Individual variation in the lifetime reproductive success of Seychelles warblers

Ellie Chesterton

Submitted in accordance with the requirements for the degree of

Doctor of Philosophy

The University of Leeds
School of Biological Sciences

January 2023

The candidate confirms that the work submitted is their own, except where work which has formed part of jointly authored publications has been included. The contribution of the candidate and the other authors to this work has been explicitly indicated below. The candidate confirms that appropriate credit has been given within the thesis where reference has been made to the work of others.

Chapter 2 (under review at *Evolution*)

This work has been submitted as a manuscript for publication to *Evolution* as follows: Chesterton, E., Sparks, A.M., Burke, T., Komdeur, J., Richardson, D.S., Dugdale, H.L. '*The impact of helping on helper life-history and fitness in a cooperatively breeding bird.*' Project was conceived by EC and HLD, with input from AMS. Data collection was done by all authors. Statistical analyses were designed and run by EC with input from HLD, AMS and DSR. EC wrote the draft, with input from all authors throughout. All authors agreed to submission.

Chapter 3

This work has been prepared as a manuscript for publication as follows: Chesterton, E., Sparks, A.M., Burke, T., Komdeur, J., Richardson, D.S., Dugdale, H.L. '*Life-long helper effects on offspring fitness in a cooperatively breeding bird.*' Project was conceived by EC and HLD, with input from AMS. Data collection was done by all authors. Statistical analyses were designed and run by EC with input from HLD, AMS and DSR. EC wrote the draft, with input from all authors.

Chapter 4

This work has been prepared as a manuscript for publication as follows: Chesterton, E., Sparks, A.M., Burke, T., Komdeur, J., Richardson, D.S., Dugdale, H.L. '*Single-generation fitness proxies as predictors of long-term genetic contributions in a cooperatively breeding bird.*' Project was conceived by EC and HLD. Data collection was done by all authors. Statistical analyses were designed and run by EC with input from HLD. EC wrote the draft, with input from all authors.

Appendix

This work has been submitted as a manuscript for publication to *Proc. R. Soc. B* as follows: Young, E.A., Chesterton, E., Lummaa, V., Postma, E., Dugdale, H.L. '*The long-lasting legacy of reproduction: lifetime reproductive success shapes expected genetic contributions of humans after ten generations.*' EC had input into statistical analysis design and code preparation, and commented on the draft prepared by EAY.

Alternative thesis style

This thesis uses an alternative style format to facilitate the dissemination of conducted work by adopting the manuscript formats of the journals to which manuscripts are/will be submitted. This thesis is constructed similarly to the 'standard' thesis format, with a general introduction, data chapters and general discussion. While the general introduction and discussion follow a standard format, the data chapters are written in the format of the corresponding journal. References are collected at the end of the thesis and follow a Harvard style referencing.

Acknowledgements

First, I would like to thank my supervisors, Hannah Dugdale, David Richardson, and Simon Goodman for all of the help and support you have provided me with over my PhD, along with the supervisors on the Seychelles warbler project, Jan Komdeur and Terry Burke. Your guidance has allowed me to get to get to this point, and I am very grateful. I would like to give a heartfelt thanks to my co-author and, more importantly, friend, Alexandra Sparks. You have helped me so much and I genuinely do not know where I would be without your guidance and unwavering support.

Thank you to the University of Leeds for providing me with the scholarship that kept me and my research afloat, and the Priestly Centre for the generous grant that allowed me to undertake fieldwork in the Seychelles. I would also like to thank everyone on the Seychelles warbler project, both past and present, for contributing to the dataset and performing the fundamental research that came before this project that allowed this research to take place.

I have met some incredible people during my time in Leeds, far too many to list them all here. However, I would like to give special thanks to Tara Cox. Your friendship is one of the most important things that I have gained from this experience. I could not have got through this PhD without you, and I know that our friendship will continue long after we have graduated. A big thanks to Lorelai Vennard for always being there for me. I treat your inbox like a journal; thank you for listening to my endless streams of consciousness and for still inviting me places during my write-up, despite my declines. Thank you to my wonderful housemate, Nicolle, for not judging me for consistently failing to do the washing up during my write-up (that's MY bit of thesis). Thank you to Rhiannon Carter, The Chat, and everyone at LPDS for keeping me sane. James Bell– we met towards the end of all this, but you have been so supportive and kind; thank you for being my daily reminder that life is wonderful. I would also like to thank Beans for being the best/worst emotional support animal, even though you will never see this acknowledgement because you are a dog and cannot read (translation: *woof woof*).

Finally, I would like to thank my parents, Stephen and Jayne Chesterton, for helping me at every step of way. Not just throughout this PhD, but for everything that came before and everything that will inevitably follow. You have helped me through every hardship I have ever faced, and I will cherish everything that you have done that has allowed me to achieve my goals. I love you both to the moon and back. I hope I have made you proud.

Abstract

Cooperative breeding is a system wherein more than two individuals raise offspring in a single breeding attempt. Helping is energetically costly, and helpers often sacrifice their personal reproduction, at least temporarily, to provide alloparental care. Why subordinates choose to help despite these apparent costs has been explored. However, studies have tended to focus on short-term fitness measures, as lifetime data are hard to obtain in most species due to system ecology. Here, I use the long-term Seychelles warbler (*Acrocephalus sechellensis*) dataset from a closed natural population with accurate fitness estimates to consider the short and life-long fitness consequences of helping behaviour to helpers (chapter 2) and helped offspring (chapter 3) and identified no positive fitness benefit in any of the metrics considered. However, I did find that the presence of a natal helper was associated with a reduced likelihood of males acquiring a dominant breeding position and reduced male lifetime reproductive success.

Whilst many studies use single-generation fitness proxies to estimate fitness, how well these proxies predict long-term genetic contributions is poorly understood. In chapter 4, I considered the relationship between single-generation life-history traits and fitness proxies and the genetic contributions of individuals to a population 15 years in the future. I found that life-history traits explained 8-33% of variation in genetic contributions, and lifetime reproductive success explained ≤56% of variation. The unexplained variation in genetic contributions is likely due to fitness having low additive genetic variance, environmental variation, and genetic drift. As such, the reproductive success of an ancestor does not necessitate the reproductive success of their descendants. My thesis improves our understanding of the evolution of cooperative breeding by highlight the importance of quantifying fitness at different life-history stages, as short-term benefits may not translate into improved longer-term fitness, and accounting for offspring sex-specific effects.

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Chapter 1

General introduction

1.1. EVOLUTION AND THE IMPORTANCE OF VARIATION

Natural selection is non-random variation in reproductive output. Variation in reproduction is determined by an individual's ability to survive and thrive in a particular environment. Individuals better adapted to their surroundings are more likely to reproduce, and those that are able to produce more offspring leave more descendant copies of their alleles, increasing their genetic representation in future populations (Darwin, 1859). Over time, in a given environment, the proportion of individuals expressing such beneficial, heritable traits that permit successful reproduction will increase in frequency from one generation to the next (Fisher, 1930). Natural selection is a strong, deterministic evolutionary force, and is the only force that invariably leads to an increase in population fitness (Lande, 1976, Rosenberg, 1988).

1.1.1. From genotype to phenotype

Genotypes, in the broadest sense, determine phenotype. Most phenotypic traits are polygenic and vary continuously between individuals; rarely are traits determined by a single genetic locus (Fisher, 1918, Goldstein, 2009, Barton et al., 2016). Indeed, complex traits tend to arise from the cumulative effect of a number of low-magnitude genetic effects and their interactions with other genetic loci and the environment (Bateson, 1907, Price and Gottesman, 1991, Andersson and Georges, 2004, Hill et al., 2008, Barros and Offenbacher, 2009, Frazer et al., 2009, Duncan et al., 2014). Genetic variation is therefore essential for evolution by means of natural selection to occur, as it is genes (and their interactions) that lead to phenotypic diversity within a population on which natural selection can then act (Darwin, 1859, Fisher, 1930).

Genetic variation can arise from a number of different sources. Fundamentally, it is different forms of mutation that drive variation in genotype (Lande, 1995, Martinsohn et al., 1999). DNA replication is an imperfect process, and random errors in replication lead to mutations within genes, giving rise to new allelic variants (Kunkel and Bebenek, 2000, Huttley et al., 2000, Tippin et al., 2004). If mutations occur within the germline, they are heritable and can be passed on to future generations (Ellegren et al., 1997, Ségurel et al., 2014). In sexually reproducing species, random assortment, recombination, and segregation of chromosomes facilitate additional variation at the genomic level, giving rise to individuals with unique allelic combinations and, consequently, unique phenotypes (Fisher, 1930, Muller, 1932, Kondrashov, 1993). If the phenotype confers a fitness advantage, the phenotype (and the alleles by which it is determined) is expected to increase in frequency as generations pass by means of natural selection.

Stochastic evolutionary forces such as genetic drift can also influence the frequency of allelic variants (and the phenotypes they confer) within a population. Genetic drift is a non-deterministic evolutionary force that occurs as a result of recombination and random sampling of gametes (Kimura, 1979, Kimura, 1983). In small populations, genetic drift can cause allelic frequencies to change rapidly – variants can be lost or arrive at fixation much quicker than in larger populations (Frankham et al., 2002). Genetic drift tends to reduce within-population and increase between-population genetic variation (Frankham et al., 2002, Futuyma, 2009, Barton et al., 2007). Migration is another stochastic force; two populations of the same species may have different allelic variants (or frequencies of those variants), gene-flow between these populations as a result of migration can then result in homogenisation and reduced inter-population variation (Waples and Gaggiotti, 2006, Goodnight, 2011). Often, migration can counteract the opposing forces of natural selection and genetic drift (Slatkin, 1987, Ellstrand, 2003). As each population has their own trajectory in terms of allelic frequencies (caused by drift and/or natural or sexual selection), migration from one population can reintroduce lost variants or reduce the frequency of common variants within the second population (Goodnight, 2011). This can have a positive impact on population fitness by introducing advantageous alleles which natural selection can then act, or a negative effect if it introduces maladapted alleles or disrupts interactions between loci conferring an advantageous polymorphic trait (Burton and Sandole, 1986, Lenormand, 2002, Garant et al., 2007).

1.1.2 Fitness and the use of proxies

'Fitness' is a relative concept referring to an individual's ability to leave descendant copies of themselves (and their alleles) compared to other conspecifics (Darwin, 1859). If a particular phenotype confers a fitness advantage, typically, we are referring to its tendency to increase the survival and subsequent reproduction of an individual relative to others within a population (Grafen, 2020). If we wish to understand how a particular trait evolved, or gain insight into its evolutionary potential, we need to consider how the trait influences variation in survival and reproductive success (Grafen, 1988, Clutton-Brock and Sheldon, 2010).

Lifetime reproductive success (LRS) is a widely used approximation of Darwinian fitness (Kruuk et al., 1999, McLoughlin et al., 2006, Sparkman et al., 2011, Le Boeuf et al., 2019), and provides a direct measure of the amount of genetic information that a breeding individual passes on to the F_1 generation. However, in wild populations, accurately quantifying LRS can be challenging. Longitudinal data are required, and individuals need to be observed from birth to death, and genetic parentage needs to be accurately assigned. Unfortunately, few study systems have access to such data. Most study systems exist in open populations with some degree of immigration and emigration, which makes life-long tracking of individuals exceptionally difficult, especially in long-lived species. And so, researchers often estimate fitness using shorter-term proxies, or consider how particular traits affect individual life-history strategies that are, in themselves, expected to correlate with reproductive success (Powers et al., 2020). For instance, researchers might consider how body condition affects the likelihood of achieving a dominant status in a socially-hierarchical species (French and Smith, 2005, van de Crommenacker et al., 2011, Giles et al., 2015, Wright et al., 2019), with dominance often being correlated with a higher LRS (von Holst et al., 2002, Schubert et al., 2007, Hodge et al., 2008).

However, the extent to which certain life-history traits can predict LRS has been questioned (Dobson et al., 2020, Neuhaus, 2006, Rubach et al., 2020). For example, breeding at an earlier age is often used as an estimate of reproductive success, as individuals that start breeding earlier could, theoretically, produce more offspring over their lifetimes (Russell et al., 2007a, Hayward et al., 2014). However, there is thought to be a negative trade-off between early reproduction and longevity, and so whether or not an earlier age at first breeding actually translates to a higher LRS is likely dependent on both the species and the context (Williams, 1957, Stearns, 1992, Blomquist, 2009). Further, fitness proxies such as LRS do not provide a measure of how much genetic information an individual contributes to generations beyond F_1. Indeed, the degree to which single-generation fitness proxies can explain longer-term genetic contributions has been questioned within the literature (Brommer et al., 2004, Reid et al., 2019b, Chen et al., 2019, Young et al., 2022, Alif et al., 2022). Still, understanding how certain phenotypes affect the reproductive success of individuals within a single-generation is an important first-step in understanding how particular traits influence long-term genetic fitness.

1.1.3. How well do fitness proxies predict genetic contributions?

The genetic contributions of an individual to a future population can be calculated to understand the relationship between life-history traits, fitness proxies, and longer-term genetic contributions. If genomic data are available, genetic contributions can be determined by considering the actual, realised amount of shared genetic information between an ancestor and their descendants (Leimar, 1996, McNamara and Houston, 1996). When genomic data are not available, genetic contributions can be estimated using genetic pedigree information based on the summed estimated relatedness between ancestors and their descendants (Chen et al., 2019, Reid et al., 2019a, Hunter et al., 2019, Alif et al., 2022, Young et al., 2022). For instance, breeding individuals share ~50% of their genetic information with their offspring (i.e., they have a relatedness coefficient (*r*) of 0.5 with each). Long-term genetic contributions can then be estimated by considering the amount of genetic information that an ancestor shares with all of their direct descendants at a given timepoint in the future. Estimated genetic contributions can be calculated as absolutes (i.e., a deceased individual with 1 living offspring and 3 grand-offspring will have a genetic representation of 1.25 in the extant population) or as a proportion of population size (i.e., the absolute estimated genetic contribution divided by the total number of individuals alive in the extant population; Reid et al., 2019). Understanding the relationship between life-history traits, fitness metrics and future genetic contributions will provide insight into how accurately these measures predict the number of descendant copies an individual contributes to future populations (that is, an estimation of their Darwinian fitness; Darwin, 1859).

1.2. COOPERATIVE BREEDING

Natural selection operates at the level of the individual, favouring traits that maximise survival and subsequent reproduction (Fisher, 1930). In his pivotal work, Darwin wrote "*natural selection will never produce in a being anything injurious to itself, for natural selection acts solely by and for the good of each*" (Darwin, 1859). Behaviours that reduce the fitness of an actor in order to benefit a recipient are, consequently, very hard to reconcile with the theory of natural selection. Yet, in some species, the behaviours of some individuals can appear almost altruistic. Perhaps one of the most striking examples of this is cooperative breeding. In cooperatively breeding species, subordinate 'helpers' will often forego their own reproduction, at least temporarily, in favour of raising non-descendant offspring (Cockburn, 2006). In addition, the help that they provide, such as incubating, defending, and provisioning offspring, has been shown to be energetically costly (Heinsohn and Legge, 1999, Dickinson and Hatchwell, 2004, van de Crommenacker et al., 2011). Why an individual would choose to help despite these apparent energetic and reproductive costs has been a topic of great interest to evolutionary biologists. Our understanding of the proximate and ultimate causes of cooperative breeding behaviour has improved considerably over recent decades (Koenig and Dickinson, 2016). However, there is a great deal of within and between species variation when it comes to cooperative behaviours, and so it is unlikely that we will arrive at a generalisable theoretical framework of cooperative breeding. Nonetheless, research can seek to understand the relative importance of the different costs and benefits associated with cooperative breeding across various taxa.

1.2.1. The evolution of delayed dispersal

Delayed, or limited, dispersal is one of the primary modes by which many (but not all) cooperative breeding groups form (Emlen, 1982, Koenig et al., 1992, Griesser et al., 2017). There are a number of hypotheses that seek to explain why an individual would delay dispersal. The 'habitat saturation' hypothesis, initially proposed by Selander (1964), suggested that a lack of available territories limits individual dispersal opportunities, causing offspring to remain in the natal territory. This hypothesis has since been expanded upon to include a number of additional ecological and demographic factors that can affect an individual's ability to disperse, giving rise to the 'ecological constraints' hypothesis (Emlen, 1982, Emlen, 1994). For instance, dispersal may be associated with heightened mortality risk (Ligon, 1990, Du Plessis, 1992, Heg et al., 2004, Griesser et al., 2006, Groenewoud et al., 2016), a reduced likelihood of acquiring territory (Emlen, 1984, Woolfenden and Fitzpatrick, 1984, Komdeur, 1992) or mates (Smith and Ridpath, 1972, Clarke, 1989, Walters et al., 1992b), or a low chance of successful breeding even if a territory were to be acquired (Reyer, 1980, Emlen, 1982, Stacey and Ligon, 1987, Curry, 1988). However, the ecological constraints hypothesis has been criticised as being insufficient to explain delayed dispersal (Stacey and Ligon, 1991). Whilst the ecological constraints hypothesis emphasises the *costs* of dispersal, unless there is also some benefit of philopatry, individuals might choose to "float" – a strategy that involves existing within a population with no association to any particular group or territory (Spinks et al., 2000, Ridley et al., 2008, Kingma et al., 2016b). Indeed, a vast majority of species experience intense competition for territory and reproduction, yet relatively few elect to delay dispersal (Stacey and Ligon, 1991, Koenig et al., 1992).

The 'benefits of philopatry' hypothesis argues that delayed dispersal occurs not because an individual is constrained in their ability to disperse, but, rather, remaining on the natal territory is associated with significant benefits (Stacey and Ligon, 1987, Waser, 1988, Stacey and Ligon, 1991). For example, foraging as a group may prove more successful than foraging solo, and more individuals may be able to better defend a territory than a single individual alone (Herrera and Macdonald, 1989, Balshine et al., 2001, Jungwirth et al., 2015). The ecological constraints and benefits of philopatry hypotheses are, however, united in the fact that they both detail a cost-benefit analysis of dispersal and philopatry, one in which philopatry is favoured because it has fewer associated costs and/or higher benefits than attempting to breed independently (Koenig et al., 1992, Komdeur, 1992, Emlen, 1994).

In addition, the life-history traits hypothesis (Arnold and Owens, 1998) predicts that certain life-history traits may predispose a population towards delayed dispersal, including an extended period of offspring dependency, high adult survival, and high reproductive rates (Gaston, 1978, Arnold and Owens, 1998, Pen and Weissing, 2000, Lukas and Clutton-Brock, 2012). Indeed, ecological constraints are not intrinsic properties of the environment itself, but a consequence of birth, death, survival, and dispersal rates of a population occupying a specific location (Kokko and Lundberg, 2001). Ricklefs (1975) suggested that cooperative breeding was most likely to occur when the rate of reproduction exceeded the death rate, leading to a surplus of adult individuals and further saturation of the environment. For short-lived species with a high rate of population turnover, cooperation is unlikely to occur because breeding vacancies arise at a faster rate, allowing individuals to disperse and reproduce independently (Kokko and Lundberg, 2001). However, there are exceptions; for instance, the long-tailed tit (*Aegithalos caudatus*) is not constrained by habitat saturation and has low adult survival, yet individuals delay dispersal and breed cooperatively (Hatchwell, 1999). The evolution of cooperative breeding is, therefore, likely to occur due to a complex interaction between existing life-history traits and ecological factors (Kokko and Lundberg, 2001; Koenig and Dickinson, 2016) as outlined by the broad constraints hypothesis (Hatchwell and Komdeur, 2000).

