or after 2000, John Maynard Smith asked:

> DO HUMAN MITOCHONDRIA RECOMBINE?
> I don't know – but nor does anyone else
> Evidence -> they do.[180]

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[173] Schley 2018.
[174] Wu 2018.
[175] Katz 2018.
[176] O'Grady 2018.
[177] Lutz-Bonengel and Parson 2019, 1821.
[178] Lutz-Bonengel and Parson 2019, 1821.
[179] Luo *et al.* 2019, 1823.
[180] Mitochondria [2000?]. JMSA Add MS 86836.

The previous discussion shows that several people would, and indeed did, disagree with this statement: their point of view was and is that we do know that they *do not* recombine and that what Maynard Smith cited as evidence is hardly able to cast doubt on this conviction. What counts as evidence and what is proper methodology was one major point of contention in the controversy after 1999, as highlighted in the referees' reports for both the original 1999 Eyre-Walker *et al.* paper and the 2004 Maynard Smith and Smith paper as well as in the *Science* exchange from 2000. The validity of theoretical assumptions, of statistical and indirect methods, of simulations, the use of data and the interpretations of results were as much discussed as the actual suggestion of recombination. The scientists disagreed on whether the research by Maynard Smith and his colleagues in fact showed human mtDNA recombination – could those homoplasies in fact be interpreted as the results of recombination – and if their methodological and data set choices were correct.

Reading White and Gemmell, later with Bryant, the problem is akin to Collins and Pinch's experimenter's regress in the case of gravitational waves: when and how do we know that the experiment – in this case, the simulation – works, giving us the correct results, if what we do not know whether what we are trying to detect – recombination in human mtDNA – actually exists? If it does occur, then a simulation showing recombination is a valid method for discovering recombination; if it does not occur, the same simulation with the same results will in fact not be a valid method. What White, Gemmell and Bryant suggest that the doubt that has been cast by the 1999 and a few later papers is reason enough to acknowledge the possibility of human mtDNA recombination and to keep working on direct and indirect methods of detection because one day, they may be ready to offer definite results.

A similar view, though less explicit, was held by Maynard Smith. Indeed, the controversies discussed in this, taken together with the previous chapter, have illuminated two things, the first being that we now have a clearer view of Maynard Smith's understanding on what science is and how it works. Second, and more focused on this chapter, by taking the long view we have not only uncovered the development of a scientific controversy but seen how closure can both be achieved and yet not be certain. This first conclusion is the result of observing Maynard Smith as an actor both on the orthodox and on the unorthodox side of a controversy. He had the confidence to welcome and defend ideas that were outside of the scientific paradigm, to use a Kuhnian term. He had welcomed palaeobiology to evolution's high table despite his own disagreements with Gould – although he later increasingly sharply pointed out these disagreements. During these debates about punctuated equilibria he several times pointed to his status as an outsider to the field. In the human mtDNA debate – although he had moved into the field via the study of bacteria and had no previous experience with sequence analysis – Maynard Smith was not an outsider in so far as it was concerned with population genetics. The confidence to question a paradigm came, first, from Maynard Smith's trust in models and simulations, a remnant of his time as an engineer and something that he had been very successful with in the development of evolutionary game theory. Second, in his fortieth year as an active researcher, an FRS, a winner of several scientific prizes, he was an established scientist. Maynard Smith knew of his intellect and was not afraid to admit that he was arrogant in that regard: 'I mean, I'm an arrogant person, but he is the one person I have associated with extensively who I recognise was cleverer than I am,' he once said being asked about his relationship with Haldane.[181] That is not to say that Maynard Smith never got things wrong. In the same interview he explained that the shortest paper he ever published was a letter to *Nature*, confirming that 'I'm afraid that Gale and Eves are quite right' after they had discovered a mistake in his work. Being wrong did not worry him too much, he added.[182]

There is a third reason why Maynard Smith did not simply back down after receiving negative reviews on their drafts or critical replies in *Science*: he liked argument. As Jim Crow pointed out in his introduction to a Festschrift for Maynard Smith,