Furthermore, cooperative breeding is not an inevitable consequence of delayed dispersal. Delayed dispersal may be necessary for the evolution of cooperative breeding in many species, but it is not sufficient (Drobniak et al., 2015, Griesser et al., 2017). Indeed, there are many species in which delayed dispersal leads to group- or family-living, in which individuals do not provide help (Cockburn, 1998, Russell, 2004). For instance, species such as the white-breasted mesite (*Mesitornis variegate*; Gamero et al., 2014) have very high survival rates and delay independent reproduction, yet do not breed cooperatively.

1.3. FITNESS BENEFITS OF COOPERATIVE BREEDING

In order for cooperative breeding to occur, there must be benefits to helping over remaining in the natal territory as a non-helping subordinate (Cockburn, 1998, Clutton-Brock, 2002, Bergmüller et al., 2007). There are two types of fitness benefits that can be obtained through helping: indirect and direct.

1.3.1. Indirect fitness benefits

Indirect fitness benefits refer to the fitness benefits obtained from facilitating the production of non-descendant kin (Hamilton, 1964). As related individuals share a certain proportion of genes that are identical by descent, helping relatives to survive and reproduce can increase a helpers genetic representation in future populations, even in the absence of direct reproduction (Nonacs, 2011, Lukas and Clutton-Brock, 2012, Komdeur et al., 2017). Hamilton was the first to explain how kin-directed cooperation might evolve using a simple formula now known as 'Hamilton's rule':

$$\boxed{\mathbf{C < B}\boldsymbol{r}}$$

Here, 'C' indicates the cost of a particular behaviour to the helper, 'B' is the benefit the behaviour provides to the recipient, and '*r*' is the level of relatedness between the two individuals (Hamilton, 1964). For natural selection to favour a helping interaction, B*r* (benefit x relatedness) must outweigh C (cost). In the context of cooperative breeding, an individual may expend valuable energetic resources providing alloparental care, which may reduce their survival and future reproductive success (C; Heinsohn and Legge, 1999). However, the care that an individual provides may result in a significant benefit to the recipients of their help; for instance, helpers may increase the number or quality of offspring produced by a breeder (B; Komdeur, 1994, Hatchwell et al., 2004). If a helper is unrelated to the recipient of their help ($r = 0$), regardless of the level of benefit they provide, the right side of the formula will always equal 0. As such, if the helper incurs any fitness cost through the interaction, the behaviour should not evolve as C will outweigh B*r* and the helper will obtain no indirect fitness benefit (Hamilton, 1964). In contrast, if the benefit to a relative is high enough, helping can evolve even if costs are incurred by the helper, as long as $C < Br$.

Whilst Hamilton's Rule may explain why an individual might choose to help a relative, it does not necessarily explain why an individual would sacrifice independent breeding in favour of helping to raise non-descendant kin. In almost all circumstances, the indirect benefits accrued through helping are thought to be less than the direct fitness benefits that could be acquired through an individual's own, personal reproduction (Brown, 1987, Oli and Armitage, 2008). However, when reproductive opportunities are limited, for instance, when habitats are saturated and there is limited opportunity for dispersal, indirect benefits could be one way in which helpers make 'the-best-of-a-bad-job.' However, in some species with lifetime monogamy and low-level promiscuity, the indirect fitness benefits obtained through helping may be sufficient to promote cooperation over independent breeding (Hughes et al., 2008, Cornwallis et al., 2010, Lukas and Clutton-Brock, 2012, Boomsma, 2013). Indeed, in social Hymenoptera where monogamy is strict and enforced, daughters raising female full-siblings can be predicted by Hamilton's rule (Boomsma, 2009).

There are different ways in which helping can increase the indirect fitness of the helper. However, the extent to which indirect fitness can be obtained through helping often depends on how dominant breeders respond to helper presence. Dominant breeders may reduce their own provisioning rate and allow helpers to compensate for their reduction in care (Crick, 1992). As a result, dominant breeders can conserve and reallocate their resources to self-maintenance and future broods, with current offspring suffering limited/no reduction in provisioning (Crick, 1992). In this way, helpers 'lighten-the-load' of the dominant breeders, which, in some species, has been shown to increase a dominant breeders tenure and lifespan (Hammers et al., 2019, Downing et al., 2021, Dammann et al., 2011, Austad and Rabenold, 1985). With this additional time to reproduce, dominant breeders may be able to produce a greater *quantity* of offspring, maximising the indirect fitness that can be obtained by helpers. Secondly, in some species, dominant breeders may only reduce their provisioning partially, or not at all, resulting in offspring receiving provisions at a higher rate than if they were cared for by dominant breeders alone (Johnstone and Hinde, 2006, Savage et al., 2013, Liebl et al., 2016). This additive care can increase the survival rate of individual offspring, enabling more offspring to be successfully produced over a given amount of time (Komdeur, 1994, Richardson et al., 2002).

Furthermore, additive care could increase the *quality* of helped offspring. Additional provisions may increase offspring body condition and, as juvenile body mass frequently predicts adult body mass (Boag, 1987, Searcy et al., 2004, Festa-Bianchet et al., 2000, Brown et al., 2022), the benefits of helpers could have long-term effects on offspring fitness. If helped offspring have a higher rate of late-life survival and reproductive success, helpers, in turn, will be able to accrue indirect fitness benefits from raising these more successful relatives (Hamilton, 1964). However, few studies have considered the long-term effects of helping on offspring fitness directly (Maccoll and Hatchwell, 2004, Vitikainen et al., 2019, Sparkman et al., 2011, Sparks et al., 2022), and so the extent to which indirect fitness benefits can be acquired in this way remains relatively unknown.

In more recent decades, the importance of indirect fitness benefits in the evolution and maintenance of cooperative breeding has been called into question. Many cooperatively breeding species are not strict monogamists, and some have surprisingly high rates of extra-pair reproduction, especially in avian taxa (Dunn et al., 1995, Griffith et al., 2002, Hughes et al., 2003, Webster et al., 2004, Kingma et al., 2009, Hellmann et al., 2015). In the cooperatively breeding Australian magpie (*Gymnorhina tibicen*), the rate of extra-pair paternity has been shown to be as high as 81.4% (Hughes et al., 2003). Indeed, true genetic monogamy is believed to occur in only 14% of passerine species (Griffith et al., 2002). If monogamy is not upheld, then the level of relatedness between helpers and helped offspring can vary dramatically (Riehl, 2013, Brouwer and Griffith, 2019). Moreover, even within majority-kin groups, cooperative behaviours are not necessarily directed toward relatives. For instance, early studies on the *Manorina* honeyeater (*Manorina melanocephala*) found a high-level of kinship between group-members and concluded that indirect fitness benefits must be driving cooperative behaviour (Painter et al., 2000). However, later studies found that most cooperative interactions within this species actually occurred between non-relatives (Wright et al., 2010). Indeed, non-kin cooperation is more common than was once thought; in ~45% of cooperatively breeding birds, helping occurs between non-relatives (Riehl, 2013). If indirect benefits were the primary incentive for cooperative breeding to occur, this level of non-kin cooperation would be unexpected.

In some species, cooperative groups composed of non-kin may even have an adaptive advantage over groups of kin (Nonacs and Kapheim, 2007, Nonacs and Kapheim, 2008). Individuals within non-kin groups vary in their skills and attributes (a cooperative strategy known as ‘social heterosis’), allowing tasks to be more efficiently partitioned between individuals. So, whilst the importance of indirect fitness benefits are undisputed in some taxa (Lukas and Clutton-Brock, 2012, Hughes et al., 2008, Nonacs, 2011), there are many instances where indirect fitness benefits are not sufficient or required to promote cooperative breeding. In many species, helping may arise due to the direct benefits of helping *generally*, as opposed to the indirect benefits of helping relatives (Clutton-Brock, 2002). Indeed, whilst indirect fitness is widely accepted as being an important driving force in cooperative breeding, studies suggest that it likely only explains ~10% of within-species variation in helping effort (Griffin and West, 2003).

1.3.2. Direct fitness benefits

Direct fitness benefits can be obtained if helping leads to an increase in the future survival (and subsequent reproduction) of the helper (Koenig and Dickinson, 2004). There are at least six hypotheses that address the direct benefits that helpers can acquire from helping.

Pay-to-stay

The pay-to-stay hypothesis proposes that helping behaviour is used as a form of ‘rent’, paid by subordinates in exchange for group membership (Gaston, 1978). Cooperation only occurs if, overall, both dominant breeders and subordinates obtain a net benefit from the interaction (West et al., 2007). As additional group members often increase reproductive and resource competition within the group (Schoepf and Schradin, 2012, Sorato et al., 2016), subordinates are unlikely to be tolerated unless their presence benefits dominant breeders (Goldstein et al., 1998). The pay-to-stay hypothesis argues that subordinates provide care to non-descendant offspring as a way of appeasing dominant breeders, allowing them to retain group benefits and avoid aggression and possible eviction from the territory (Bergmüller and Taborsky, 2005). As a result, dominant breeders benefit from the help that subordinates provide to offspring, and subordinates benefit from group membership. Notable benefits of group membership to subordinates include resource/territory access, possible mating opportunities (Hellmann et al., 2015) and reduced predation rates (Groenewoud et al., 2016).

However, if subordinates impose little or no cost to dominant breeders, rent is neither required nor enforced, as the costs associated with eviction are likely to be higher than allowing subordinates to stay (Kokko et al., 2002). For instance, aggression could lead to physiological stress and reduce the body condition of dominant breeders (Young et al., 2006). Additionally, eviction from the territory could reduce the survival and reproductive success of a subordinate (Gilchrist, 2006), which will then translate into a loss of inclusive fitness to the dominant breeder should the subordinate be a relative (Quinones et al., 2016). Dominant breeders are therefore likely to have a higher tolerance for ‘lazy’ subordinates if they are related, as punishing them could reduce their own fecundity (Marshall and Rowe, 2003). Indeed, in species with high levels of relatedness, subordinate-directed aggression is often absent (Quinones et al., 2016). If related subordinates face minor (or no) punishment for laziness, then the fact that they still provide care could suggest that other benefits are more important for the evolution of cooperative breeding.

Co-breeding

'Reproductive skew' describes how the reproduction within a social group is partitioned between group members (Keller and Reeve, 1994). In some cooperatively breeding species, reproduction is completely monopolised by a single breeding pair (Jarvis, 1981, Field and Foster, 1999). In others, the extent of reproductive skew is less extreme, with dominant breeders conceding a proportion of reproduction to subordinates (Keller and Reeve, 1994, Johnstone, 2000, Nonacs and Hager, 2011). In some species, subordinates may help to raise the offspring of the dominant pair in exchange for these reproductive concessions (Reeve et al., 1998, Clutton-Brock, 1998, Reeve and Shen, 2006). So, rather than individuals paying to stay (and receiving benefits associated with group-living), subordinates are paying for the opportunity to breed (Balshine-Earn et al., 1998, Downing et al., 2018). Co-breeding allows group members to obtain direct fitness despite holding a subordinate position, and might provide an incentive for individuals to help (Richardson et al., 2002, Groenewoud et al., 2018, Kim et al., 2022). In situations where independent breeding is unlikely to be successful, or the costs of dispersal are likely to be high, helping to raise non-descendant offspring in exchange for a share of a group's direct reproduction might be a strategic alternative (Reeve and Shen, 2006, Shen and Kern Reeve, 2010). However, it has been suggested that, if the benefits of philopatry or future reproductive opportunities are sufficiently high, subordinates may benefit from helping even in the absence of co-breeding (Koenig, 1990, Kokko and Johnstone, 1999). For instance, in a study by Koenig (1990), helpers still provided alloparental care when potential co-breeding partners were experimentally removed from the group. This might suggest that, in some species, co-breeding is more of an opportunistic behaviour, enabling subordinates to obtain direct fitness benefits when, or if, they are able to, rather than being a driver of cooperative breeding (Kokko et al., 2002).

Group augmentation

The 'group augmentation' hypothesis posits that individuals living in larger social groups benefit from higher fitness (Woolfenden, 1975). As such, by helping to raise offspring (irrespective of genetic relatedness), individuals increase the survival and subsequent recruitment of additional group members and obtain the benefits associated with a larger social unit (Clutton-Brock et al., 1999, Kokko et al., 2001, Bergmüller et al., 2007). Research documenting the benefits of large groups is widespread. For instance, in the cooperative meerkat (*Suricata suricatta*), larger groups are better able to defend themselves against predators (Clutton-Brock et al., 1999), and in the yellow-eyed Junco (*Junco phaeonotus*), individuals in larger groups spend more time foraging, as scanning for predators is shared between more individuals (Caraco, 1979). However, whether or not individuals engage in cooperative breeding for the explicit purpose of increasing group size is debated in the literature.

The group augmentation hypothesis describes two classes of benefit associated with large groups, those that are short-term and those that are long-term (Kokko et al., 2001). Short-term, mutualistic benefits are derived from the presence of additional group members, such as a reduced mortality or an increase in foraging success (Kingma et al., 2014). Long-term (active) benefits, on the other hand, are associated with an increase in the future reproductive success of the helper (Kokko et al., 2001). For instance, by helping to raise more offspring, individuals increase the number of future subordinates that might help them to raise their offspring should they acquire a dominant breeding position (Kokko et al., 2001, Kingma et al., 2011). The long-term benefits of group augmentation are an example of delayed reciprocity; subordinates invest in offspring on the premise that they will obtain future direct fitness as a result of increased offspring survival (Bergmüller et al., 2007). However, evidence for helping as a means of group augmentation is limited and mixed (Woolfenden, 1975, Wiley and Rabenold, 1984, Khan and Walters, 2000, Gilchrist, 2007, Kingma et al., 2011, Browning et al., 2012), and the hypothesis has been criticised within the literature as being poorly defined, and failing to make predictions that are sufficiently distinct from other fitness benefits such as indirect fitness (Cockburn, 1998, Wright, 2007). Whilst the group augmentation hypothesis could explain some interesting behaviours e.g., in white-winged choughs (*Corcorax melanorhamphos*), adults have been observed 'kidnapping' unrelated young to serve as helpers in their territory (Heinsohn, 1991), such behaviours are yet to be observed in additional taxa, and so the extent to which group augmentation applies to other systems remains a point of contention.

Social prestige

The 'social prestige' hypothesis, originally proposed by Zahavi (1995), argues that subordinates help as a way of signalling their phenotypic quality to group members and potential mates (Roberts, 1998, Lotem et al., 2003). Helping behaviour is presumed to be an honest signal, as only high-quality individuals with a surplus of resources can afford to engage in behaviours that are so energetically costly (Heinsohn and Legge, 1999, van de Crommenacker et al., 2011, Cram et al., 2015).

For helping behaviours to evolve due to social prestige, the level of investment that a subordinate provides must first be observed by a potential mate and increase the actors future breeding prospects (Nomano et al., 2013). Subordinates must therefore time their help to increase the likelihood of the intended audience being present to observe them (Zahavi, 1995). Indeed, early research supports this, for instance, Arabian babbler (*Turdoides squamiceps*) helpers made loud vocalisations and waited for group members to arrive before provisioning offspring (Carlisle and Zahavi, 1986). Helpers were also found to compete with one another to provide for nestlings by physically interfering and preventing others from helping (Zahavi, 1995). However, later studies on the same population of Arabian babblers found no evidence to suggest that subordinates pause after vocalising for social prestige, but, rather, such behaviour is sentinel, as synchronised feeding reduces predation at the nest-site (Wright et al., 2001). In addition, the competitive altruism noted by Zahavi (1995) was observed during a single season following a productive breeding season the year prior. Consequently, there was an abnormally large number of subordinates in the population, and so it is possible that dominance displays between these group members were erroneously interpreted as competition for social prestige (Wright, 1999).

Whilst some additional studies have provided evidence for social prestige, such as those on the bell miner (*Manoria malnophyrs*; McDonald et al., 2008) and sociable weaver (*Philetairus socius*; Doutrelant and Covas, 2007), it has been argued that the observed effects can likely be explained by observer-induced disturbances (McDonald et al., 2007), predator deterrence (Doutrelant and Covas, 2007), or the fact that helping behaviour is often correlated with other phenotypic markers of individual quality such as body size (McDonald et al., 2008). Evidence rejecting the social prestige hypothesis, however, is more abundant (Wright, 1997, Raihani et al., 2010, Kingma et al., 2011, Nomano et al., 2013, Brügger et al., 2018, Teunissen et al., 2021). Indeed, social prestige likely involves a high-level of cognitive processing and the use of information that many species are unlikely to be able to obtain (Wright, 2007, Wright et al., 2010, McDonald and Wright, 2011)

Territory inheritance

The 'territory inheritance' hypothesis describes how helping might be favoured if it increases the probability of an individual inheriting a high-quality territory (Woolfenden and Fitzpatrick, 1978). By helping to raise the offspring of dominant breeders, subordinates are tolerated in the territory, allowing them to remain in the breeding "queue" (Balshine-Earn et al., 1998, Pen and Weissing, 2000, Kokko and Ekman, 2002). Eventually, after the death of a dominant breeder, the subordinate helper may inherit the territory and obtain a dominant breeding position (Kinnaird and Grant, 1982, Stacey and Ligon, 1987, Wild and Koykka, 2014).

Cooperatively breeding species typically have longer lifespans than non-cooperative species (Arnold and Owens, 1998, Beauchamp, 2014). A longer life means lengthy breeding tenure for dominant breeders, resulting in the production of more subordinates than there ever will be vacant breeding positions (Arnold and Owens, 1998, Pen and Weissing, 2000, Downing et al., 2015). Life-history theory states that as lifespan increases, future reproductive potential increases relative to current investment (Roff, 1993), and so helping now in order to acquire territory in the future is potentially a good reproductive strategy. Mathematically, even in the absence of direct reproduction as a subordinate, an increased likelihood of territory inheritance and future reproduction may be enough of an incentive for a subordinate to provide help to non-descendant offspring (Kokko et al., 2002). However, the individual that occupies a territory following the death of a dominant breeder is not always the one that has been queueing the longest (Russell and Rowley, 1993). In fact, some studies have shown that it is rare for a helping subordinate to acquire a breeding position in their natal territory (Komdeur and Edelaar, 2001).

Studies assessing the importance of territory inheritance often overlook the impact that helping has on dominant breeder survival, and the consequences this would then have on territory inheritance (Khan and Walters, 2002). If helping behaviour lightens the load for dominant breeders, dominant breeders are able to reallocate their resources into self-maintenance as opposed to caring for current offspring (Crick, 1992). As a result, their lifespan (and their breeding tenure) could be extended (Austad and Rabenold, 1985, Dammann et al., 2011, Hammers et al., 2019, Downing et al., 2021), reducing the chance that a subordinate will inherit the territory. It seems unlikely, therefore, that helping behaviour evolved as a way for subordinates to remain in the breeding queue if helping ultimately reduces the likelihood of there being a future breeding vacancy (Shreeves and Field, 2002). However, it could be that helping has evolved as a way for subordinates to remain within the vicinity of other high-quality territories. Whilst helping may reduce the likelihood of inheriting of the natal territory, assuming spatial autocorrelation in habitat quality, helping may allow subordinates to remain in high-quality neighbourhoods in which a breeding vacancy may become available (Wiley and Rabenold, 1984, Zack, 1990, Komdeur and Edelaar, 2001, Kokko and Ekman, 2002, Ribeiro et al., 2012)

Parental experience

The ‘skills’ hypothesis suggests that by helping to raise non-descendant offspring, subordinates obtain valuable breeding experience that makes future breeding attempts more successful (Selander, 1965). In this way, subordinates obtain delayed direct fitness benefits in exchange for current investment in non-descendant offspring (Komdeur, 1996). Early support for the skills hypothesis comes from research on the Seychelles warbler (*Acrocephalus sechellensis*); when subordinates were translocated to neighbouring islands and free to acquire a dominant breeding position, individuals that had previous experience as a helper bred much faster in their first breeding attempt than those with no experience (Komdeur, 1996). Females with helping experience took approximately 4 months to produce their first brood, whereas females without helping experience took more than a year (Komdeur, 1996). Experienced females also manufactured stronger nests, and spent more time incubating the brood than the inexperienced (Komdeur, 1996). This could suggest that helping equips subordinates with the necessary skills to successfully fledge young. Consequently, in long-lived species such as the Seychelles warbler, helping may be an important investment for the success of future breeding attempts, and so it might be in a subordinate's best interest to provide help while waiting for a breeding vacancy to arise.

However, the study by Komdeur (1996) was conducted before the level of co-breeding in the Seychelles warbler had been quantified (see (Richardson et al., 2001)), and so genetic parents may have been misidentified as subordinate helpers. As such, it cannot be concluded that *helping* experience specifically increased breeding success, as the helpers in this particular study may have bred previously. In fact, Komdeur (1996) is one of the only studies to have found parental experience to be a direct fitness benefit of helping. Studies on other cooperative breeders such as the long-tailed tit (Meade and Hatchwell, 2010), acorn woodpecker (*Melanerpes formicivorus*; Koenig and Walters, 2011), red-cockaded woodpecker (*Leuconotopicus borealis*; Khan and Walters, 1997), and white-fronted bee-eater (*Merops bullockoides*; Emlen and Wrege, 1989) found no effect of prior helping experience on short-term breeding success. Few studies have considered how helping affects the long-term reproductive success of helpers, likely due to a lack of longitudinal data in most systems (DuVal, 2013, Busana et al., 2022b), and this thesis aims to fill this knowledge gap.

1.3.3. No singular benefit

Depending on the species and the context, different direct and/or indirect fitness benefits can provide an incentive for subordinates to provide alloparental care. It is unlikely that there is one prevailing benefit applicable to all taxa, but, rather, that helping is associated with a combination of costs and benefits unique to the system being studied (Kingma et al., 2010, Kingma et al., 2011). For instance, indirect fitness benefits have been shown to be exceedingly important in cooperatively breeding mammals (Lukas and Clutton-Brock, 2012) and eusocial insects (Hughes et al., 2008, Nonacs, 2011), yet appear to play less of a role in cooperative breeding in avian taxa where non-kin cooperation is commonplace (Riehl, 2013). Even within species, there are likely to be different costs and benefits of helping depending on the context. For example, in some species, subordinates migrate to non-natal habitats and provide care to non-relatives, a situation where they gain no indirect fitness benefit (Dunn et al., 1995, Richardson et al., 2002, Wright et al., 2010, Riehl, 2013, Groenewoud et al., 2018). However, the dominant breeders within this territory might award the helper with reproductive concessions (Balshine-Earn et al., 1998). Indeed, previous studies have suggested that, in some cooperative species, dominant breeders may be more likely to allow non-kin helpers to co-breed than they are related helpers, in order to maintain their cooperation (Nonacs, 2017). In the natal territory, however, helpers may obtain future direct fitness benefit or indirect fitness (Nonacs, 2011). The benefits of helping within species can therefore vary depending on the context.

The intra- and interspecific variation in helper effort and the costs and benefits associated with helping makes it notoriously difficult to develop a generalisable framework of cooperative breeding. However, as more data is collected on different taxa, we can contrast and compare the costs and benefits of helping in different lineages in an attempt to understand the evolutionary contexts in which helping behaviour evolved.

1.3.4. Inclusive fitness

Whilst direct and indirect fitness are often studied in isolation, it is their combined effect that leads to an individual's overall fitness – that is, their inclusive fitness. Hamilton (1964) stated that, in order to obtain an individual's inclusive fitness value, '*all components which can be considered as due to the individual's social environment*' should first be subtracted from the individual's reproductive success, and then added to the effect of that individual on conspecifics, weighted by the relationship coefficient between them. If the reproductive success of an individual is unaffected by the actions of conspecifics, and the fitness of conspecifics unaffected by that particular individual's actions, the fitness of the individual will be equal to their reproductive success, as there are no additional influences to be stripped (Oli, 2003). However, if the fitness of an individual is influenced by behavioural interactions with others, the effect of these interactions should be accounted for when calculating inclusive fitness (Hamilton, 1964). If social effects are not accounted for, this may lead to 'double accounting' in which different individuals (e.g., helpers *and* breeders) are credited for the same contribution to an individual's reproductive success (Creel, 1990).

In cooperatively breeding species, the behaviours of others can significantly impact an individual's reproductive success. For instance, alloparental care provided by helpers within a breed group might affect a breeder's rate of reproduction or the number of offspring that survive to a point of sampling (Komdeur, 1994, Richardson et al., 2007). In this way, a breeder with a higher rate of personal reproduction is not solely responsible for their increased reproductive success. As such, whilst a breeder may possess certain traits that correlate with their reproductive success, an increased reproductive success cannot be truly attributed to the breeders' behaviours without first accounting for the effect of the social environment (Oli, 2003). One way in which the effect of helpers could be accounted for is by stripping the average effect of one individual on another's reproductive success (Creel, 1990), considered on a per-breeding-season basis (Lucas et al., 1996).

Often, the nuances of inclusive fitness are misconstrued within the literature. For instance, Ricklefs and Miller (2001) describe inclusive fitness as '*the fitness of an individual plus the fitness of its relatives, weighted according to the coefficient of relatedness.*' Similarly, Griffin and West (2002) define inclusive fitness as '*the effect of one individual's actions on everybody's number of offspring, weighted by the relatedness.*' These definitions suggest that inclusive fitness can be quantified as a calculation of an individual's reproductive success and indirect fitness. However, it has been argued that, whilst such definitions highlight important components of fitness, they do not accurately describe fitness itself (McGraw and Caswell, 1996), nor are they consistent with Hamilton's original definition of inclusive fitness.

1.3.5. Helper effects on individual offspring fitness

One of the more general assumptions of cooperative breeding is that helping provides a benefit to helped offspring. Whilst progress is being made in analysing the early-life benefits of receiving help (*e.g.,* Lehmann and Keller, 2006), few studies have considered how the presence of a helper can affect the long-term fitness of individual offspring. Indeed, a number of studies have shown that helpers can improve the early-life survival and body condition of offspring (Solomon, 1991, Hatchwell et al., 1999, Dickinson et al., 1996, Koenig and Dickinson, 2004, Hodge, 2005, Salomon and Lubin, 2007, Kingma et al., 2010). In some instances, these early benefits have the capacity to continue into reproductive age. For instance, in the cooperatively breeding meerkat (*Suricata suricatta*), individuals raised with helpers are more likely to obtain a dominant breeding position and start breeding at a younger age (Russell et al., 2007a). This could suggest that the presence of helpers has a significant effect on long-term offspring fitness, as individuals that obtain dominance are responsible for the majority of within-group reproduction (Clutton-Brock et al., 2001). However, whilst links have been made between helpers and the reproductive *potential* of offspring, few studies have analysed how helpers affect the lifetime reproductive success of offspring directly (Vitikainen et al., 2019, Sparkman et al., 2011, Sparks et al., 2022). Therefore, assuming that because helpers have an apparent early-life benefit that this will result in an overall lifetime fitness benefit may prove inaccurate. Unless we are able to empirically quantify the effect of helpers on offspring fitness, the links we draw between early and late-life fitness are tenuous at best. Unfortunately, long-term studies on offspring fitness are rare in the literature, perhaps because they require comprehensive, longitudinal datasets that are not available for most systems. Additionally, open systems are not always able to follow individuals over their lifetime.

1.4. THE SEYCHELLES WARBLER

1.4.1. A conservation success story

The Seychelles warbler is a small (13-19g; Fig. 1a) facultative cooperatively breeding passerine endemic to the archipelagic island country of Seychelles (Safford and Hawkins, 2020, Komdeur et al., 2016). In the 1870s, the Seychelles warbler populated numerous islands across the Seychelles including Mahé, Marianne, Félicité, and Cousine (Oustalet, 1878). Although, a study by Spurgin et al. (2014) using museum specimens from the 1800s revealed a large effective population size, suggesting that the distribution of the Seychelles warbler was historically much larger than this. By the early 1900s, the number of Seychelles warblers had dramatically declined. Native vegetation had been almost completely destroyed to clear space for coconut (*Cocos nucifera*) plantations, and mammalian predators had been introduced to many islands across the Seychelles. Consequently, the Seychelles warbler had been completely extirpated from almost every island that it once inhabited. By the 1960s, there were only 26–50 individuals left (Crook, 1960, Loustau-Lalanne, 1968, Spurgin et al., 2014), confined to one remnant population on Cousin island (*ca* 29 ha; 04°20'S, 55°40'E; Fig. 1b) which remained predator-free (Collar and Stuart, 1985). The Seychelles warbler was critically endangered.

In 1968, Cousin Island was purchased by BirdLife International (then the International Council for Bird Preservation) and made a designated nature reserve for the explicit purpose of saving the Seychelles warbler from extinction. Intense conservation efforts began, and by 1982, the habitat on Cousin had been almost completely restored to native forestry (Bathe and Bathe, 1982). The Seychelles warbler population was able to flourish and reach carrying capacity (~320 adult individuals). Individuals were then translocated to four additional islands to establish new populations of this once endangered species: Aride and Cousine in 1988 and 1990, respectively (Komdeur, 1994), Denis in 2004 (Richardson et al., 2006), and Frégate in 2011 (Wright et al., 2014). Of the translocated populations, Aride and Cousine are now at carrying capacity (1,850 and 210 individuals, respectively; Wright et al., 2014), while the populations on Denis and Frégate continue to increase (424 birds on Denis in 2015; Doblas et al., 2015) and 141 birds on Frégate in 2016; Johnson et al., 2018). Now, the total number of Seychelles warblers is believed to be around 2750 individuals, and the conservation status of the Seychelles warbler has been reduced from endangered to vulnerable (IUCN, 2013).

FIGURE. 1. **A)** A fledgling Seychelles warbler (*Acrocephalus sechellensis*) in the hand after being ringed, blood sampled, and processed. **B)** An aerial photograph of Cousin Island, taken by Martin Harvey, courtesy of Nature Seychelles.

1.4.2. A model system

The entire population on Cousin has been monitored since 1985, during both the minor (January-March) and major (July-September) breeding seasons, although more rigorous study began in 1997. The vast majority of birds (>96% since 1997) have been blood sampled and ringed with a unique combination of three coloured rings, along with a British Trust for Ornithology metal ring, enabling individual recognition and tracking (Richardson et al., 2001). Blood samples are used for genetic analysis and sexing, and allowed the extensive Seychelles warbler pedigree to be established (Richardson et al., 2001, Hadfield et al., 2006, Sparks et al., 2021). The pedigree is based on up to 30 microsatellite markers and consists of all sampled individuals hatched between 1991 and winter 2018, with 89% of fathers and 86% of mothers assigned at ≥80% accuracy (Edwards et al., 2018, Sparks et al., 2021). Despite having the wing morphology capable of migration, inter-island dispersal is exceedingly rare (<0.1%; Komdeur et al., 2004, Komdeur et al., 2016). This lack of migration, along with an extremely high resighting rate (0.92 ± 0.02 for <2-year-olds and 0.98 ± 0.01 for older birds; Brouwer et al., 2010) means that individuals that are not observed for two or more consecutive field periods can be confidently presumed dead. Seychelles warbler adults have no predators, and can live up to 19 years (Hammers and Brouwer, 2017), with a mean post-fledging lifespan of 5.5 years (Komdeur, 1991). These factors facilitate the lifetime monitoring of individual Seychelles warblers, allowing fitness at different life-history stages to be accurately quantified. Thus, the Seychelles warbler is an excellent model system to answer evolutionary questions about the short- and long-term fitness consequences of cooperative breeding behaviours.

There are *ca.* 115 Seychelles warbler territories on Cousin, each occupied by a dominant breeding pair and 0–5 helping and non-helping subordinates (Komdeur, 1992, Richardson et al., 2002). The dominant breeding pair are determined through behavioural observations of mate-guarding and contact calls (Richardson et al., 2002). Subordinates are identified as all other sexually mature adults that reside within the territory, and 'helpers' are subordinates that provide help to non-descendant kin within the territory in the form of incubating or provisioning (Komdeur, 1994). Helper statuses are determined during 60-90-minute nest watches performing during the incubation and feeding stages (Komdeur, 1994). Roughly 42% of female subordinates help, compared to only 20% of male subordinates (Hammers et al., 2019). Whilst both sexes help, the tasks that they perform are split differently between the sexes; both sexes provision offspring, however, females are the only sex to incubate, and males often provide alloparental in ways that are not used to determine helper status, such as nest-guarding and territory defence (Komdeur, 1994). Helpers are often, but not always, the offspring of the dominant breeding pair from a previous clutch (Kingma et al., 2016a). Approximately 50% of territories on Cousin breed cooperatively, with at least one subordinate providing alloparental care to non-descendant offspring (Kingma et al., 2016a). The existence of non-helpers within the population is important, as it allows us to disentangle the benefits of helping from the benefits of a larger group size. Offspring can remain dependent upon caregiver provisions for up to 3 months, which is extremely long compared to other passerine birds.

The Seychelles warbler is socially monogamous and highly territorial year-round; once paired, individuals tend to remain on the same territory with their mate until one of them dies (Komdeur, 1992). Despite their social monogamy, the rate of extra-pair reproduction in this species is considerably high. Extra-pair paternity is common, with 41% of offspring being sired by extra-group dominant males (Richardson et al., 2001; Hadfield et al., 2006); subordinate males, on the other hand, rarely gain paternity, siring just 0.6% of offspring (Sparks et al., 2021). In addition, approximately 44% of subordinate females have the opportunity to co-breed alongside the dominant female, producing 11% of all offspring within a territory (Richardson et al., 2001, Raj Pant et al., 2019, Sparks et al., 2021). The high rates of extra-pair paternity and co-breeding means that helpers have a relatedness coefficient to offspring that is substantially lower than first-order relatives (mean $r = 0.16$; Richardson et al., 2003), which limits the amount of indirect fitness benefit a subordinate can gain through helping non-descendant kin.

1.4.3. The benefits of helping in the Seychelles warbler: a summary to-date

Dominant breeders, helpers, and helped offspring all stand to benefit from cooperative breeding behaviour, and the evolutionary stability of the system is likely dependent upon a complex interaction between the costs and benefits incurred by these group members.

In the Seychelles warbler, helpers have been shown to provide a significant fitness benefit to dominant breeders. Helpers provide additive compensatory care to offspring; dominant breeders reduce their provisioning rate in the presence of helpers, and helpers compensate for this reduction as well as providing additional food resources (van Boheemen et al., 2019). Indeed, in the presence of a helper, dominant breeders reduced their provisioning rate by ~12.9% (from 8.5–8.1 feeds per hour). The presence of a single helper increases the rate of nestling provisioning by 30.5% (from a total of 17.0 to 22.2 feeds per hour; van Boheemen et al., 2019). Dominant females that receive help have been shown to have longer breeding tenures and lifespans, which may allow them to produce more offspring than dominant females that do not receive help (Hammers et al., 2019). In addition, helpers have been shown to compensate for age-related declines in dominant breeder provisioning, enabling dominant breeders to be more productive in their older years (Hammers et al., 2021). By helping their parents to be more successful in their breeding attempts, helpers can acquire indirect fitness benefits. However, the level of relatedness between helpers and offspring tends to be low due to extra-pair paternity (mean r = 0.13; Richardson et al., 2003) and helping between non-kin is not uncommon (Groenewoud et al., 2018).

Evidence for the direct fitness benefits associated with helping is mixed in the Seychelles warbler. Helping has no effect on the likelihood of a helper inheriting their natal territory (*see*: territory inheritance section; Komdeur and Edelaar, 2001), and helping is unlikely to act as 'rent' paid to dominant breeders in exchange for territory membership, as helping is neither required nor enforced (*see*: pay-to-stay section; Komdeur and Edelaar, 2001). Most individuals help on their natal territory (but not all), which they rarely inherit, and so helping is unlikely to serve as a way for helpers to advertise their phenotypic quality to potential mates (*see*: social prestige section; Komdeur, 1992, Komdeur et al., 2016). In fact, helping has been recently shown to *decrease* the likelihood of female subordinates acquiring dominance (Busana et al., 2022a).

Co-breeding could be a potential incentive for females to help on non-natal territories, as previous research has shown that immigrant females that help are more likely to be awarded reproductive concessions than immigrant females that do not help (*see*: co-breeding section; Groenewoud et al., 2018). Whether females must help before they are allowed to co-breed on the natal territory (where helping primarily takes place), however, remains to be seen. Subordinate males rarely gain paternity, and so reproductive concessions are unlikely to be a motivating factor for males to provide care to non-descendant offspring (Sparks et al., 2021). Helping may also provide helpers with breeding 'skills' that enable them to be more successful breeders later in life (*see*: parental experience section; Komdeur, 1996). Translocated females with helping experience bred faster and were more successful in their first breeding attempt than individuals with no helping experience, which could have an effect on lifetime fitness (Komdeur, 1996). However, the level of co-breeding in the Seychelles warbler was not considered in Komdeur (1996), and so 'helpers' may have actually been co-breeders experienced with direct reproduction. Importantly, a more successful first breeding attempt does not translate into higher lifetime reproductive success as a recent analysis found that female helpers and non-helpers do not differ in their lifetime reproductive success (Busana et al., 2022a).

Helping has been shown to improve the quantity of offspring that can be fledged by dominant breeders (Komdeur, 1994, Hammers et al., 2015). In addition, helping has been shown to increase the likelihood of individual offspring fledging (Komdeur, 1994) and surviving to adulthood (Brouwer et al., 2012). However, the long-term fitness consequences of having a natal helper on individual offspring fitness have not yet been fully addressed. Previous studies have shown that helpers are associated with an increased offspring mass at fledging (Komdeur, 1994), and increased offspring mass is a strong predictor of adult mass in the Seychelles warbler (Brown et al., 2022). Adult mass, in turn, is associated with dominance (van de Crommenacker et al., 2011) and increased adult survival rates (Brown et al., 2022). Helpers may therefore have long-term effects on offspring fitness if they increase offspring reproductive success. However, a recent study considering parental age effects on offspring fitness controlled for helper presence and found that helpers have negative effect on female LRS (Sparks et al., 2022), which is thought to be driven by within-mother effects. Further research is needed to determine the long-term fitness consequences of natal helpers on helped offspring fitness.