> One of the articles is a book review in which the author takes strong exception to tone of JMS's ideas about the evolution of language. I am sure that John loves it and is eagerly looking forward to an argument.[183]

Remembering the previous chapter and Maynard Smith's use of Karl Popper's ideas, we can see that even though he argued against the philosophy of science influencing one's science, his love for argument has distinct Popperian features. Popper emphasised the need for constant critical thinking in science as the way for science to progress. The distinction

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[181] Maynard Smith 1999.
[182] Maynard Smith 1999.
[183] Crow 2000, 2.

between 'normal' and 'extraordinary, or revolutionary, science' (Kuhn's terms) is the major point of contention between Popper and Thomas Kuhn (and their respective followers). It is explicit in the 1969 volume *Criticism and the Growth of Knowledge*, collecting the papers from and follow-ups to the International Colloquium in the Philosophy of Science that took place in London in 1965. Kuhn argued that in normal science, scientists work within the current paradigm as puzzle-solvers; they do not actively try to depose of the current theory.[184] Popper replied that Kuhnian normal science exists; '[i]t is the activity of the non-revolutionary, or more precisely, the not-too-critical professional'. He felt, however, that this uncritical nature of normal science was 'a danger to science' and that to consider it as the 'normal' state of science was hugely problematic.[185] The disagreement lies in Kuhn and Popper's interpretations of scientific orthodoxy and unorthodoxy. As Steve Fuller put it, for Kuhn scientific paradigms are a 'source of stability' while Popper saw in them a 'problem to overcome'.[186] Maynard Smith's lack of fear in the face of controversy marks him a Popperian; apart from calling Popper explicitly his 'favourite philosopher of science', he once – in reply to Charles Taylor of UCLA sending him Margaret Masterman's article in *Criticism and the Growth of Knowledge*[187] – made it clear that he was unconvinced by Kuhn:

> On Kuhn, I can only repeat my point, which is that if the molecular biology revolution was not a 'paradigm shift' – and I gather we agree about that – then the concept of a paradigm shift seems pretty useless. It doesn't apply to the most significant change in outlook in biology since Darwin.[188]

His view was the same as Popper's in that they both believed that 'science is essentially critical' and that controversy is a healthy, indeed essential, part of science.[189] In the previous chapter we saw, for example, that Maynard Smith published *Evolution Now*, a collection of controversial scientific papers with the explicit aim of making them accessible to a non-specialist audience. He has also said that 'it is precisely by abandoning the claim to absolute certainty that science has been able to progress at such a fantastic speed in obtaining an understanding of what the universe is like.'[190] As Hasok Chang has suggested, Kuhn's

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[184] Kuhn 1976.
[185] Popper 1976, 52.
[186] Fuller 2003, 54.
[187] Taylor to Maynard Smith, 31 January 1985. JMSA Add MS 86590.
[188] Maynard Smith to Taylor, 15 February 1985. JMSA Add MS 86590.
[189] Popper 1976, 55.
[190] Maynard Smith 1964, Talk I, p.4. JMSA Add MS 86606.

emphasis on normal science in which certain ideas are taken for granted in order to work with them is important but best taken *together* with Popper's emphasis on critical thinking to avoid close-mindedness.[191]

The second conclusion we can draw from this chapter relates to the nature of scientific controversies and their position within science. In fact, behind the one controversy on whether human mitochondrial DNA recombines are at least two others that show similar characteristics: the precise evolutionary origin of mitochondria and the existence of mitochondrial Eve. All three controversies form layers of the one overarching question of human evolution.