1.5. THESIS OUTLINE

Cooperative breeding is a breeding system in which individuals help to raise offspring that are not their own. It is a comparatively rare breeding system in avian taxa, occurring in just 9% of bird species (Cockburn, 2006). Often, helpers sacrifice their own personal reproduction, at least temporarily, to raise the offspring of others (Cockburn, 2006). Why individuals would choose to help despite these apparent energetic and reproductive costs has been studied across different taxa (see Lehmann and Keller, 2006 for review). However, the majority of studies focus on the short-term fitness consequences of helping; comparatively few studies have considered how helping affects the long-term fitness of helpers (Maccoll and Hatchwell, 2004; DuVal, 2013, Busana et al., 2022). Further, few studies have considered the effect of helping on long-term measures of helped offspring fitness (*see* Maccoll and Hatchwell, 2004, Sparkman et al., 2011, Vitikainen et al., 2019, Sparks et al., 2022), although progress is being made in understanding the short-term consequences of having a natal helper (Lehmann and Keller, 2006). In chapters 2 and 3, I aim to quantify the short and long-term fitness consequences of helping for helpers and helped offspring. In chapter 4, I consider how well life-history traits and single-generation fitness proxies predict longer term genetic contributions to future populations.

1.5.1. Individual reproductive success as a first step

Inclusive fitness is difficult to quantify, as it requires the accurate quantification of both direct and indirect fitness benefits. In order to accurately quantify direct fitness, lifetime data are required; individuals need to be studied from birth to death and genetic parentage needs to be accurately defined. In addition, direct fitness should be first isolated from the benefits or costs associated with an individual's particular social environment (Hamilton, 1964). Indirect fitness may then be calculated as the additional, shared genetic information that an individual helps to transfer to the next generation by helping to raise non-descendant relatives (Oli, 2003). This could be calculated by considering how many offspring a breeding relative would produce *without* the helper and comparing it to the number of offspring that they produce *with* the helper (Koenig et al., 2023). The difference can then be attributed to the additional care that a helper provides and, after considering the relatedness coefficient between the helper and the breeding individual, provide a measure of the helper's indirect fitness (Koenig et al., 2023). The direct and indirect fitness can then be summed together, resulting in the helper's inclusive fitness.

Quantifying reproductive success is the first step to calculating inclusive fitness; the reproductive success of individuals must be calculated in order to derive their direct fitness, and the reproductive success of breeders (with and without a helper) must be calculated in order to determine a helper's indirect fitness (Hamilton, 1964). As chapters 2 and 3 focus on how helping affects the reproductive success (and associated life-history traits) of helpers and helped offspring, they provide a fundamental first step in calculating inclusive fitness, providing a basis for future study.

1.5.2. Chapter summaries

Chapter 2: The impact of helping on helper life-history and fitness

Chapter 2 addresses the effect of helping on a number of key helper breeding and fitness-related parameters. Specifically, I consider if helping experience influences the likelihood of an individual acquiring dominance, the age at which they acquire dominance, their dominant breeding tenure, the number of offspring they produce throughout their dominant tenure, and their lifetime reproductive success. Chapter 2 is, therefore, an exploration of both the short and long-term fitness consequences of helping. The model considering the number of offspring produced throughout an individual's dominant breeding tenure directly tests the 'skills' hypothesis – the idea that helping equips individuals with important caregiving skills that enable them to be more successful breeders when they acquire dominance (Selander, 1965). Whilst evidence for the skills hypothesis in wild populations is mixed (Emlen and Wrege, 1989, Dickinson et al., 1996, Khan and Walters, 1997, Hatchwell et al., 1999, Meade and Hatchwell, 2010; Koenig and Walters, 2011), a previous study on the Seychelles warbler found that helping experience improves short-term breeding success (Komdeur, 1996). The effect of helping on long-term helper fitness, however, has only been considered by a few studies (MacColl and Hatchwell, 2003; Duval, 2013; Busana et al., 2022a). Importantly, we separate helpers from co-breeders, as co-breeders have experience with direct reproduction as opposed to just helping.

Chapter 3: Life-long helper effects on offspring fitness

Chapter 3 considers the effect of having a natal helper on different measures of offspring breeding performance and fitness in the Seychelles warbler. We consider how the presence of a natal helper affects the likelihood of an individual acquiring dominance, age at first breeding attempt, lifetime reproductive success, and lifespan. In other cooperatively breeding taxa, helpers have been shown to improve short-term measures of offspring fitness, such as juvenile growth and/or survival (Solomon, 1991, Hatchwell et al., 1999, Dickinson et al., 1996, Koenig and Dickinson, 2004, Hodge, 2005, Salomon and Lubin, 2007, Kingma et al., 2010). It is possible that these early benefits carry over into reproductive age and affect long-term measures of offspring breeding and reproduction, such as lifetime reproductive success, although this has only been explored in a few studies (e.g., Sparkman et al., 2011; Vitikainen et al., 2019; Sparks et al., 2022). In the Seychelles warbler, helpers provide additive compensatory care; helped offspring receive provisions at a higher rate than offspring without natal helpers, despite dominant breeders reducing their provisioning rate in the presence of helpers (van Boheemen et al., 2019). It is possible that this additive care provides a benefit to offspring in key breeding and fitness-related parameters, which is explored here.

Chapter 4: Single-generation fitness proxies as predictors of long-term genetic contributions

Individual life-history traits and single-generation fitness proxies are often used to estimate fitness. How well these proxies predict long-term genetic contributions to future populations, however, is poorly understood. Recently, a handful of studies have considered the relationship between fitness proxies, such as LRS, and genetic contributions to future generations (Chen et al., 2019, Reid et al., 2019, Alif et al., 2022, Young et al., 2022). However, studies are yet to consider how life-history traits relate to future genetic contributions. As life-history traits are often used as approximations of fitness, understanding how they relate to genetic contributions provides important insight into how useful they are as proxies. In chapter four, we consider how the acquisition of a dominant breeding position, age at first breeding attempt, length of dominant breeding tenure, lifespan, and lifetime reproductive success affect individual genetic contributions to a population 15 years in the future.

Chapter 2

The impact of helping on helper life-history and fitness in a cooperative breeder

Submitted as a manuscript to Evolution

2.1. ABSTRACT

Cooperative breeding occurs when helpers provide alloparental care to the offspring of a breeding pair. One hypothesis as to why helping behaviour occurs is that helpers gain valuable experience (skills) that may increase their own future reproductive success. However, research has typically focused on the effect of helping on short-term measures of reproductive success. Fewer studies have considered how helping experience affects long-term fitness measures. Here, we analyse how helping experience is linked to key breeding and fitness-related parameters in the Seychelles warbler (*Acrocephalus sechellensis*). Importantly, we control for females that have previously co-bred, as these individuals will have experience with direct reproduction as opposed to helping. Helping experience alone had no impact on any of the fitness or life-history metrics looked at, except that helpers had an older age at first dominance. However, this did not equate to differences in reproductive success as helpers and non-helpers had the same length of dominance tenure. Interestingly, females that had previously co-bred produced more adult offspring as dominant breeders and had a higher lifetime reproductive success than females that had never co-bred. Our results suggest that helping experience alone does not lead to an increase in the fitness of helpers for any of the metrics considered, and highlights the importance of separating the effects of helping from that of co-breeding. Our findings also emphasise the importance of analysing the effect of helping on various life-history stages, as short-term fitness measures may not lead to an overall increase in lifetime fitness.

Key words: helper fitness benefits, cobreeding, cooperative breeding, Seychelles warbler, skills hypothesis, lifetime reproductive success

2.2. INTRODUCTION

Cooperative breeding is a breeding system wherein more than two individuals help to raise offspring. These helpers often forgo their own reproduction, at least temporarily, to help raise non-descendant offspring (Sherman et al., 1995) which is energetically costly (Heinsohn and Legge, 1999). Why an individual would choose to help despite these apparent reproductive and energetic costs has been a topic of great interest to evolutionary biologists.

The evolution of cooperative breeding can be separated into two complementary processes: the decision to delay dispersal, and the decision to help. Delayed dispersal may evolve, for example, due to ecological constraints (Selander, 1964, Brown, 1974, Gaston, 1978, Stacey, 1979) or the benefits of philopatry (Stacey and Ligon, 1987, Stacey and Ligon, 1991, Waser, 1988). The benefits of philopatry and ecological constraints hypotheses both involve a cost-benefit analysis of dispersing to an independent breeding position or remaining in the natal territory (Koenig et al., 1992, Emlen, 1994, Emlen, 1997) that ultimately leads to delayed dispersal being favoured. If the risks of dispersal are high e.g., there is a reduced likelihood of independent breeding due to habitat saturation (Selander, 1964, Walters et al., 1992a) or a low probability of finding a mate (Rowley, 1965, Clarke, 1989) and/or there are benefits to delaying dispersal such as survival benefits from remaining on a high-quality territory (Stacey and Ligon, 1991, Pasinelli and Walters, 2002), then an evolutionary transition towards family-living may occur. Additionally, the life-history hypothesis states that certain life-history traits such as an extended lifespan and reduced adult mortality are important in the transition toward family-living, as they lead to a surplus of individuals that are constrained in their ability to reproduce independently (Ricklefs, 1975, Arnold and Owens, 1998, Mourocq et al., 2016). The broad constraints hypothesis (Hatchwell and Komdeur, 2000) proposes that the ecological constraints, benefits of philopatry and life-history hypotheses may act at the same time, and the dual benefits hypothesis proposes that helper benefits can be split into resource defence and collective action (Nelson-Flower, 2018).

However, cooperative breeding is not an inevitable consequence of delayed dispersal (Gayou, 1986, Veltman, 1989, Ekman and Griesser, 2016), despite it being a pre-requisite in the majority of cases (Griesser et al., 2017). Individuals could choose to delay dispersal and reside on the natal territory without providing help to offspring, as they do in many species (Drobniak et al., 2015). A number of hypotheses seek to explain why an individual would choose to help in terms of direct fitness benefits, such as the pay-to-stay (Gaston, 1978), group augmentation (Woolfenden, 1975), territory inheritance (Woolfenden and Fitzpatrick, 1978), social prestige (Zahavi, 1995), and skills (Selander, 1965, Lehmann and Keller, 2006) hypotheses. Additionally, helpers can gain indirect fitness benefits from helping to raise related individuals (Hamilton, 1964). For instance, 'Hamilton's Rule' states that helping behaviours may evolve if the cost of helping is lower than the benefit obtained by a recipient, weighted by the relatedness between the two individuals ($C < Br$; Hamilton, 1964). Helpers may incur significant energetic costs from providing alloparental care, which may reduce their survival and future reproductive success (Heinsohn and Legge, 1999). However, as long as the benefit to the relative outweighs this cost, and the relatedness coefficient between the relatives is sufficiently high, helpers can gain indirect fitness benefits as they share a proportion of the same genetic information with the individuals they are helping (Hamilton, 1964). These hypotheses suggest that helping serves as a way for subordinates to make 'the-best-of-a-bad-job' and acquire fitness benefits in the absence of independent breeding. However, the benefits that apply to particular systems are heavily debated; for instance, indirect benefits are exceedingly important in cooperatively breeding mammals (Lukas and Clutton-Brock, 2012) and eusocial insects (Hughes et al., 2008, Nonacs, 2011), yet the existence of non-kin helpers in 45% of bird species brings the importance of indirect fitness into question (Riehl, 2013). It is likely, therefore, that the benefits of helping are both species and context dependent.

The 'skills hypothesis' proposes that helpers obtain valuable breeding experience from helping, and that helpers may be more successful and proficient breeders later in life than non-helpers (Selander, 1965). Helpers may therefore gain delayed direct fitness benefits through their helping behaviour by maximising their future reproductive potential. Initial support for the skills hypothesis came from the Seychelles warbler (*Acrocephalus sechellensis*), where females with prior helping experience bred faster, built stronger nests and incubated longer in their first breeding attempt as a dominant breeder (Komdeur, 1996). In long-tailed tits (A*egithalos caudatus)*, helpers that gained a dominant breeding position built more successful nests than individuals that had never helped (Hatchwell et al., 1999). Despite this, helping experience had no effect on breeding success in their first or second year (Meade and Hatchwell, 2010). Studies on other cooperative breeders, such as the acorn woodpecker (*Melanerpes formicivorus*; Koenig and Walters, 2011), red-cockaded woodpecker (*Leuconotopicus borealis*; Khan and Walters, 1997), and white-fronted bee-eater (*Merops bullockoides*; Emlen and Wrege, 1989) found no effect of prior helping experience on short-term breeding success. In the Western bluebird (*Sialia mexicana*), helpers fledged fewer chicks in their first year as dominant breeders compared to non-helpers (Dickinson et al., 1996). Consequently, support for the skills hypothesis, in wild populations, is mixed.

Whilst a number of studies have considered how helping experience affects short-term breeding success, fewer studies have considered the effect of helping on longer-term fitness metrics, such as lifetime reproductive success (LRS), that ultimately determine the amount of genetic material passed on to the next generation (Link et al., 2002). The limited number of studies considering the longer-term fitness benefits of helping is likely because longitudinal data are required; life-long data from birth to death are needed, which many studies cannot obtain due to system ecology. The few studies that have considered the effect of helping on LRS, such as those on the lance-tailed manakin (*Chiroxiphia lanceolata;* DuVal, 2013), long-tailed tit (Maccoll and Hatchwell, 2004), and female Seychelles warblers (Busana et al., 2022) have shown that helping has no effect on the LRS of helpers compared to non-helpers. Further work is needed to determine whether there are longer-term fitness consequences of having helping experience, and at what life history stages these effects are seen.

Here, we investigate the fitness benefits of being a helper in the cooperatively breeding Seychelles warbler population on Cousin Island, where breeding positions are saturated. Previously, helping experience was found to have positive short-term fitness effects (Komdeur, 1996). When female subordinates were translocated to unoccupied islands, those with helping experience bred faster in their first breeding attempt (Komdeur, 1996), built stronger nests, and spent more time incubating than females without helping experience (Komdeur, 1996). However, 44% of subordinate females co-breed (Richardson et al., 2001, Sparks et al., 2021) which was not accounted for in Komdeur (1996). As such, it cannot be concluded that helping experience *per se* increased future breeding success, as females may have had direct breeding experience. Since 1997, >96% of warblers on Cousin have been ringed (Richardson et al., 2001), with 98% of ringed birds having been blood sampled and genotyped (Sparks et al., 2021), allowing genetic parentage and the rate of co-breeding to be accurately determined (Richardson et al., 2001, Hadfield et al., 2006, Sparks et al., 2021). With genetic parentage established, we can now test whether any initial reproductive benefits of having helping experience translate into longer-term fitness benefits. Busana et al. (2022) found that female helpers were less likely to obtain a dominant breeding position and had similar LRS to non-helpers. However, Busana et al. (2022) did not analyse male helpers, and co-breeders and helpers were not separated. In addition, whilst Busana et al. (2022) considered the effect of helping on female LRS, they did not consider the number of offspring produced after acquiring dominance, so did not address the skills hypothesis.

Seychelles warblers rarely disperse between islands (<0.1% of all birds studied; Komdeur et al., 2004) and the yearly resighting probability on Cousin is high (0.92 ± 0.02 for <2-year-olds and 0.98 ± 0.01 for older birds; Brouwer et al., 2010). If a warbler is not seen for two consecutive field seasons, we can therefore confidently assume that they are dead (Brouwer et al., 2006), thus lifetime fitness can be calculated accurately, which is rare in natural populations. Consequently, it is possible to analyse the effect of helping on helper fitness at various life-history stages, allowing us to test for effects during both early and late-life whilst controlling for additional, potentially confounding variables. If helping improves the short-term breeding success of helpers, helping may be an important investment in long-term fitness (Selander, 1965, Komdeur, 1996), especially in long-lived species such as the Seychelles warbler (maximum lifespan: 19 years; Hammers and Brouwer, 2017).

Using a 21-year genetic pedigree spanning a maximum of 12 generations, we investigate short and long-term fitness consequences of helping experience in both sexes. Specifically, we test the predictions that helpers, compared to non-helpers, have an: increased likelihood of obtaining a dominant breeding position (i.e., prestige hypothesis), older age at acquiring dominance and shorter breeding tenure (as they spend time helping), produce more offspring as dominant breeders (i.e., skills hypothesis), and have a similar overall LRS (as helping and non-helping are both stable strategies). Importantly, we control for the effect of previous co-breeding experience.

2.3. METHODS

2.3.1. Study system and data collection

There are *ca.* 320 adults in the closed population of Seychelles warblers on Cousin Island (0.29 km^2; 4°20'S, 55°40'E) (Komdeur et al., 2016). The Seychelles warbler project began in 1985, with more intensive monitoring from 1997 onwards (Richardson et al., 2002). The population is studied during the major (June–September) and minor (January–March) breeding seasons (Richardson et al., 2002). The island contains ~115 Seychelles warbler territories (Komdeur, 2003), each of which is occupied by a breed group consisting of a dominant breeding pair and 0-5 helping and non-helping subordinates (Komdeur, 1992, Richardson et al., 2002). Roughly 42% of female and 20% of male subordinates help (Hammers et al., 2019). Breeding statuses are determined through behavioural observations. The dominant breeding pair in each territory are determined by observations of contact calls and mate-guarding (Richardson et al., 2002). Subordinates are defined as additional, sexually mature individuals that reside within the territory. One hour nest watches are performed to see whether subordinates help, either by incubating or provisioning offspring (Komdeur, 1994). Co-breeding females are subordinates that are the genetic mother of an offspring in their territory (Richardson et al., 2001).

Each season, as many individuals as possible are caught in mist-nests or as nestlings in the nest. Unringed birds are ringed with a unique combination of three ultraviolet-resistant colour rings, along with a British Trust for Ornithology metal ring. Blood samples (*ca*. 25µl) are then taken from all birds via brachial venepuncture and stored at room temperature in 100% ethanol for later DNA extraction and analysis. Up to 30 microsatellite loci (Richardson et al., 2000) are used to determine genetic parentage, and molecular sexing is performed using 1–3 loci (Sparks et al., 2021). The R package MASTERBAYES 2.52 (Hadfield et al., 2006) was used to assign parentage to 1809 offspring that hatched between 1991 and the minor season in 2018 (Edwards et al., 2018, Sparks et al., 2021), with fathers and mothers assigned to 86% and 82% of offspring, respectively, at ≥80% accuracy.

Groups typically produce one egg per season (Komdeur, 1996), although ~20% of clutches consist of 2–3 eggs (Richardson et al., 2001). Subordinate females occasionally lay eggs in the dominant female's nest, with ~11% of offspring being the product of co-breeding (Raj Pant et al., 2019, Sparks et al., 2021) by 44% of subordinate females (Richardson et al., 2001, Raj Pant et al., 2019, Sparks et al., 2021). Intra-specific egg dumping does not occur (Richardson et al., 2001). Extrapair paternity is common, with 41% of offspring sired by dominant males from a different territory (Raj Pant et al., 2019). Within-group subordinate males rarely gain paternity, siring just 0.6% of offspring (Sparks et al., 2021).

Seychelles warblers are territorial and insectivorous, so territory quality was estimated based on the amount of arthropod prey available within each territory (Komdeur, 1992, Brouwer et al., 2009), averaged across all monthly estimates taken during each breeding season. Missing territory quality data (151 territories across 40 seasons, n=703/1108 datapoints) were estimated using the mean territory quality values of the previous and subsequent breeding season of the same season-type (following Brouwer et al., 2006), as there is seasonal variation in territory quality (Dowling et al., 2001, Komdeur and Daan, 2005).

2.3.2. Estimation of life-history traits and fitness metrics

We investigated the relationship between helping experience and five measures of life-history and fitness: likelihood of becoming a dominant breeder, the age at which they become a dominant breeder, the length of an individual's dominant breeding tenure, the number of offspring produced during their dominant breeding tenure, and their LRS. Likelihood of dominance was a binary metric of whether an individual was ever assigned a dominant breeding status. For age at first dominance, dominance tenure, and number of offspring produced as a dominant breeder, only individuals that had obtained dominance at some point during their lifetime were included. Age at first dominance was the time difference between an individual's estimated hatch date and the midpoint of the first breeding season that they were assigned a dominant breeding status. Length of dominance tenure was calculated as the total length of time that an individual spends in a dominant breeding position. The number of offspring produced throughout an individual's dominant breeding tenure was calculated as the total number of genetic offspring that an individual produced as a dominant breeder, determined using the Seychelles warbler genetic pedigree. Only offspring that survived to adulthood (≥1 year old) were included, as they were capable of propagating the lineage. LRS was calculated in the same way, except instead of the number of offspring (≥1 year old) produced over an individual's breeding tenure, it was the total number of offspring (≥1 year old) produced over an individual's lifetime. LRS therefore included offspring that were produced pre- and post-dominance, either through co-breeding (females) or subordinate extra-pair paternity (males). In addition, LRS provided a measure of fitness for individuals that never acquired dominance and, instead, remained life-long subordinates.

2.3.3. Dataset and statistical analyses

For all analyses, generalised linear mixed-effects models (GLMMs) were performed in *R* 4.2.1. (R Core Team, 2022) using glmmTMB 1.1.4 (Brooks et al., 2017).

The dataset included deceased individuals that had hatched from 1997 to the minor breeding season in 2018. Only individuals that survived to independence (≥3 months) were included in the models to remove potential biases in the dataset; nests located high in the canopy are hard to reach, so individuals raised in these nests are often only ringed and sampled after they have fledged and are independent (~3 months). For age at first dominance, dominance tenure, and number of offspring produced as a dominant breeder, only individuals that had obtained dominance at some point during their lifetime were included. Individuals that had not been assigned a helper status *prior to dominance* and lived during a field period in which their helper status could not be determined (e.g., if no nest-watch had been performed on a known nest) were excluded from these analyses (males: *n*=175 males; females: *n*=125), resulting in a dataset of 340 individuals (males: *n*=161; females: *n*=188), of which 34 males and 62 females had previous helping experience. For the likelihood of obtaining dominance and LRS models, if, during any field period within an individual's *lifetime*, a bird with no assigned helper status lived during a field period in which their status could not be determined, they were excluded from these analyses (males: *n*=279; females: *n*=231), resulting in a dataset of 545 individuals (males: *n*=251; females: *n*=294), of which 57 males and 120 females had previous experience as a helper.

Models were run separately for each sex. 42% of female and 20% of male subordinates help in the Seychelles warbler (Hammers et al., 2019), and males and females differ in their life-history strategies; they have different dispersal tactics (Komdeur, 1992, Kingma et al., 2016a), age-related differences in territory acquisition (Eikenaar et al., 2008a), and greater variance in male than female lifetime reproductive success (Sparks et al., 2022), and so analysing them separately allowed for the disentanglement of sex-related benefits. The same fixed and random effects were included in the models for both sexes, the exception being that the female models included an additional variable addressing whether they had co-bred as a subordinate either before dominance (for the age at first dominance, length of dominance breeding tenure, and number of offspring produced throughout dominant breeding tenure models) or at any point over their lifetime (for the likelihood of dominance and LRS models). This was not appropriate for the male models as subordinate males rarely gain paternity (0.6%; Sparks et al., 2021).

All models included the following fixed effects: whether the individual had experience as a helper (factor: yes/no), maternal age at conception (years) as both linear and squared variables to control for maternal effects that affect reproductive success (Sparks et al., 2021), and territory quality as this can affect individual dispersal (Komdeur, 1992; Komdeur et al., 1995) and reproductive success (Sparks et al., 2022). Territory quality was incorporated in different ways depending on the model and our hypotheses. For the likelihood of dominance models, natal territory quality was included. For the age at first dominance model, territory quality was incorporated as the mean territory quality prior to obtaining dominance. For the dominance tenure and number of offspring produced during dominance models, the mean territory quality during dominance was included. For the LRS models, the mean territory quality over an individual's lifetime was incorporated. For the male likelihood of acquiring dominance model, whether the focal individual received help when they were a nestling (i.e., had a "natal helper") was also included, as males with helpers have a reduced likelihood of acquiring dominance (Chapter 3). For the dominance tenure and number of offspring produced during dominance models, the proportion of years as a dominant breeder that an individual had helpers was also included, as the presence of helpers can affect dominant breeder lifespan (Hammers et al., 2019) and reproductive success (Komdeur, 1994, Hammers et al., 2021). Cohort, genetic mother ID, and social father ID were included as random effects.

All models were checked for over-dispersion and zero-inflation using PERFORMANCE 0.5.1 (Lüdecke et al, 2021), and variance inflation factors (all <3; (Dormann et al., 2013). Model fit was determined by assessing plots of the observed values against the simulated squared residuals using DHARMa 0.3.3.0 (Hartig, 2022), as well as comparing the AIC values of candidate models, with the model of lowest AIC being preferred (Akaike, 1973). We fitted the following error distributions: binomial (likelihood of dominance models), negative binomial (male age at first dominance), quasi-Poisson distribution (female age at first dominance and breeding tenure models), and zero-inflated Poisson (number of offspring produced during tenure and LRS). Non-significant maternal age^2 effects were removed from the models to facilitate the interpretation of first-order age effects (see Table S1 for full models). Significance of random effects were determined using likelihood ratio tests comparing models with and without each random effect. For each model, the marginal effect and predicted counts of each variable of interest were calculated using GGEFFECTS 1.1.0 (Lüdecke, 2018). Marginal effects refer to the effect size of a variable of interest, after adjusting for all other variables within a model.

2.4. RESULTS

Dominance acquisition

Having helping experience had no effect on whether a male or female Seychelles warbler acquired dominance (Table 1). 36 out of 57 males that had helping experience became a dominant breeder (63.2%, 95% CI: 50.6–75.7%) compared to 84 out of 194 males that had no prior experience (60.8%, 95% CI: 53.9–67.7%). 78 out of 120 females with experience went on to become dominant breeders (65%, 95% CI: 56.5–73.5%), compared to 108 out of 174 that had no experience (62.1%, 95% CI: 54.9–69.3%). However, males that had natal helpers were less likely to become dominant breeders than males that did not have natal helpers (Table 1). In contrast, females hatched on higher quality territories were more likely to become dominant breeders than females hatched on lower quality territories (Table 1), but this was not the case in males.

Age at first dominance

For both male and female Seychelles warblers, having experience as a helper was associated with becoming a dominant breeder at an older age (Table 2; Fig. 1a). The mean age for a male to become a dominant breeder was 1.54 years (95% CI: 1.39–1.70 years, *n*=161). Males that had experience as a helper became a dominant breeder at 2.66 years (95% CI: 2.22–3.10 years, *n*=33) compared to males that had no helping experience that became dominant breeders at 1.25 years (95% CI: 1.18–1.33 years, *n*=128). The mean age for a female to become a dominant breeder was 1.88 years (95% CI: 1.68–2.08 years, *n*=181). Females with experience as a helper became dominant breeders at 3.04 years (2.67–3.41 years, *n*=62) compared to females that had never helped that became dominant breeders at 1.31 years (95% CI: 1.23–1.39 years, *n*=126). Female co-breeders also acquired dominance later than females that did not co-breed (Table 2; Fig. 1b).

Breeding tenure

Having experience as a helper had no significant effect on the tenure of dominant breeding in either sex (Table 3). For males that acquired a dominant breeding position, the mean length of dominance tenure was 3.33 years (95% CI: 2.92–3.74 years, *n*=161). Dominant males that had experience as a helper prior to acquiring dominance had a mean dominant breeding tenure of 2.64 years (95% CI: 1.79–3.45 years, *n*=33) compared to males that had no experience helping that had a mean dominant breeding tenure of 3.51 years (95% CI: 3.04–3.98 years, *n*=128). For females that have acquired a dominant breeding position, the mean length of tenure as a dominant breeder is 3.61 years (95% CI: 3.22–4.01 years, *n*=187). Dominant females that had experience as a helper had a mean breeding tenure of 3.59 years (95% CI: 2.91–4.27 years, *n*=62) compared to 3.62 years (95% CI: 3.14–4.11 years, *n*=125) for females that had no prior helping experience. In addition, dominant females that had helpers for a greater proportion of their breeding tenure had longer breeding tenures than dominant females that had helpers for a lower proportion of their breeding tenure (Table 3).

Number of offspring produced as a dominant breeder

We found no association between having experience as a helper and the number of offspring that an individual produces during their dominant breeding tenure in either males or females (Table 4). Males that had helping experience produced a mean number of 1.2 offspring (95% CI: 0.8–1.6, range: 1–6, *n*=33) compared to males with no helping experience that produced 1.7 offspring (95% CI: 1.3–2.0, range: 0–15, *n*=128). Females that had helping experience produced a mean number of 1.4 offspring (95% CI: 1.0–1.8, range: 0–8, *n*=62) compared to females with no helping experience that produced 1.7 offspring (95% CI: 1.4–2.0, range: 0–9, *n*=126). However, females that had co-bred prior to obtaining dominance produced more offspring during their dominant breeding tenure than females that did not co-breed (Table 4; Fig. 3). In addition, dominant females that had helpers over a greater proportion of their dominant tenure produced more offspring during this period than dominant females who had helpers for a lower proportion of their dominant tenure (Table 4). Females hatched by younger mothers also produced more offspring during their dominance tenure than females hatched by older mothers (Table 4).

Lifetime reproductive success

We found no relationship between having experience as a helper and the LRS of either males or females (Table 5). The mean lifetime reproductive success of males with helping experience was 0.8 offspring (95% CI: 0.6–1.1, range: 0–6, *n*=57) compared to males that had never helped that had a mean lifetime reproductive success of 1.1 offspring (95% CI: 0.8–1.3, range: 0–15, *n*=193). The mean lifetime reproductive success of females with helping experience was 1.5 (95% CI: 1.2–1.8, range: 0–8, *n*=120) compared to females that had never helped that had a lifetime reproductive success of 1.1 (95% CI: 0.9–1.3, range: 0–9, *n*=174). However, females that had co-bred had a higher LRS than females that had never co-bred (Table 5; Fig. 3). Females hatched by younger mothers also produced more offspring that survived to adulthood over their lifetimes than females hatched by older mothers (Table 5).

Table 1. Socio-ecological predictors of whether an individual becomes a dominant breeder in the Seychelles warbler, estimated using sex-specific GLMMs with binomial error distributions. Total number of males: 251 (males with helping experience: 57; males with natal helper: 55), total number of females: 294 (females with helping experience: 120, females with co-breeding experience: 54). The parameter estimate, standard error (SE), z-value, and p-value are given for each fixed effect, along with the conditional r^2 for each model. Significant results are shown in bold. Territory quality = natal territory quality. Reference level for helped ever/ natal helper/ co-bred ever = no.

		Males (*n*=251)					**Females (*n*=294)**				
Fixed effect	Levels	Estimate	SE	z	p	r^2	Estimate	SE	z	p	r^2
(Intercept)		0.52	0.50	1.04	0.298	0.28	0.10	0.36	0.29	0.771	0.09
Helped ever	Yes	0.35	0.41	0.85	0.395		0.20	0.29	0.68	0.496	
Co-bred ever	Yes	/	/	/	/		-0.14	0.36	-0.38	0.704	
Maternal age		0.43	1.01	0.43	0.670		-0.34	0.67	-0.51	0.611	
Natal helper	Yes	**-1.04**	**0.42**	**-2.47**	**0.014**		/	/	/	/	
Territory quality		0.63	1.68	0.38	0.707		**2.80**	**1.32**	**2.12**	**0.034**	
Random effect		Levels	Variance	p			Levels	Variance	p		
Mother ID		184	0.05	0.955			203	0.00	1.000		
Social father ID		177	0.61	0.483			196	0.02	0.960		
Cohort		**22**	**0.44**	**0.048**			22	0.20	0.139		

Table 2. Socio-ecological predictors of the age that Seychelles warblers become dominant breeders, estimated using sex-specific GLMMs with a quasi-Poisson distribution (nbinom2) for males and negative binomial distribution (nbinom1) for females. Total number of males: 161 (males with helping experience: 34); total number of females: 188 (females with helping experience: 62, females with co-breeding experience: 19). The parameter estimate, standard error (SE), z-value, and p-value are given for each fixed effect, along with the conditional r^2 for each model. Significant results are shown in bold. Territory quality = mean territory quality prior to dominance. Reference level for helped/co-bred before dom (dominance) = no

		Males (*n*=161)					**Females (*n*=188)**				
Fixed effect	Levels	Estimate	SE	z	p	r^2	Estimate	SE	z	p	**r^2**
(Intercept)		**6.06**	**0.10**	**59.64**	**<0.001**	0.54	**6.14**	**0.08**	**74.33**	**<0.001**	0.70
Helped before dom	Yes	**0.74**	**0.08**	**9.06**	**<0.001**		**0.67**	**0.07**	**9.35**	**<0.001**	
Co-bred before dom	Yes	/	/	/	/		**0.51**	**0.09**	**5.53**	**<0.001**	
Maternal age		0.09	0.20	0.45	0.654		-0.07	0.18	-0.41	0.681	
Territory quality		0.02	0.38	0.06	0.950		0.09	0.30	0.31	0.754	
Random effect		Levels	Variance	p			Levels	Variance	p		
Mother ID		129	0.03	0.111			**145**	**0.07**	**0.024**		
Social father ID		128	0.00	1.000			136	0.00	0.882		
Cohort		**21**	**0.02**	**0.035**			20	0.00	0.887		

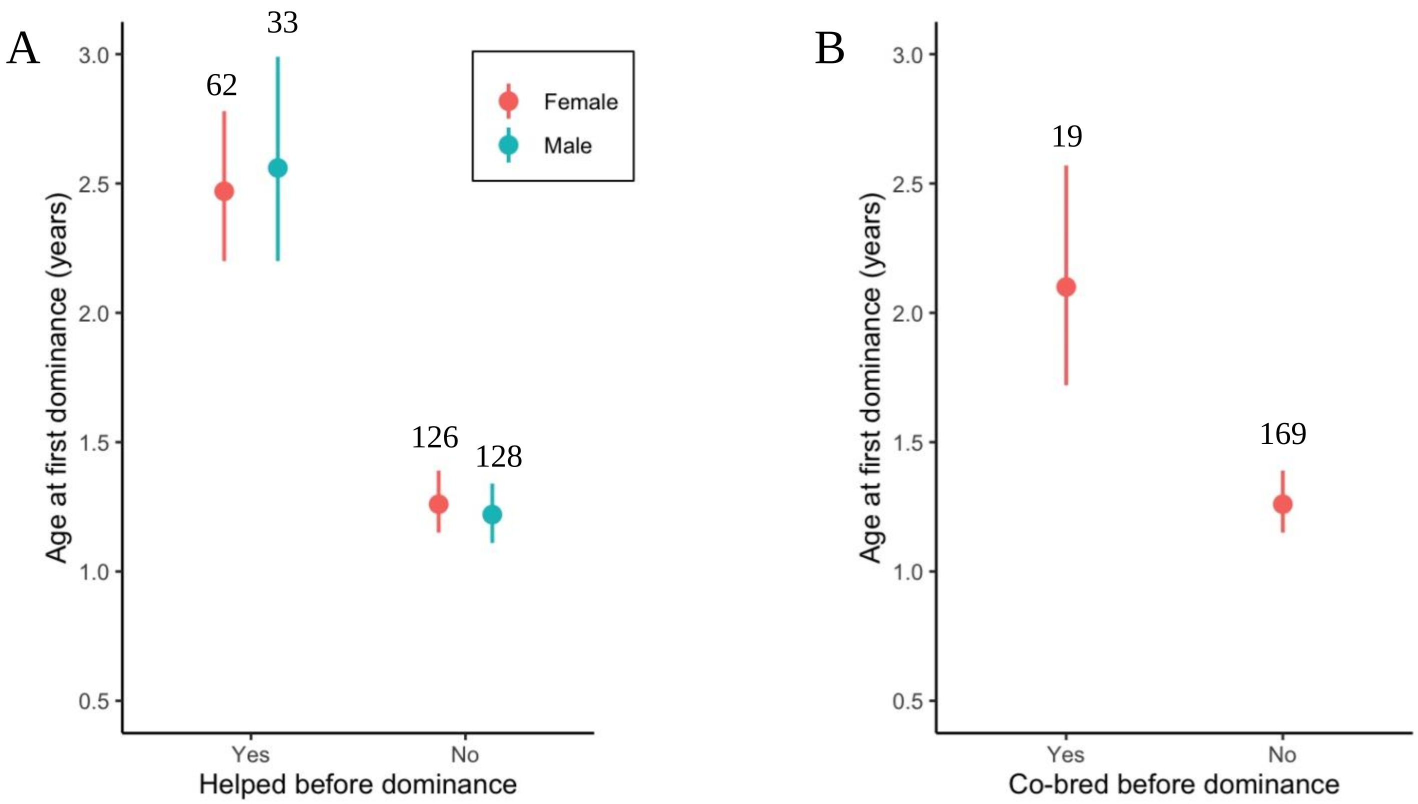


Fig. 2. Marginal effects of having experience as a helper (**A**; males and females) or co-breeding experience (**B**; females only) on the age that an individual first becomes a dominant breeder. The ggpredict function from the GGEFFECTS package (Lüdecke, 2018) in R was used to calculate the marginal effects and create the graphs: the solid points indicate the mean predicted value for each group, with associated 95% confidence intervals, after adjusting for all other model variables (Table 2). Numbers indicate the sample size for each group.