First, Lynn Margulis' endosymbiotic theory is still not fully established or universally accepted. Built to an extent onto this theory which used the discovery of mtDNA as an argument, the second idea in this chapter was put forward in the 1987 paper by Rebecca Cann, Mark Stoneking and Allan Wilson. Mitochondrial Eve spoke to palaeontological and anthropological debates on evolution of anatomically modern human; the team's research weighed in on the side of the 'Out of Africa' model as opposed to the multiregional model by bringing new research methods into play (molecular biology). Third, the research done by Maynard Smith and his various co-authors (and by Hagelberg *et al.*) addressed taken-for-granted assumptions underlying the mtEVE story. Depending on who you ask, all of these have either reached closure; originally unorthodox views have either reached the status of a new orthodoxy (evolution of mitochondria, mitochondrial Eve) or have been swallowed by the existing orthodoxy (recombination in human mtDNA).

By taking the long view, going beyond Maynard Smith's direct involvement, we have seen that this idea of closure is too simplistic. There are now several cases in which recombination in animal mtDNA has been shown, which appears much less controversial. (As we saw, both the original 1999 controversy and the recent 2018/19 case spilled over into news sections in both professional and popular publications. The involvement of creationists too suggests that when it comes to human origins, there is widespread engagement with otherwise very localised scientific ideas and disputes.) Ideas that have been

[191] Chang 2004, 236f.

suggested once are hard to suppress completely. Ernan McMullin defined closure of scientific controversies as opposed to resolution of controversies: no solution has been found, but there is a sense in which a decision has been reached to not discuss the issue anymore; to close it.[192] Here, too, the solution appears not to have been a resolution; while the orthodoxy was re-established, it keeps being challenged in small instances. Popperian critical thinking is working within Kuhnian normal science, keeping the orthodoxy on its toes.

192 McMullin 1987, 78ff.

8 Conclusion

8.1 John Maynard Smith's legacy

Before his death, John Maynard Smith expressed the wish that his papers would be deposited with the British Library. He visited the Library on 21 June 2001: he had lunch with the then chairman, John Ashworth, and the curator of manuscripts, Anne Summers, after which he was shown around.[1] The same year of his visit to the Library, Maynard Smith was interviewed by Robert Wright. Wright asked about his views on spirituality and legacy. Maynard Smith answered that while he did not believe in any spiritual existence or afterlife, he did hope to have made some lasting contributions to science and to be recognised and remembered for his achievements. Donating his archive created a lasting physical legacy that ties in with and helps understanding Maynard Smith's contributions to science and British public life beyond the fifty years of his career as one of Britain's foremost evolutionary biologists.

In years to come, this archive will need to make its way to the top of historians of science's list of resources. It is invaluable not only as a source but also in prompting further research questions that will need to go beyond the archive and Maynard Smith. Considering the lack of attention paid to Maynard Smith in the history of science so far – philosophy of science here is one step ahead with a special issue in *Biology and Philosophy* (2005), as is biology itself with a special issue in the *Journal of Theoretical Biology* (2006) – this thesis therefore takes on three different roles: it functions as an introduction to the archive; it serves as a stepping stone for future research; and importantly, it is the first major historical contribution on John Maynard Smith.

Taking these together, it will be obvious that the thesis does not address everything there is to address about Maynard Smith, his scientific contributions, or his place in British public life. The thesis did not set out to do so. Instead, it is a focused study of the material in terms of Maynard Smith's working life, which turned out to be rich, diverse, and

[1] BL Acquisition File "John Maynard Smith".

revealing – and one which complicates some previously held assumptions about evolutionary biology and biologists of the twentieth century.

8.2 Questions answered?

I asked at the beginning, how does John Maynard Smith fit into post-war evolutionary biology and what role does science communication play in that context? What do his involvements in scientific controversies tell us, first, about his philosophy of science and the state of evolutionary biology in the second half of the twentieth century? It is time to look at what answers the thesis has provided.

8.2.1 Popular science

Maynard Smith's popular science activities were the focus of the first two chapters which discussed his writing and broadcasting for broad audiences. The most striking fact that emerged is that Maynard Smith operated on a reverse timeline to the usual development of a research scientist's involvement with science communication to non-specialists: most would first establish themselves as experts in their profession and then move onto more popular platforms. Even though he had published a successful book for non-specialists as an early-career scientist, Maynard Smith did not switch careers (again). He stayed in research, keeping up science communication at the side.

As Michael Ruse's analysis shows, many other twentieth-century evolutionary biologists who were both publishing research scientists and popular science writers would also keep their specialist and non-specialist writings quite distinct from each other. Maynard Smith, on the other hand, made no clear distinction, at least not in his writing which he could control more than how he was presented on radio or television. *The Theory of Evolution* blends genres and audiences, which resulted in mixed uses. For many, it was an introduction to evolutionary biology, but this could be both in an individual capacity, reading the book as a popular science book, or it could be structured, when it was used as a textbook at university. The sharing of knowledge is apparent in the broadcasts as well: Maynard Smith, as I pointed out, explained, defended, and critically discussed (evolutionary) science.

8.2.2 Professional science

In terms of Maynard Smith's professional life, focused within academia, we have taken a look at some of the ideas that he is best known for: kin selection and evolutionary game theory. Situated in the context of peer-reviewing, intellectual property, and collaboration, these two chapters illuminated one of the most fundamental issues in science – the origin of scientific ideas and who gets scientific priority.

In both cases, the story started with Maynard Smith reviewing a manuscript, suggesting publication but also a few changes. In the first case, the story turns into one of conflict. In the second case, it turns into one of collaboration. Different levels of communication and presentation were obvious in both, with the private world of correspondence usually working behind, and more openly than in, the public world of publication. At the same time, Maynard Smith made use of different types of publication to assert his priority in evolutionary game theory, an idea that gets presented and discussed in both popular and professional venues. The state of professional evolutionary biology was increasingly consolidated, and with kin selection theory and evolutionary game theory received two of its most influential concepts and approaches of the twentieth century. Maynard Smith's insistence on the utility of mathematics for biology is vindicated. At the same time, the advance of computers introduced new ways of doing science, and on the insistence of George Price, Maynard Smith taught himself programming to run the simulations for their Hawk and Dove (Mouse) Game.

8.2.3 Controversial science

The Hamilton case already gave us a controversy, but one that was not about scientific *ideas* but rather about scientific *conduct*. For the most part, it was handled in private; only the letters reveal the full scale of the accusations and the resolution. It is fair to say that neither participant enjoyed this controversy, as it was highly personal. The later, truly scientific, controversies showed us another side of Maynard Smith, one that did enjoy controversy. When it comes to scientific ideas, he cherished and even encouraged critical engagement. This was the result of a personal philosophy of science influenced by Karl Popper's concepts. Maynard Smith used Popper to demarcate science from the pseudo-science creationism, yet at the same time asserted that philosophy should be kept out of the actual activity of science. His high regard for critical thinking and scientific challenges and controversies however illustrated how far Popperian thinking about what science is and how it should be done have filtered into Maynard Smith's working life. The early influence of Sir Peter Medawar, one of Popper's biggest proponents, on Maynard Smith the student and early-career researcher at University College may have played a part in this.

Overall, we have seen that controversies made up a visible part of the scientist's professional life. Maynard Smith took them as opportunities to further science, consequently not minding being both the defender and the challenger of orthodoxy.

8.3 Further research options: JMS and BIOLS

Figure 30. John Maynard Smith after moving to Sussex, ca. 1965. © University of Sussex.

This thesis could not cover the entire archive and scientific work of Maynard Smith, nor did it aim to do so. One important part of Maynard Smith's working life that needed to be cut as other stories grew is his relation to the University of Sussex. As the founding dean of the School of Biological Sciences, or BIOLS, he had the freedom to shape a research environment without any previous institutional memory to break with. BIOLS was inaugurated after the School of Physical Sciences (which housed experimental and theoretical physics, chemistry and mathematics), in line with the University's vision to do away with the traditional departmental system.[2] The schools aimed at interdisciplinary, general studies rather than specialisations.[3] In terms of BIOLS, therefore,

[2] B-S. 1963, 10.
[3] Briggs 2011.