Table 3. Socio-ecological predictors of the length of breeding tenure, estimated using sex-specific GLMMs with a quasi-Poisson distribution (nbinom2) for males and negative binomial distribution (nbinom1) for females. Total number of males: 161 (males with helping experience: 33); total number of females: 187 (females with helping experience: 62, females with co-breeding experience: 19). The parameter estimate, standard error (SE), z-value, and p-value are given for each fixed effect, along with the conditional r^2 for each model. Significant results are shown in bold. Territory quality= mean territory quality during dominance. Reference level for helped/co-bred before dom (dominance) = no

		Males (*n*=161)					**Females (*n*=187)**				
Fixed effect	Levels	Estimate	SE	z	p	r^2	Estimate	SE	z	p	r^2
(Intercept)		**6.87**	**0.29**	**23.95**	**<0.001**	0.27	**6.95**	**0.20**	**35.03**	**<0.001**	0.181
Helped before dom	Yes	-0.27	0.20	-1.36	0.173		-0.22	0.15	-1.49	0.137	
Co-bred before dom	Yes	/	/	/	/		**0.36**	**0.23**	**1.59**	**0.113**	
Maternal age		0.31	0.48	0.64	0.521		0.05	0.33	0.14	0.887	
Territory quality		-0.13	0.91	-0.14	0.888		0.30	0.50	0.61	0.544	
Proportion of tenure with helpers		0.76	0.66	1.14	0.254		**1.19**	**0.36**	**3.32**	**<0.001**	
Random effect		Levels	Variance	p			Levels	Variance	p		
Mother ID		129	0.00	0.999			145	0.00	1.000		
Social father ID		128	0.00	0.999			136	0.03	0.784		
Cohort		21	0.21	0.007			20	0.08	0.016		

Table 4. Socio-ecological predictors of the number of offspring an individual produces after acquiring a dominant breeding position, estimated using sex-specific GLMMs with zero-inflated Poisson distributions. Total number of males: 161 (males with helping experience: 33); total number of females: 187 (females with helping experience: 62; females that co-bred prior to dominance: 19). The parameter estimate, standard error (SE), z-value, and p-value are given for each fixed effect, along with the conditional r^2 for each model. Significant results are shown in bold. Territory quality = mean territory quality during dominance. Reference level for helped/co-bred before dom (dominance) = no

		Males (*n*=161)					**Females (*n*=187)**				
Fixed effect	Levels	Estimate	SE	z	p	r^2	Estimate	SE	z	p	r^2
(Intercept)		0.73	0.38	1.91	0.056	0.60	**1.02**	**0.29**	**3.56**	**<0.001**	0.42
Helped before dom	Yes	-0.28	0.26	-1.09	0.278		-0.33	0.19	-1.70	0.090	
Co-bred before dom	Yes	/	/	/	/		**0.56**	**0.26**	**2.16**	**0.031**	
Maternal age		-0.62	0.56	-1.11	0.266		**-1.01**	**0.46**	**-2.18**	**0.029**	
Territory quality		-0.93	1.01	-0.92	0.356		-0.86	0.85	-1.01	0.314	
Proportion of tenure with helpers		0.68	0.69	0.99	0.320		**1.50**	**0.64**	**2.36**	**0.018**	
Zero-inflated model											
(Intercept)		**-1.16**	**0.34**	**-3.39**	**<0.001**		**-1.18**	**0.31**	**-3.83**	**<0.001**	
Random effect		Levels	Variance	p			Levels	Variance	p		
Mother ID		129	0.00	1.000			145	0.18	0.244		
Social father ID		128	0.29	0.176			136	0.00	1.000		
Cohort		**21**	**0.43**	**<0.001**			20	0.02	0.596		

Table 5. Socio-ecological predictors of lifetime reproductive success in the Seychelles warbler, estimated using sex-specific GLMMs with zero-inflated Poisson models. Total number of males: 250 (males with helping experience: 57); total number of females: 294 (females with helping experience: 120; females that had co-bred: 54). The parameter estimate, standard error (SE), z-value, and p-value are given for each fixed effect, along with the conditional r^2 for each model. Significant results are shown in bold. Territory quality = mean territory quality over lifetime. Reference level for helped/co-bred ever = no.

		Males (*n*=250)					**Females (*n*=294)**				
Fixed effect	Levels	Estimate	SE	z	p	r^2	Estimate	SE	z	p	r^2
(Intercept)		0.38	0.47	0.81	0.415	0.68	**1.02**	**0.43**	**2.34**	**0.019**	0.54
Helped ever	Yes	-0.17	0.26	-0.64	0.521		-0.16	0.19	-0.81	0.418	
Co-bred ever	Yes	/	/	/	/		**0.68**	**0.24**	**2.91**	**0.004**	
Maternal age		-0.52	0.58	-0.90	0.371		**-1.17**	**0.44**	**-2.65**	**0.008**	
Territory quality		-0.91	1.31	-0.69	0.489		-1.21	1.28	-0.94	0.346	
Zero-inflated model											
(Intercept)		-0.33	0.23	-1.43	0.154		-0.44	0.29	-1.51	0.132	
Random effect		Levels	Variance	p			Levels	Variance	p		
Mother ID		183	0.00	1.000			**203**	**0.26**	**0.007**		
Social father ID		176	0.35	0.368			196	0.00	1.000		
Cohort		**22**	**0.83**	**<0.001**			22	0.11	0.152		

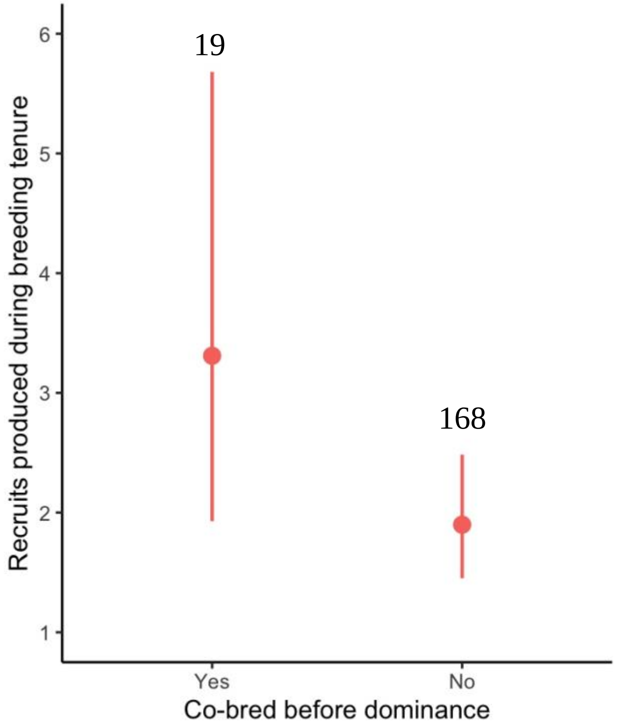


Fig. 3. Marginal effects of having co-bred prior to dominance on the number of offspring a female Seychelles warbler produces during their dominant breeding tenure. The ggpredict function from the ggeffects package (Lüdecke, 2018) in R was used to calculate the marginal effects and create the graphs: the solid points indicate the mean predicted value for each group, with associated 95% confidence intervals, after adjusting for all other model variables (Table 4). Numbers indicate the sample size for each group.

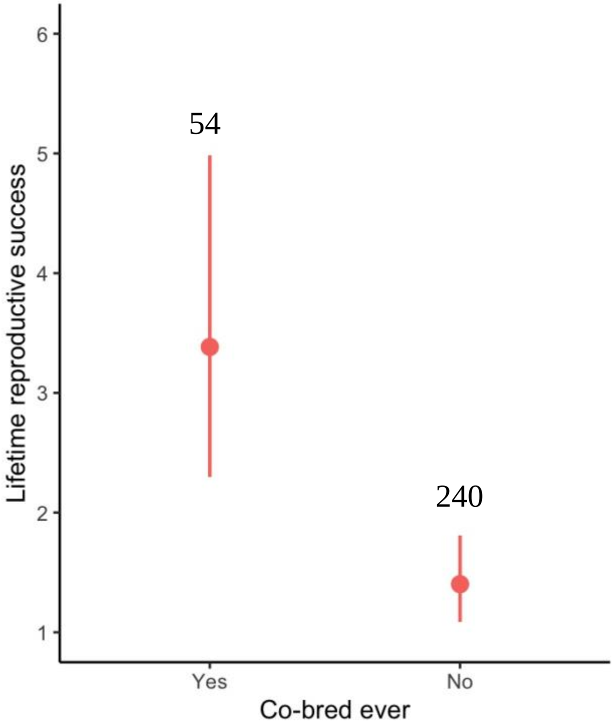


Fig. 4. Marginal effects of having co-bred on the lifetime reproductive success of female Seychelles warblers. The ggpredict function from the ggeffects package in R (Lüdecke, 2018) was used to calculate the marginal effects and create the graphs: the solid points indicate the mean predicted value for each group, with associated 95% confidence intervals, after adjusting for all other model variables (Table 5). Numbers indicate the sample size for each group.

2.5. DISCUSSION

In this study, we found that having helping experience had no effect on the likelihood of an individual acquiring dominance, length of breeding tenure, number of offspring produced as a dominant breeder, or LRS in either male or female Seychelles warblers. We only found an effect of helping experience on age at first dominance: individuals that helped, and females that co-bred, had a higher age at first dominance. Additionally, females that had co-bred as a subordinate produced more offspring as dominant breeders and had an overall higher LRS.

We found that experience as a helper had no effect on whether an individual acquired dominance in either males or females. At first sight, this finding conflicts with a previous study on the Seychelles warbler, which found that female helpers were *less* likely to acquire a dominant breeding position than female non-helpers (Busana et al., 2022a). However, Busana et al. (2022a) analysed female subordinate non-helpers versus female subordinate helpers, whereas we analysed all subordinate helpers versus any bird with no helping experience, which includes birds that had no subordinate status and went straight to first being a floater or a dominant, as well as a subordinate non-helper.

Our findings indicate that helping experience has no effect on the likelihood of an individual becoming a dominant breeder, which could provide evidence against the 'social prestige' hypothesis in the Seychelles warbler (Zahavi, 1995). The social prestige hypothesis posits that helping serves as a way for an individual to advertise their phenotypic quality and caregiving abilities, making them more attractive to potential mates, thus providing future direct fitness benefit (Zahavi, 1995). The social prestige hypothesis has limited evidence in other taxa, with the majority of studies finding that helping has no effect on an individual's likelihood of acquiring dominance or future breeding opportunities (Wright et al., 2001, Wright, 2007, McDonald et al., 2008, Nomano et al., 2013). Indeed, it has been argued that social prestige likely requires a level of cognitive processing that most species are unlikely to be capable of (Wright, 2007, McDonald et al., 2008). In addition, studies on other taxa have shown that helping may be associated with an increased likelihood of obtaining dominance (Field et al., 2006, Cockburn et al., 2008), not due to social prestige, but because helping serves as a way for an individual to remain in the 'breeding queue' on their natal territory (Wiley and Rabenold, 1984, Koenig and Dickinson, 2004, Stacey and Koenig, 1990). However, in the Seychelles warbler, the majority of dominant statuses are acquired when a subordinate moves to a vacant breeding position on a territory other than their natal; subordinates rarely inherit their natal territory (Komdeur and Edelaar, 2001), which may explain why we found no effect of helping on dominance acquisition.

Whilst we found no effect of helping experience on dominance acquisition, we did find that helpers became dominant breeders later in life than those that did not help. This result is consistent with previous studies on female Seychelles warblers (Busana et al., 2022a) and the lance-tailed manakin (Duval et al. 2013). If individuals spend time helping prior to dominance, it follows that they may become a dominant breeder at an older age compared to individuals that did not help and, instead, acquired dominance at their earliest opportunity.

Even though helpers become dominant breeders at an older age, there was no significant difference in dominant breeding tenure between birds that have helping experience and those that do not. If helpers obtain dominance at an older age yet there is no significant difference in the length of tenure, this could suggest that helpers have longer lifespans than birds without helping experience. Indeed, after running a supplementary analysis on our dataset, we found that dominant females that had previously helped had significantly longer lifespans than dominant females that had never helped (Table S2). This complements the findings of Hammers et al., (2013), where Seychelles warblers that delayed reproduction had delayed late-life survival senescence. Our findings, therefore, provide additional support for the 'disposable soma' hypothesis–a trade-off between early-life reproductive investment and late-life declines in reproduction and survival (Kirkwood, 1997. Kirkwood and Rose, 1991). As female helpers spend time helping, they delay independent reproduction which is linked to increased longevity. The reason this effect was found in females, and not males, could be because female birds bear the cost of egg production (Nilsson and Råberg, 2001, Nager et al., 2003, Williams, 2005) and, in the Seychelles warbler, dominant breeding females provide more parental care than dominant breeding males: only females incubate (Komdeur, 1994) and dominant breeding males have lower provisioning rates than dominant breeding females (van Boheemen et al., 2019).

Having helping experience did not increase the number of offspring produced as a dominant, providing evidence against the skills hypothesis. Previous research has shown that female Seychelles warblers with helping experience build stronger nests and make their first breeding attempt quicker than non-helpers after acquiring dominance (Komdeur, 1996). It was suggested that these early reproductive benefits could then translate into improvements in long-term reproductive success. Having tested this here, despite any initial improvements in breeding performance (Komdeur, 1996), future reproductive success as a dominant did not differ with helping experience. However, Komdeur (1996) did not separate helpers and co-breeders, and so the early reproductive benefits that were identified could possibly be attributed to co-breeders that had experience with direct reproduction. Indeed, here, we found that females with prior experience as a co-breeder produced more offspring throughout their dominant breeding tenure than females that had never co-bred. This suggests that experience of direct reproduction improves the future reproductive success of dominant females, as opposed to helping experience. One potential explanation for this is that females with co-breeding experience are more proficient breeders, producing more successful offspring per unit time. Indeed, in other species, individuals with prior breeding experience can be more successful at raising offspring (Limmer and Becker, 2009, Buston and Elith, 2011, Baran and Adkins-Regan, 2014), although this is not the case in all taxa (Cichoñ, 2003, Pärt, 1995). Some studies have questioned whether the apparent benefits of prior breeding experience are, in fact, due to age-related effects i.e., that older individuals are better at foraging or increase their breeding effort with age (see Forslund and Pärt (1995) for review; Cichoñ, 2003). Whilst we did not consider age-related effects directly, the fact that both helpers and co-breeders commence breeding at an older age, yet only co-breeders benefit from an increase in reproductive success throughout their dominant breeding tenures, suggests that this effect is not simply due to age-related improvements in reproductive performance, but prior breeding experience specifically.

Alternatively, it might not be that co-breeding experience causes an improvement in reproductive success throughout an individual's dominant breeding tenure. But, rather, underlying factors that result in a female co-breeding also enable them to be more successful dominant breeders later in life. For instance, better quality females may be more likely to co-breed alongside a dominant female (van de Crommenacker et al. (2011), and, because of their higher quality, may also be more successful breeders once they acquire dominance. However, whether co-breeders are, in fact, in better condition than helpers or non-helping subordinates is yet to be tested in the Seychelles warbler.

Helping experience had no effect on male or female LRS (offspring that survived to ≥1 year of age), as predicted, and as previously demonstrated in female Seychelles warblers using offspring that survived to at least 6 months of age (Busana et al., 2022). As there was no difference between the LRS of helpers and non-helpers of either sex, helping and non-helping could be viewed as equally successful life-history strategies in terms of reproductive success. Additionally, co-breeding increased the LRS of females. Many females never produce offspring (58.6%; Chapter 3) and, by definition, co-breeding females produce at least one offspring. It is unsurprising, therefore, that co-breeders had a higher LRS than females that did not co-breed.

Whilst we found no effect of helping on any of the fitness metrics measures, it must be noted that individuals may gain indirect fitness benefits from helping to raise relatives (Hamilton, 1964). Indeed, previous studies on the Seychelles warbler have shown that helpers enable dominant breeders to produce a greater number of offspring (Komdeur, 1994, Richardson et al., 2007). If helpers are related to these offspring, this will increase the amount of shared genetic material that is passed on to the next generation (Hamilton, 1964). Whilst the level of relatedness between helpers and non-descendant offspring is relatively low in the Seychelles warbler due to high levels of extra-pair paternity (0.13 ± 0.23 and 0.08 ± 0.25 for male and female subordinates, respectively; Richardson et al., 2002), when direct reproduction is not an option, the indirect fitness benefits obtained through helping may not be insignificant.

2.6. CONCLUSION

We demonstrate that helping experience has no positive effect on the fitness of Seychelles warblers in any of the metrics considered. Our results do not align with the skills hypothesis, as helping had no effect on the future breeding success of helpers. Helping~~,~~ consequently, is an equally successful life-history strategy in terms of future reproductive success compared to Seychelles warblers that have no helping experience. Our findings highlight the importance of separating helpers from co-breeders, as co-breeders produced more offspring as dominants and had higher lifetime reproductive success than females that did not co-breed. Whilst previous Seychelles warbler studies have shown helping experience to have short-term reproductive benefits, here, we have shown that this does not result into an overall increase of lifetime fitness. Future studies on cooperative breeders should therefore consider the benefits of helping at various life-history stages, as any effect of helping on short-term breeding success may not translate into longer-term fitness benefits.

2.7. SUPPLEMENT

Table S1. Maternal age (quadratic) as a predictor dominance likelihood, age at first dominance, dominance tenure, number of offspring produced as a dominant breeder, and lifetime reproductive success in the Seychelles warbler. The parameter estimate, standard error (SE), z-value, and p-value for the maternal age (quadratic) fixed effect, prior to removal from the final model of the same title (Tables 1–5) to facilitate the interpretation of first-order effects. The sample size (n) is also given for each model.

	Males					**Females**				
	Estimate	**SE**	**z**	**p**	**n**	**Estimate**	**SE**	**z**	**p**	**n**
Dominance likelihood										
Maternal age^2	-0.58	4.96	-0.12	0.906	251	-0.82	2.54	-0.32	0.745	294
Age at first dominance										
Maternal age^2	0.66	0.94	0.70	0.483	161	0.68	0.61	1.11	0.268	188
Dominance tenure										
Maternal age^2	2.21	2.48	0.89	0.373	161	-1.16	1.31	-0.89	0.374	187
Number of offspring produced as a dominant breeder										
Maternal age^2	2.57	2.81	0.91	0.360	161	-2.52	-1.71	-1.48	0.139	187
LRS										
Maternal age^2	1.88	2.78	0.68	0.499	251	-1.55	1.65	-0.94	0.350	294

Table S2. Socio-ecological predictors of the lifespan of dominant breeders in the Seychelles warbler, estimated using sex-specific GLMMs with quasi-Poisson distribution (nbinom2). Total number of males: 161 (males with helping experience: 33); total number of females: 187 (females with helping experience: 62; females that co-bred prior to dominance: 19). The parameter estimate, standard error (SE), z-value, and p-value are given for each fixed effect, along with the conditional r^2 for each model. Significant results are shown in bold. Territory quality = mean territory during dominance. Reference level for helped/co-bred before dom (dominance) = no.

		Males (*n*=161)					**Females (*n*=188)**				
Fixed effect	Levels	Estimate	SE	z	p	r^2	Estimate	SE	z	p	r^2
(Intercept)		**7.22**	**0.18**	**39.84**	**<0.001**	0.277	**7.48**	**0.16**	**47.79**	**<0.001**	0.183
Helped before dom	Yes	0.10	0.13	0.78	0.434		**0.24**	**0.11**	**2.15**	**0.032**	
Co-bred before dom	Yes	/	/	/	/		**0.43**	**0.18**	**2.45**	**0.014**	
Maternal age		0.35	0.31	1.12	0.263		**-0.54**	**0.27**	**-2.03**	**0.043**	
Territory quality		-0.34	0.54	-0.62	0.535		0.26	0.54	0.49	0.624	
Random effect		Levels	Variance	p			Levels	Variance	p		
Mother ID		129	0.00	1.000			145	0.00	0.999		
Social father ID		128	0.04	0.543			136	0.00	0.999		
Cohort		**21**	**0.08**	**0.001**			**20**	**0.04**	**0.052**		

Chapter 3

Life-long helper effects on offspring fitness in a cooperatively breeding bird

3.1. ABSTRACT

Cooperative breeding occurs when more than two individuals help to raise offspring in a single breeding attempt. In many instances, subordinate helpers assist in raising the offspring of a dominant breeding pair. Why these helpers elect to do this, often at the expense of their own reproduction and energetic resources, is of great interest to evolutionary biologists. Typically, research on the costs and benefits of helping has focused on the fitness of helpers or of the dominant breeders; studies have rarely considered the effect that helping has on the long-term fitness of offspring. Here, we analyse the effect of the presence of a natal helper on offspring fitness, recorded across different life-history stages in a long-term dataset of the Seychelles warbler (*Acrocephalus sechellensis*). Specifically, we consider natal helper effects on the likelihood of an offspring becoming a dominant breeder, the age at first breeding attempt, lifetime reproductive success, and lifespan. Surprisingly, we found no evidence that helpers improve offspring fitness in any of these metrics. However, we found that males with a natal helper were less likely to become a dominant breeder and had lower lifetime reproductive success than males without a natal helper, perhaps due to increased local competition for dominant breeding vacancies. Our findings highlight the importance of analysing the costs and benefits of helping at different offspring life-history stages, as previously identified benefits of helping, such as improved nestling mass and early-life survival, may not translate into long-term fitness increases.