> the various branches of biology will be studied as a unity, and this study will be based on a firm foundation of physical, chemical and mathematical knowledge. Undergraduates majoring in this School will follow two foundation courses; one dealing with biophysics, biochemistry and genetics, and the other with living organisms in relation to their environment. In the third year, there will be opportunity for specialization in most branches of biological science.[4]

Despite being a core value, interdisciplinarity was implemented with varying success. The arts and the sciences, for instance, were supposed to cross over, such as with seminars on genetics for sociology students but the seminar series was dropped, much to Maynard Smith's regret.[5] Yet within the biological sciences he had the freedom to break with old teaching traditions. Even though he had no previous experience in administration and 'hate[d] running things,' Maynard Smith was

> very impatient with the way that biology was being taught […] in most British universities. It was still dominated by departments of zoology and botany and genetics and biochemistry who never talked to one another […]. And it (moving to Sussex) did give me an opportunity of starting a department in which biology was a unified science and in which it was, sort of, taught in a modern way.[6]

The Sussex vision thus fitted his own ideals of integrated science teaching. At the same time, the new administrative duties took their toll on his research: after his move to Sussex in 1965, Maynard Smith abandoned experimental biology (*Drosophila* genetics) and turned his full attention to theory; there was no time for fruit fly farming and long-term experiments.[7] Arguably, this shift was for the better; as Maynard Smith remarked twenty years later:

> I was quite a competent geneticist. But the world is full of competent geneticists, and it *isn't* terribly full of people who can do mathematics *and* apply it to animals. The world is also full of mathematicians and many, many people are enormously better at mathematics than I am. What it isn't very full of is people who can apply mathematics to the real world.[8]

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4 B-S. 1963, 10.
5 Maynard Smith and Dawkins 1997, https://www.webofstories.com/play/john.maynard.smith/61.
6 Maynard Smith and Dawkins 1997, https://www.webofstories.com/play/john.maynard.smith/35. Maynard Smith appears to have told the story that Haldane inspired him to take the post (cf. Stern 2013, 17) but his other major influence, Medawar, was instrumental in actually getting him the job, as we saw in Chapter 1.
7 Maynard Smith 1985, 350f; see also Maynard Smith and Dawkins 1997, https://www.webofstories.com/play/john.maynard.smith/35.
8 Maynard Smith 1988, 137 (emphasis in original).

After original struggles, particularly financially,[9] BIOLS turned into a centre for much biological research in Britain during the 1970s.[10] Claudio Stern, who took his degrees at the School, remembers it as 'an extraordinary environment in the 1970s. Many people agree that most of this was due to the vision of John Maynard Smith'.[11] Frequent seminars with outside speakers, full of provocation and discussion, were one part of the curriculum.[12] One angle to take on this part of Maynard Smith's working life, in conjunction with an institutional history of BIOLS, is the nature of the research school(s) around Maynard Smith – and whether he indeed built any in the traditional sense. Gerald Geison has defined research schools as

> small groups of mature scientists pursuing a reasonably coherent programme of research side-by-side with advanced students in the same institutional context and engaging in direct, continuous social and intellectual interaction.[13]

Maynard Smith, however, never took on many research students as a supervisor, 'mainly because he preferred people to get on with their own ideas'[14] – and reversely, because he preferred 'to think on his own'.[15] At the same time, the archive contains a folder related to "Visitors to population biology group" and linked correspondence. This material allows the tracing of visiting students and scholars, their subjects and nationalities, primarily for the late 1970s to the early and mid-1980s.[16]

Maynard Smith's last years as dean – he officially retired in 1985 but stayed on as professor emeritus – coincided with Margaret Thatcher's premiership. In the early 1980s, he asked Lewontin, '[a]ny jobs at Harvard? Mrs T is planning to close down the universities here.'[17] Towards the end of the decade, he informed another colleague that '[u]nfortunately,

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[9] The school had originally been promised £180,000 to equip the building in its various stages; the funds were cut before they could be spent, as planned, in 1968:

> In consequence we have no money to equip our third-year teaching laboratories, which will be occupied for the first time in October, and no money to equip a bio-chemistry research laboratory, headed by a professor and a reader, which is to open in October (Maynard Smith 1967, 9).

[10] Briggs 2011.
[11] Stern 2013, 17.
[12] Stern 2013, 19.
[13] Geison 1981, 23.
[14] Charlesworth and Harvey 2005, 263.
[15] 'Professor John Maynard Smith' 2004, 31.
[16] JMSA Add MS 86767 and 86868A-B. The University of Sussex's records, housed at The Keep in Brighton, would also be relevant.
[17] Maynard Smith to Lewontin, 19 July [1981]. JMSA Add MS 86615.

the evolutionary biology group here has disintegrated (thanks to Mrs T)'.[18] There are suggestions that the financial troubles hitting BIOLS during the 1980s were linked to Maynard Smith's dislike for administration. Being 'hopeless at academic politics', the *Times* obituary says, Maynard Smith

> never attended committee meetings in London if he could avoid it. So when Margaret Thatcher's funding cuts hit higher education, Sussex was almost completely undefended, and his department was decimated.[19]

8.4 Final reflections

I said at the beginning that I would not write a traditional biography but that I would instead take a non-biographical, yet still largely chronological, thematic approach to the working life and archive of John Maynard Smith. As the above answers to and reflections on the original research questions show, this proved to be highly illuminating:

1) The theme of popular science emerged first, counter to what we traditionally believe the typical trajectory into popular science to be. Also counter to the typical view, neither career – communicator or researcher – eclipsed the other; Maynard Smith was established in both and maintained a respectable research output as well as broadcasting and publishing to non-specialists.
2) Maynard Smith had a varied research profile, moving from fruit fly genetics to the evolution of senescence and sex through to bacteria and mitochondria. But his name is most closely linked to ideas he promoted and developed mid-career, ideas about which he was still contacted after having moved on to different research interests.
3) Firm in his position and reputation, with both public and professional visibility, he was involved in several scientific controversies towards the end of his career, defending not only orthodox but also unorthodox views.

At the same time, all three aspects – the popular, professional, and controversial – always interacted and were never isolated from each other. The instances where all three meet are spread throughout the thesis: think, for example, of how Maynard Smith first introduced

[18] Maynard Smith to Robson, 3 July 1989. JMSA Add MS 86588.
[19] 'Professor John Maynard Smith' 2004, 31.

evolutionary game theory in an essay collection aimed at a non-specialist audience, or of how he discussed religion on the radio, debated creationists, and exchanged public letters with Stephen Jay Gould in the *New York Review of Books*.

Given what we have learned about Maynard Smith and his working life as a man of science with a public presence, can we say any more about how typical or atypical he was? As established in the thesis's early chapters, Maynard Smith's original involvement with writing science for non-specialist audiences was no surprise given how he himself learned much of science: 'by reading books and essays by scientists,' precedents which convinced him 'that it is possible for scientists to convey their ideas, and their enthusiasm for those ideas, to a non-professional readership'.[20] Scientists from a variety of disciplines had been successfully writing about science to non-specialists since the nineteenth century; in Bowler's words there had been a 'Victorian ideal of communicating with the public'.[21] Many of the scientists the early-career Maynard Smith worked with and knew in the 1950s – Haldane, Spurway, Medawar, Lack, Tinbergen, and others – all wrote (or had written) for both specialist and non-specialist audiences in the form of books and articles. Throughout its run between 1945 and 1960, for example, *New Biology* published articles by many famous names, some of whom had previously written popular science books (like Lancelot Hogben) or were going to start broadcasting careers next to or after their research careers (e.g. Harold Munro Fox). Aubrey Manning is another name on that list. Manning is an interesting point of comparison given that he and Maynard Smith were friends and fellow undergraduates at UCL. Manning then went on to Oxford and in 1956 published 'Bees and flowers' in *New Biology*. But in contrast to Maynard Smith, his career as science broadcaster only started after his retirement from Edinburgh in 1997: he headed the BBC series *Earth Story* in 1998 (despite being an ethologist and not a geologist) and afterwards worked on several other projects both on radio and television.[22]