Keywords: helper benefits, cooperative breeding, Seychelles warbler, lifetime reproductive success, early-life effects

3.2. INTRODUCTION

Until relatively recently, it was believed that effects of the early-life environment would be most pronounced during the early life stages. It was thought that long-term fitness would be predominantly determined by stochastic environmental processes that accumulate over an individual's lifetime, and that these processes would override any effect of the early-life environment (van de Pol et al., 2006). However, numerous studies have shown that early-life conditions can have long-term consequences for individual fitness (Lindström, 1999, Lummaa and Clutton-Brock, 2002, Beckerman et al., 2002, Hamel et al., 2009). For example, in humans, nutrient availability *in utero* can affect the future adult body weight of offspring; offspring conceived during famine were more likely to be obese as adults (Ravelli et al., 1999), which increases the likelihood of obesity-related diseases such as diabetes (Phillips, 1998) and coronary heart disease (Barker, 1999). In addition, nutrient availability and the provisioning rate of caregivers can affect the long-term survival and/or reproduction of other species such as the hamster (*Mesocricetus auratus*; Huck et al., 1986), wild house mouse (*Mus musculus*; Meikle and Westberg, 2001), house sparrow (*Passer domesticus*; Schwagmeyer and Mock, 2008), Seychelles warbler (*Acrocephalus sechellensis*; Brown et al., 2022) and solitary bee (*Osmia cornuta*; Bosch and Vicens, 2006). However, different species exist in different social and environmental contexts, which limits our ability to arrive at universal conclusions and draw cross-species comparisons. Nonetheless, the fact that the early-life environment has been shown to have long-term effects across a variety of taxa provides a basis for studying early-life caregiving effects in additional species. The amount that caregivers invest in offspring, both prenatally and postnatally, is potentially a very important early-life variable that can have lasting fitness consequences for offspring in a variety of species, and should be investigated (Boag, 1987).

Cooperative breeding is a breeding system wherein more than two individuals help to raise offspring (Cockburn, 2006). Cooperative breeders tend to live in social groups consisting of a dominant breeding pair and a number of helping and non-helping subordinates (Stacey and Koenig, 1990). In avian species, helpers typically help by incubating and/or provisioning offspring (Heinsohn and Legge, 1999). As helped offspring often receive different levels of care to non-helped offspring (Brown, 1987, Heinsohn, 2004), helping could have long-term consequences on offspring fitness. Unfortunately, we have a limited understanding of the costs and benefits to the offspring being helped in cooperatively breeding systems, especially in regard to longer term fitness metrics.

Dominant breeders, helpers, and helped offspring all potentially stand to benefit from cooperative breeding behaviour, and the evolutionary stability of the system is likely dependent upon a complex interaction between the costs and benefits incurred by these group members. Many hypotheses have been developed that explain cooperative breeding in terms of the benefits associated with helping. However, these hypotheses typically focus on the direct and indirect benefits accrued by helpers and dominant breeders. For instance, by helping to raise related offspring, helpers may increase the amount of shared genetic information passed on to the next generation and improve their indirect fitness (Hamilton, 1964). Helpers may also gain direct fitness benefits if helping increases their own future breeding prospects e.g., by allowing them to remain in the 'breeding queue' and inherit a high-quality territory (Woolfenden and Fitzpatrick, 1978, Pen and Weissing, 2000, Kokko et al., 2002, Stiver et al., 2006), or by enabling them to be more successful in their future breeding attempts (Selander, 1965, Komdeur, 1996, Hatchwell et al., 1999). As long as helpers do not impose much of a cost on dominant breeders, for instance, by depleting territory resources (Kokko et al., 2002), dominant breeders can benefit from the presence of helpers. Indeed, previous research has shown that helpers can 'lighten-the-load' of dominant breeders; dominant breeders may reduce their caregiving in the presence of helpers, allowing them to invest more in self-maintenance and future reproductive efforts (Crick, 1992). This, in turn, can extend a dominant breeder's reproductive lifespan (Hammers et al., 2019, van Boheemen et al., 2019) or increase their rate of reproduction (Komdeur, 1994, Richardson et al., 2002), thus maximising their reproductive output and direct fitness. Alternatively, dominant breeders could continue to invest in current offspring at the same rate and allow helpers to make an additive contribution to offspring care (Brown, 1987, Heinsohn, 2004); additive care could lead to higher quality offspring, which may be more likely to survive and reproduce in the future (Komdeur, 1994, Brouwer et al., 2012). Notably, many of the proposed benefits of helping to helpers and dominant breeders rely on helping having a beneficial effect on offspring fitness. Whilst progress is being made in analysing the early-life benefits of being helped (*e.g.,* Lehmann and Keller, 2006), comparatively little research has considered how helpers affect the long-term reproductive fitness of offspring.

Across a variety of taxa, offspring raised with helpers can benefit from an improvement in juvenile growth and/or survival (Solomon, 1991, Hatchwell et al., 1999, Dickinson et al., 1996, Koenig and Dickinson, 2004, Hodge, 2005, Salomon and Lubin, 2007, Kingma et al., 2010). In some instances, these early-life benefits may have the potential to carry over into reproductive age. For instance, juvenile growth rates frequently predict adult body mass (Boag, 1987, Searcy et al., 2004, Festa-Bianchet et al., 2000, Brown et al., 2022), and a larger adult mass is often associated with dominance status (Russell et al., 2003a, Russell et al., 2003b, Russell et al., 2007a, van de Crommenacker et al., 2011) and an earlier onset of reproduction (Russell, 2004, Hodge, 2005, Russell et al., 2007a). In the Seychelles warbler (*Acrocephalus sechellensis*), a higher juvenile weight is also associated with higher survival throughout an individual's lifetime (Brown et al., 2022). However, there are likely to be trade-offs between early- and late-life fitness, and so focusing exclusively on early-life benefits may lead to an overestimation of the impact of helpers on lifetime fitness (Williams, 1957, Stearns, 1992).

The presence of helpers may influence long-term fitness components of the offspring being helped, although few studies have considered this directly. The reason for the lack of studies is likely due to the difficulty of obtaining longitudinal lifetime data. In the long-tailed tit (*Aegithalos audatus*), individuals raised in a nest with a natal helper had a marginal, but reduced, likelihood of fledging offspring of their own (Maccoll and Hatchwell, 2004). Sparkman et al. (2011) is one of few previous studies to have analysed the effect of helpers on offspring lifetime reproductive success (LRS). Sparkman et al. (2011) identified a sex-specific effect of helpers on offspring LRS in red wolves (*Canis rufus*) – helpers were associated with an increased LRS in female offspring and a reduced LRS in males. In banded mongooses (*Mungos mungo*), offspring of both sexes that were escorted more closely had higher body mass at sexual maturity and higher LRS (Vitikainen et al 2019). Additional studies are needed across a variety of taxa, as this would allow us to build a more accurate and nuanced picture of how helpers affect the long-term fitness of offspring.

Here, we use 21 years (1997–2018) of individual lifetime data from deceased Seychelles warblers to investigate how natal helper presence affects an offspring's fitness. In the Seychelles warbler, inter-dispersal between islands is rare (<0.1% of all individuals studied; Komdeur et al., 2004) and the resighting probability is high (0.92 ± 0.02 for <2-year-olds and 0.98 ± 0.01 for older birds; Brouwer et al. 2010). If a warbler is not seen for two or more consecutive field seasons, we can confidently assume that it is dead and that it has not dispersed (Brouwer et al., 2006). The ability to separate dispersal and death means that all individuals are accounted for, and lifetime fitness estimates can be accurately calculated, which is rare in natural populations. In addition, the Seychelles warbler is a facultative cooperative breeder; the occurrence of non-helpers allows for the effect of helpers to be separated from that of group size (van Boheemen et al., 2019).

Fitness benefits of natal helpers may be expected as Seychelles warbler helpers provide additive compensatory care, such that helped offspring receive more provisions than they would from dominant breeders alone (van Boheemen et al., 2019). Natal helpers have been positively associated with short-term measures of Seychelles warbler offspring fitness such increased as mass at fledging (Komdeur, 1994), survival to independence (Komdeur, 1994) and improved first-year survival (Brouwer et al., 2012). Whether these short-term benefits translate into longer-term improvements in different components of reproductive success remains to be seen. One Seychelles warbler study testing for parental age effects on offspring fitness controlled for natal helper presence, which indicated that females with a natal helper had reduced LRS than females without a natal helper (Sparks et al 2022). Here, we test whether natal helper presence affects an offspring's acquisition of a dominant breeder position, age at first breeding attempt, LRS, and lifespan. Our study differs from Sparks et al., (2022), as we focus on individuals that survived to independence (≥3 months) to remove potential biases in the dataset (Raj Pant et al 2020). This is because nests located high in the canopy are hard to reach, and so nestlings often cannot be ringed until after independence, and catching effort varies across years such that offspring are caught at different ages. Sparks et al., (2022), however, considered all individuals that had been assigned genetic parentage. We predict that natal helper presence will have a positive benefit on an offspring's age at first breeding attempt and likelihood of dominance (due to the positive association between nestling and adult body mass), and a negative effect on offspring lifespan and lifetime reproductive success (due to trade-offs in early-life growth and reproduction and late-life survival senescence).

3.3. METHODS

3.3.1. Study system and data collection

The Seychelles warbler is a small, insectivorous passerine endemic to the Seychelles archipelago (Komdeur et al., 2016). Our closed population on Cousin Island (0.29 km^2; 4°20'S, 55°40'E) consists of *ca.* 320 adult individuals, monitored each year over two breeding seasons: the major breeding season (June–September) and the minor breeding season (January–March; Richardson et al., 2002). The population has been studied since 1985, with more intensive monitoring from 1997 onwards (Richardson et al., 2002, Davies et al., 2021).

On Cousin, there are approximately 115 distinct Seychelles warbler territories (Komdeur, 2003). Each territory is occupied by a breed group consisting of a dominant pair and 0–5 helping or non-helping subordinates (Komdeur, 1992, Richardson et al., 2002). Whilst capable of reproducing within their first year of life, individuals often delay independent breeding and, instead, remain on their natal territory or, less often, disperse to another group to help to raise the offspring of dominant breeders (Komdeur, 1992, Komdeur et al., 2016, Groenewoud et al., 2019). Approximately 42% of female subordinates help, compared to 20% of male subordinates (Hammers et al., 2019). When helpers are present, dominant breeders reduce their provisioning rates and helpers additively compensate for this reduction in care (van Boheemen et al., 2019). Subordinate females sometimes lay eggs in the dominant female's nest, with ~11% of offspring having a within-group subordinate mother (Richardson et al., 2001, Raj Pant et al., 2019). In contrast, only 0.6% of offspring are sired by within-group subordinate males (Raj Pant et al., 2019). Seychelles warblers typically produce one clutch per season of just a single egg (Komdeur, 1996) or, less often, 2–3 eggs (~20% of nests; Richardson et al, 2001). Intraspecific egg dumping does not occur (Richardson et al., 2001).

Each year, as many Seychelles warblers as possible are caught in mist nets or captured in the nest as nestlings during the breeding season. Caught birds are ringed with a British Trust for Ornithology metal ring, as well as a unique colour combination of three ultraviolet-resistant rings. Blood samples (*ca.* 25 µl) are then taken using brachial venepuncture and stored in 100% ethanol at room temperature for later DNA extraction and analysis. Molecular sexing was performed with 1–3 markers to confirm sex, and up to 30 microsatellite loci were used to genotype individuals and determine genetic parentage (Sparks et al., 2021). The Bayesian R package MASTERBAYES 2.52 (Hadfield et al., 2006) was used to assign parentage to 1853 offspring that hatched between 1992 and 2018 (Sparks et al., 2021), with 89% of offspring assigned a father and 86% of offspring assigned a mother with ≥80% confidence.

The breeding status of all individuals within a territory are determined through behavioural observations. The dominant breeding pair is determined by observations of contact calls and mate guarding (Richardson et al., 2002). Subordinates are defined as all other sexually mature individuals that reside within the territory. To determine helper status, one hour nest watches are performed to identify birds that incubate or provision non-descendant offspring (van Boheemen et al., 2019).

Seychelles warblers are territorial and insectivorous, so territory quality is estimated by the amount of arthropod prey available. Arthropod counts are performed monthly at 14 locations across the island, where the number and type of arthropods on the underside of 10 leaves of the 5 most abundant plant species are counted (Komdeur, 1992, Brouwer et al., 2009). For breeding seasons where data were not available, territory quality was estimated based on the mean territory quality of the previous and following field period of the same season-type (following Brouwer et al. 2006), as territory quality on Cousin varies temporally(Dowling et al., 2001, Komdeur and Daan, 2005).

3.3.2. Estimation of fitness metrics

Dominant breeding position acquisition (yes/no) was calculated using behavioural breeding statuses; if an individual was assigned dominance at any point within their lifetime, they were said to have acquired dominance. Age at first breeding attempt was calculated as the time between an individual's estimated hatch date and the midpoint of the first season that they were assigned a dominant breeding status or the estimated hatch date of their first genetic offspring, to account for co-breeding, whichever came first. LRS was calculated as the total number of adult offspring (≥1 year old) produced by an individual, assigned using the genetic pedigree. Lifespan was calculated as the length of time between an individual's estimated hatch date and the midpoint of the last season that they were assigned a status, or the last date that they were observed or caught in the field, whichever came last.

3.3.3. Dataset and statistical analyses

We estimated the relationship between helper presence and four offspring life-history traits and fitness measures: the likelihood of acquiring a dominant breeding position, the age at the first breeding attempt, LRS, and lifespan. The dataset included individuals hatched between 1997 and the minor breeding season of 2018. Only deceased individuals were included in the analyses to ensure the accuracy of long-term fitness measures, as the long-term fitness measures of living individuals still have the capacity to change. Individuals with more than one helper were excluded from the dataset to avoid complications, as multiple helpers could be detrimental to fitness due to increased competition (Komdeur, 1994) and represented a small proportion of the dataset (2.9% of individuals had >1 helper). In addition, only individuals that were not translocated and survived to independence (≥3 months) were included in the models. Our final dataset consisted of 1010 individuals (506 males, 504 females), of which 196 had a natal helper (94 males, 102 females).

For all analyses, sex-specific generalised linear mixed models (GLMMs) were performed in *R* 4.2.1 (R Core Team, 2022) using glmmTMB 1.0.2.1 (Brooks et al, 2017). In all models, we included the presence of a helper (factor: yes/no) and group size (covariate, range: 0–7) as fixed effects which allowed us to separate the effect of helping from those of increased group size. We additionally included four fixed effects that are known to affect offspring fitness in this system: the age of the genetic mother (years) as both linear and squared terms to control for parental effects (Sparks et al., 2021), the presence of a nestmate (factor: yes/no) to control for sibling competition for resources (Bebbington et al., 2016) and natal territory quality as this affects individual dispersal (Komdeur, 1992; Komdeur et al., 1995) and reproductive success (Spurgin et al., 2018). All continuous predictor variables were rescaled using SCALES 1.1.1 (Wickham and Seidel, 2022) to facilitate interpretation and allow comparison of model coefficients. All models initially included interactions between helper presence and maternal age (both linear and squared; Table S3 (Hammers et al., 2019, Sparks et al., 2021). Any non-significant interactions and squared terms were removed sequentially, with the term of least significance removed first, to facilitate interpretation of the first-order effects. No interactions were significant in any model (Table S3), so all interactions were removed from the final models. Cohort, genetic mother ID, and dominant male ID were included as random effects.

All models were checked for over-dispersion and zero-inflation using PERFORMANCE 0.5.1 (Lüdecke et al, 2021) and variance inflation factors (all <3; Dormann et al., 2013). Model fit was determined by assessing plots of the observed values against the simulated squared residuals using DHARMa 0.3.3.0 (Hartig, 2022), as well as comparing the AIC of candidate models (Akaike, 1973), with the model of lowest AIC value being preferred. Ultimately, sex-specific dominance likelihood models were fitted using binomial error distributions, age at first breeding attempt models were run using quasi-Poisson distributions (nbinom1), LRS models with zero-inflated quasi-Poisson (nbinom1) distributions, and the lifespan model was run using a negative binomial (nbinom2) distribution. For each model, the marginal effect and predicted counts of each variable of interest were then calculated using GGEFFECTS 1.1.0 (Lüdecke, 2018). Marginal effects refer to the effect size of a variable of interest, after adjusting for all other variables within a model.

3.4. RESULTS

Dominant breeding position acquisition

Having a natal helper was associated with a significant reduction in the likelihood that a male became a dominant breeder (Table 6; Fig. 5), but not females. Out of 506 males and 504 females included within our analyses, 327 males (64.6%; 95% CI: 61.1–68.1%) and 300 females (59.5%; 95% CI: 55.9–63.1%), respectively, went on to become a dominant breeder at some point during their lifetime. After adjusting for all model effects, the predicted likelihood that males with a natal helper acquired a dominant breeding position was 49% (95% CI: 35–63%, *n*=94) versus 69% (95% CI: 62–76%, *n*=412) for males raised without a natal helper. Having a natal helper had no effect on the likelihood of a female acquiring a dominant breeding position (Table 6). After adjusting for all model effects, the predicted likelihood that a female raised with a natal helper acquired dominance was 55% (95% CI: 0.42–0.67, *n*=102), compared to 60% (95% CI: 52–67%) for females raised without a natal helper. No other fixed effects were significant.

Age at first breeding attempt

Having a natal helper had no effect on the age of the first breeding attempt in either males or females (Table 7). Within our dataset, 333 males and 327 females attempted to breed at some point during their lifetime. After adjusting for all model effects, males raised with a natal helper had a mean age at first breeding attempt of 1.6 years (95% CI: 1.4–1.8 years, *n*=52), compared to 1.6 years for males raised without a natal helper (95% CI: 1.5–1.7 years, *n*=281). Females raised with a natal helper had a mean age at first breeding attempt of 1.8 years (95% CI: 1.5–2.1 years, *n*=57), compared to 1.6 years for females raised without a natal helper (95% CI: 1.5–1.7 years, *n*=270). No other fixed effects were significant in either the male or female models.

Lifetime reproductive success

Having a natal helper had a significant negative association with male, but not female, LRS (Table 8; Fig. 6). After controlling for all model variables, the predicted LRS of helped males was 0.7 offspring (95% CI: 0.4–1.2, range: 0–10, *n*=94) compared to males without helpers that had a predicted LRS of 1.1 offspring (95% CI: 0.8–1.6, range: 0–15, *n*=412). In addition, maternal age, the presence of a nestmate, and natal territory quality all had a significant positive association with male LRS (Table 8). In females, the predicted LRS of females raised with a natal helper was 1.0 offspring (95% CI: 0.6–1.7, range: 0–7, *n*=102) compared to females without a natal helper that had a predicted LRS of 1.4 offspring (95% CI: 1.0–2.1, range: 0–9, *n*=402), which was not significant. For females, maternal age had a significant, negative association with LRS; females hatched by younger mothers produced more offspring over their lifetimes (Table 8).