That this separation of careers did not occur in Maynard Smith's working life reflects his intellectual upbringing and environment; communicating science to non-specialists must have appeared to Maynard Smith to be part of the job. The generation of biologists before

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[20] '11. PARTICULAR POINTS to be emphasised in promotion…' Author's Agreement for *Did Darwin Get It Right?* (undated). JMSA Add MS 86578.
[21] Bowler 2009, 276.
[22] Sington 2018. See also Grant 2013.

him had been and still were writing to numerous audiences through the first half of the twentieth century, and his colleagues at UCL helped the publication of Maynard Smith's first book with discussion and proof-reading. Haldane even wrote a piece on 'How to write a popular scientific article'.[23] But there were also changes happening. J.W. Atkinson, writing about the popular writings of the American embryologist E.G. Conklin, noted that 'a good deal more popular material may be found in the first fifty than the last thirty years' of the twentieth century.[24] In Britain Bowler noted that with the declining interest in serious self-education literature after World War Two and an increasing number of science writers and correspondents, scientists appeared less willing to write for non-specialist audiences.[25] At the very least, they often only started doing so after having had a successful research career, like Manning did. Maynard Smith is therefore atypical in achieving visibility in both professional and public circles by communicating to both continuously since the very beginning of, and then throughout, his career, while (at least in the late 1960s) also pushing for other scientists to contribute more to science communication.

The merging of these two careers into being two aspects of one job was helped by the fact that even though he was a visible scientist and public intellectual, Maynard Smith never reached fame (and sometimes, notoriety) of the kind that some of the next generation of science communicators like Richard Dawkins have. Maynard Smith's public visibility remained mostly within the British context, having the BBC as his primary outlet for TV and radio work. The archived notebook of fees and royalties received between 1976 and 2000, for instance, records only eight international appearances out of 111 media appearances.[26] Books are a different matter of course; due to their translations, Maynard Smith's books had audiences beyond the Anglo-American context. As noted in the first part of the thesis, *The Theory of Evolution* was translated into five different languages. This was already more than H. Munro Fox's Penguin book on *The Personality of Animals* (1940), which was translated into Italian and Japanese.[27] Neither compares to the audiences more recent

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[23] Haldane 1986, 154ff.
[24] Atkinson 1985, 32.
[25] Bowler 2009, 274f.
[26] Notebook 1. Add MS 86831. These fees and royalties include repeat fees, making this number larger than the total of approximately 100 appearances suggested in Chapter 2.
[27] Smith 1968, 216.

books like Dawkins' *Selfish Gene* have reached; *The Selfish Gene* has been translated into over twenty languages and the 'title has become a set phrase in the English language'.[28]

There are at least two reasons for this wider reach. First, Dawkins' style differs from Maynard Smith's. Although influenced by Maynard Smith's work, which as we saw provided the basis for several parts in *The Selfish Gene*, Maynard Smith's emphasis on 'doing the sums' in biology moved into the background. Dawkins translates evolutionary game theory and other ideas into non-mathematical, at times metaphorical, language and does not include formulae or equations in his popular writings. This contributed to the book having a wider appeal than Maynard Smith's which, as shown by its usage in teaching environments, was technical enough to serve as a textbook. *The Selfish Gene* was also helped along by being depicted as controversial in early promotional material, being the basis of the 1976 *Horizon* episode of the same name (even though the episode did not make the link clear, the publisher did), and by being linked to E.O. Wilson's *Sociobiology* (1975) which was already being discussed widely in both the media and scientific circles.[29]

Maynard Smith's public visibility raises the question of whether he could be considered a scientific celebrity. In their study 'Scientific celebrity, competition, and knowledge creation: the case of stem cell research in South Korea', Hyunsung D. Kang and Jeongsik J. Lee define scientific celebrities in contrast to star scientists: the latter are known for their productivity in science, the former extend their influence – scientific, political, and otherwise – beyond the scientific community.[30] Kang and Lee focus primarily on positive spillover effects of scientific celebrities like their 'encouraging entries of new scientists' and 'helping direct increased funding resources from the public sector', both encouraging greater knowledge production in their field.[31] (Negative spillover effects could be exploitation of status for personal or financial gain.[32]) Maynard Smith definitely helped encourage a number of people to enter evolutionary biology as the appreciations mentioned in Chapter 1 show.[33] He was an inspiring and encouraging teacher but at the same time he 'rarely applied for grant support' and there are indications that he was even less actively

[28] De Chadarevian 2007, 32.
[29] De Chadarevian 2007, 33.
[30] Kang and Lee 2016, 27.
[31] Kang and Lee 2016, 42.
[32] Kang and Lee 2016, 42f.
[33] Cf. p.53.

involved in the politics of education due to a dislike of administration.[34] As a result, and notwithstanding the public image he had built up by then, his department at the University of Sussex was decimated when Margaret Thatcher's government instituted funding cuts for higher education in the 1980s.

At the same time, Maynard Smith shares aspects of Kang and Lee's star scientist-idea which focuses on visibility within the scientist's profession. For Maynard Smith, this visibility is summarised by Marek Kohn's naming him the "senior statesman" of British evolutionary biology and it takes a number of typical forms: publishing, acting as a referee as well as president to organisations like the European Society for Evolutionary Biology, organising and attending conferences, as well as corresponding internationally with other scientists. A study of his work at the School of Biological Sciences at Sussex could add another dimension by looking at his teaching activities, which were not part of this thesis.

Especially in the context of mathematics in biology and evolutionary game theory, Maynard Smith's visibility, involvement, and both research and promotional efforts put him in an influential position. First, his mathematical abilities and perspective on biology resulted in the textbook *Mathematical Ideas in Biology* (1968). This attempt to shape the course of the discipline, at least within evolutionary biology, translated into disciplinary power when editors called on Maynard Smith to review mathematically complex research like Bill Hamilton's work on inclusive fitness. But second, he was probably even more influential as an early gatekeeper in evolutionary game theoretical studies: he was the go-to reviewer for many papers (in addition to which he published much himself and, again, wrote the definite textbook). I cited Alan Grafen in the chapter on game theory when he noted that, when new research appeared in the field and its merits were discussed, 'Maynard Smith will know. He is nearly always right, and always sensible.'[35]

The problematic side of this much influence is not hard to see, of course: there is a danger of one-sidedness in research directions or suppression of competition when one person shapes the development of a field as much as Maynard Smith shaped evolutionary game theory. He was certainly a defining character for at least a decade, before he eventually took a backseat and moved on to a different research area. This was in part an

34 Charlesworth and Harvey 2005, 262.
35 Grafen 1983.

acknowledgement that some of the work being done in evolutionary game theory had gone beyond his skills. The other part was Maynard Smith's tendency to change research areas when a new problem struck him as interesting and worth working on, rather than specialising deeply in one area. (Here he again emulated Haldane, whose research interests varied widely and changed throughout his career.) What gives coherence to his research output is the unwaveringly neo-Darwinian perspective and the emphasis on adaptation. In these changes of research direction also lies another reason why no research school of 'Maynard Smith-style evolutionary biology' evolved at Sussex. The main source for Maynard Smith's disciplinary power lay in his own research and his refereeing activities which ensured a professional visibility that matched, if not exceeded, his public visibility.

In summary, these findings show that non-specialist science very much constituted a part of, and even consolidated, Maynard Smith's professional ideas and provided a platform for working through controversial issues. As such, *only* taken together do they completely illustrate and illuminate the working life of John Maynard Smith as a man of science with a public presence.

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JMSA – John Maynard Smith Archive. The British Library, London.

MWP – Maurice Wilkins Papers. King's College London Archives, London.

PA – Penguin Archive, Special Collections, Bristol.

WHP – William D. Hamilton Papers. The British Library, London.

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