Lifespan

Having a natal helper had no significant effect on individual lifespan in either male or female Seychelles warblers (Table 9). After adjusting for all model effects, males with a natal helper had a predicted lifespan of 2.9 years (95% CI: 2.3–3.6, range: 0.3–16.4, *n*=94) compared to males without a natal helper that had a predicted lifespan of 3.3 years (95% CI: 2.9–3.7, range: 0.3–15.5, *n*=412). Females reared by a natal helper had a predicted lifespan of 3.2 years (95% CI: 2.7–3.9, range: 0.3–19.4, *n*=102) compared to 3.5 years (95% CI: 3.1–3.9, range: 0.3–15.5, *n*=402) for females raised without a natal helper. In addition, maternal age had a negative association with female lifespan, but not males (Table 9). No other fixed effects were significant.

Table 6. Natal socio-ecological predictors of whether an individual becomes a dominant breeder or not in the Seychelles warbler, estimated using sex-specific GLMMs with binomial distributions. Total number of males: 506 (males with helpers: 94); total number of females: 504 (females with helpers: 102). The estimate, standard error (SE), z-value, and p-values are given for each fixed effect. Conditional r^2 values are provided for each model. Significant results ($p<0.05$) are shown in bold. Reference level for natal helper/ nestmates= absent.

		Males (*n*=506)					**Females (*n*=504)**				
Fixed effect	Levels	Estimate	SE	z	p	r^2	Estimate	SE	z	p	r^2
(Intercept)		0.34	0.29	1.18	0.238	0.114	**0.57**	**0.27**	**2.11**	**0.035**	0.095
Group size		0.45	0.78	0.58	0.562		-0.11	0.67	-0.16	0.871	
Natal helper	Present	**-0.86**	**0.31**	**-2.82**	**0.005**		-0.18	0.27	-0.66	0.509	
Maternal age		0.56	0.57	0.99	0.322		-0.82	0.49	-1.68	0.093	
Nestmates	Present	0.05	0.33	0.15	0.880		0.01	0.33	0.03	0.973	
Territory quality		4.30	2.43	1.77	0.077		2.94	2.50	1.18	0.239	
Random effect		Levels	Variance	p			Levels	Variance	p		
Mother ID		290	0.00	1.000			274	0.00	0.999		
Social father ID		278	0.09	0.650			267	0.00	1.000		
Cohort		**22**	**0.19**	**0.041**			**22**	**0.28**	**0.013**		

Table 7. Natal socio-ecological predictors of the age of first breeding attempt in the Seychelles warbler, estimated using sex-specific GLMMs with a quasi-Poisson distribution (nbinom1) for males and a negative binomial distribution (nbinom2) for females. Total number of males: 333 (males with helpers: 52; males without helpers: 281); total number of females: 327 (females with helpers: 57, females without helpers: 270). The estimate, standard error (SE), z-value, and p-values are given for each fixed effect. Conditional r^2 values are provided for each model. Significant results are shown in bold. Reference level for natal helper/ nestmates= absent.

		Males (*n*=333)					**Females (*n*=327)**				
Fixed effect	Levels	Estimate	SE	z	p	r^2	Estimate	SE	z	p	r^2
(Intercept)		**6.30**	**0.06**	**101.82**	**<0.001**	0.113	**6.41**	**0.07**	**86.21**	**<0.001**	0.100
Group size		0.08	0.16	0.50	0.614		0.04	0.19	0.23	0.818	
Natal helper	Present	0.00	0.07	0.02	0.981		0.12	0.08	1.45	0.147	
Maternal age		0.10	0.13	0.82	0.414		-0.14	0.15	-0.94	0.349	
Nestmates	Present	0.03	0.07	0.39	0.698		0.02	0.10	0.16	0.874	
Territory quality		-0.08	0.39	-0.19	0.848		-0.33	0.46	-0.71	0.478	
Random effect		Levels	Variance	p			Levels	Variance	p		
Mother ID		221	0.01	0.553			215	0.01	0.789		
Social father ID		217	0.00	0.949			211	0.00	1.000		
Cohort		**21**	**0.01**	**0.017**			**20**	**0.01**	**0.013**		

Table 8. Natal socio-ecological predictors of lifetime reproductive success in the Seychelles warbler, estimated using a sex-specific zero-inflated GLMMs with quasi-Poisson distributions (nbinom1). Total number of males: 506 (males with helpers: 94) total number of females: 504 (females with helpers: 102). The estimate, standard error (SE), z-value, and p-values are given for each fixed effect. Conditional r^2 values are provided for each model. Significant results are shown in bold. Reference level for natal helper = no; reference level for nestmates = no.

		Males (*n*=506)					**Females (*n*=504)**				
Fixed effect	Levels	Estimate	SE	z	p	r^2	Estimate	SE	z	p	r^2
(Intercept)		-0.28	0.29	-0.96	0.336	0.235	**0.59**	**0.26**	**2.26**	**0.024**	0.272
Group size		0.14	0.61	0.22	0.824		0.12	0.46	0.26	0.792	
Natal helper	Present	**-0.52**	**0.25**	**-2.09**	**0.037**		-0.39	0.23	-1.71	0.087	
Maternal age		**0.84**	**0.41**	**2.04**	**0.042**		**-0.87**	**0.38**	**-2.30**	**0.022**	
Nestmates	Present	**0.46**	**0.23**	**2.02**	**0.043**		0.15	0.22	0.69	0.489	
Territory quality		**2.21**	**1.04**	**2.13**	**0.033**		0.39	0.79	0.49	0.625	
Zero-inflated model											
(Intercept)		**-1.22**	**0.53**	**-2.30**	**0.021**		**-0.81**	**0.33**	**-2.49**	**0.013**	
Random effect		Levels	Variance	p			Levels	Variance	p		
Mother ID		290	0.00	1.000			274	0.00	0.999		
Social father ID		278	0.00	0.999			267	0.00	0.999		
Cohort		**22**	**0.33**	**<0.001**			**22**	**0.37**	**<0.001**		

Table 9. Natal socio-ecological predictors of lifespan in the Seychelles warbler, estimated using a sex-specific zero-inflated GLMMs with quasi-Poisson distributions (nbinom1). Total number of males: 506 (males with helpers: 94) total number of females: 504 (females with helpers: 102). The estimate, standard error (SE), z-value, and p-values are given for each fixed effect. Conditional r^2 values are provided for each model. Significant results are shown in bold. Reference level for natal helper = no; reference level for nestmates = no.

		Males (*n*=506)					**Females (*n*=504)**				
Fixed effect	Levels	Estimate	SE	z	p	r^2	Estimate	SE	z	p	r^2
(Intercept)		**6.92**	**0.13**	**51.74**	**<0.001**	0.261	**7.20**	**0.14**	**51.31**	**<0.001**	0.270
Group size		-0.21	0.29	-0.70	0.482		0.17	0.26	0.65	0.516	
Natal helper	Present	-0.09	0.12	-0.79	0.431		-0.04	0.11	-0.31	0.757	
Maternal age		0.17	0.21	0.81	0.417		**-0.67**	**0.21**	**-3.20**	**0.001**	
Nestmates	Present	0.15	0.13	1.16	0.247		0.12	0.14	0.83	0.408	
Territory quality		1.28	0.88	1.46	0.145		0.44	0.96	0.46	0.649	
Random effect		Levels	Variance	p			Levels	Variance	p		
Mother ID		290	0.00	0.999			274	0.00	0.999		
Social father ID		278	0.00	0.999			267	0.00	0.999		
Cohort		**22**	**0.14**	**<0.001**			**22**	**0.18**	**<0.001**		

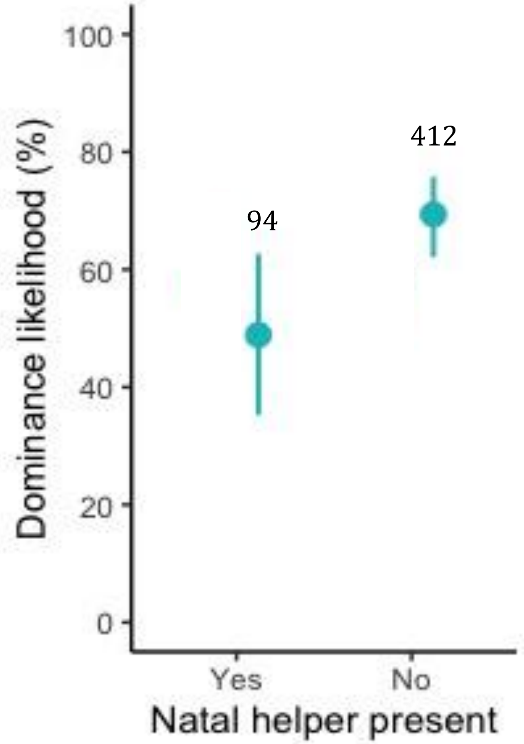


Fig. 5. Marginal effects of natal helper presence on the likelihood of a male Seychelles warbler becoming a dominant breeder. The ggpredict function from the GGEFFECTS package in R (Lüdecke, 2018) was used to calculate the marginal effects and create the graphs: the solid points indicate the mean predicted value for each group, with associated 95% confidence intervals (error bars), after adjusting for all other model variables (Table 3). Numbers indicate the sample size for each group.

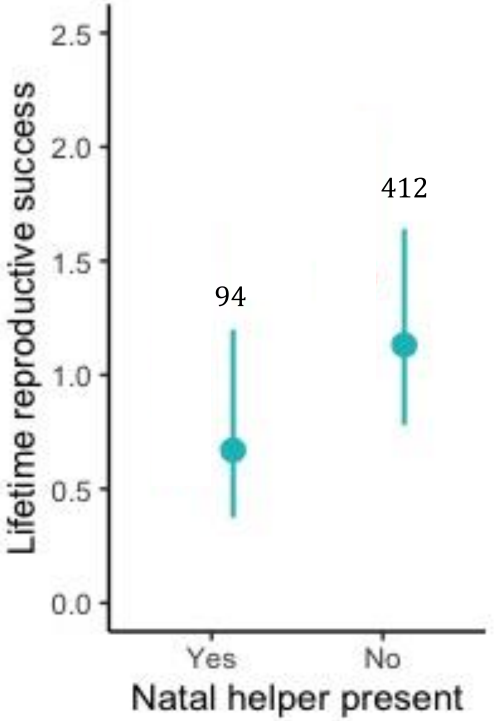


Fig. 6. Marginal effects of natal helper presence on the lifetime reproductive success of male Seychelles warblers. The ggpredict function from the GGEFFECTS package in R (Lüdecke, 2018) was used to calculate the marginal effects and create the graphs: the solid points indicate the mean predicted value for each group, with associated 95% confidence intervals (error bars), after adjusting for all other model variables (Table 5). Numbers indicate the sample size for each group.

3.5. DISCUSSION

Here, we found that the presence of a natal helper had no effect on an individual's fitness at any of the life-history stages or fitness metrics measured, except that the presence of a natal helper reduced the likelihood of a male acquiring dominance and their LRS.

The presence of a natal helper significantly reduced the likelihood that males, but not females, became dominant breeders later in life. This finding was surprising, as natal helpers increase the mass of Seychelles warblers at the point of fledging (Komdeur, 1994). Juvenile mass is, in turn, a strong predictor of adult body mass (Brown et al., 2022), and males with a larger adult body mass are more likely to be dominant breeders (van de Crommenacker et al., 2011). Indeed, our study contrasts with findings in other taxa; for instance, in the cooperatively breeding meerkat (*Suricata suricatta*), helpers are associated with an increased likelihood of offspring becoming dominant breeders (Russell et al., 2007a). Similarly, Solomon (1991) found that helpers increase the weight of prairie voles (*Microtus ochrogaster*), and that larger prairie voles are more likely to mate (Solomon, 1993). The fact that natal helpers *reduce* the likelihood of male Seychelles warblers becoming a dominant breeder is, therefore, an unexpected result.

One explanation for the association between helpers and a reduced likelihood of male offspring becoming dominant breeders is that the presence of a helper may lead to increased competition for future dominant breeding vacancies. Individuals only adopt subordinate positions as helpers when local population density is high and all available breeding positions on high-quality territories are occupied (Komdeur, 1992, Komdeur et al., 1995). The presence of helpers therefore indicates a lack of available breeding vacancies on territories nearby, as the helpers would have themselves dispersed to fill them (Komdeur, 1992, Komdeur et al., 1995). If there are more individuals competing for a limited number of dominant breeding vacancies, this reduces the likelihood of any one individual obtaining it. However, if local population density is driving a reduction in dominance likelihood, we might expect the presence of a natal helper to reduce the dominance likelihood of both male and female offspring. Yet, we found no effect of natal helper presence on the likelihood of female offspring becoming dominant breeders. However, this could be explained by sex-differences in dispersal strategies. Females tend to disperse further than males (Eikenaar et al., 2008b, Kingma et al., 2017), and are more likely to adopt a subordinate position on a non-natal territory while they wait for a dominant breeding vacancy (Groenewoud et al., 2018). By dispersing to a territory with fewer competitors, females may be more likely to acquire dominance than males that remain closer to their natal territory.

While we identified an effect of natal helpers on the likelihood of males becoming dominant breeders, we found no effect of natal helpers on the age at which individuals make their first breeding attempt. This finding conflicts with studies on other species that have shown that individuals with helpers start breeding at a younger age (Hodge, 2005, Russell et al., 2007, but see Sparkman et al., 2011). For instance, in the banded mongoose (*Mungo mungo*), helpers increase juvenile mass, allowing offspring to start breeding at an earlier age (Hodge, 2005). However, such studies often focus on species where individuals can disperse and establish new breeding groups elsewhere or have low reproductive skew (Russell et al., 2007a). In species with low reproductive skew, reproduction is shared between dominant breeders and subordinates at a higher rate compared to species with high reproductive skew where dominant breeders account for the majority of reproduction within a group (Keller and Reeve, 1994, Johnstone, 2000, Nonacs and Hager, 2011). As such, in species with low reproductive skew, the effect of helpers on life-history traits associated with breeding performance, such as age at first breeding, may be more pronounced, as more subordinates may have the opportunity to breed than in species with a high reproductive skew.

On Cousin, the population of Seychelles warblers is at carrying capacity (~320 adults) and all available territories are occupied by dominant breeders (Komdeur et al., 2016). In the Seychelles warbler, reproductive skew is relatively high; dominant breeders account for the majority of reproduction within a group. Subordinate males rarely gain paternity (0.6%; Sparks et al., 2021) and just ~11% of subordinate females have been shown to co-breed alongside the dominant female (Sparks et al., 2022). Even if helpers reduced the time taken of an offspring to arrive at sexual maturity, this would not change the availability of dominant breeding vacancies. As the demotion of dominant breeders to subordinate positions is relatively rare (13.7% of females, 3% of males; Richardson et al., 2007), individuals typically only acquire a dominant breeding position once a dominant breeder of the same sex dies or is translocated to another island by researchers (Komdeur and Edelaar, 2001). The rate at which dominant breeding positions become available therefore remains relatively constant over time. So, whilst helpers may influence *which* offspring are able to obtain dominance, they cannot change the rate at which breeding vacancies become available. This could explain why we find no effect of helpers on the age at which individuals make their first breeding attempt.

Importantly, we also found that having a natal helper reduces a male's LRS. This result was to be expected, given our finding that natal helpers reduce the likelihood of male offspring acquiring dominance and the fact subordinate males rarely gain paternity (0.6%; Raj Pant et al., 2019, Sparks et al., 2021). Consequently, if helpers reduce the likelihood of a male becoming a dominant breeder, it follows that the LRS of helped male offspring would also be reduced. Indeed, when dominance (yes/no) was included as a variable in the LRS model for males, natal helpers no longer had a significant effect on male LRS (Table S4). It is likely, therefore, that the effect of natal helpers on male LRS is driven by the effect of natal helpers on the likelihood that a male will obtain a dominant breeding position. Our study conflicts with previous research conducted by Sparks et al., (2022) which found that females, but not males, with natal helpers have a reduced LRS. However, in this study, we considered individuals that made it to independence (≥3 months old), whereas Sparks et al., (2022) included all individuals assigned a genetic parent within their analysis. The differences in our findings likely derive from natal helper effects that occur prior to independence. Few previous studies have considered the impact of helpers on offspring LRS. Sparkman et al. (2011) found that male red wolves with helpers had reduced LRS, whereas females had increased LRS, compared to males or females without helpers, respectively. Sparkman et al. (2011) found that helped pups benefit from increased mass, and suggested that the sex-differences in LRS associated with natal helper presence may arise due to trade-offs between pup mass and late-life declines in male reproductive success. In banded mongooses, however, offspring of both sexes that we more closely helped had higher mass at sexual maturity and higher LRS than offspring that were less closely helped (Vitikainen et al 2019).

Finally, we found no effect of natal helper presence on offspring lifespan in either males or females, which was also concluded by Sparks et al (2022). Interestingly, this could suggest that natal helpers have a limited effect on offspring body condition. According to life-history theory, there will be trade-offs between growth, reproduction, and longevity (Williams, 1957, Stearns, 1992). In several species, faster growth rates have been linked to reduced lifespans (Rollo, 2002, Olsson and Shine, 2002, Metcalfe and Monaghan, 2003, Dmitriew, 2011, Lee et al., 2013). Indeed, in the Seychelles warbler, faster growth rates increase the rate of telomere attrition (van de Crommenacker et al., 2011), which is a key predictor of mortality (Barrett et al., 2012). The fact we found no effect of natal helpers on offspring lifespan might, therefore, suggest that the presence of a natal helper does not have a significant effect on offspring growth rates. Further support for this hypothesis comes from our finding that helping has no effect on the likelihood of females, and a reduced likelihood of males, acquiring a dominant breeding position. In the Seychelles warbler, larger juvenile mass is positively associated with adult body mass (Brown et al., 2022), which, in turn, is associated with dominance (van de Crommenacker et al., 2011). Helpers having a limited effect on offspring body mass could explain these findings. Whilst a previous study on the Seychelles warbler found helpers to be associated with an increased mass at fledging (Komdeur, 1994), this study was conducted over few years (1985-1991), prior to intensive monitoring of the population. Further studies are required to determine the effect of helpers on offspring body condition. However, such data is not easily obtained and can be subject to bias, as only nestlings from nests located in low-level vegetation can be accessed for sampling.

In the Seychelles warbler, helpers provide additive compensatory care, with helped offspring receiving provisions at a higher rate than offspring with no helpers (van Boheemen et al., 2019), which could have a positive effect on offspring quality. However, whilst helped offspring receive more provisions overall, the amount of provisioning visits that they receive from the dominant breeders is reduced (van Boheemen et al., 2019). It is possible that helpers provide lower quality food items than dominant breeders, either intentionally or because of their inexperience, which may mask any effect of an increased provisioning rate. Across different taxa, the relationship between provisioning rate and offspring mass is contentious, with studies showing that provisioning rate does not necessarily predict offspring body mass (MacLeod et al., 2015, Preston et al., 2016). For instance, in the rifleman (*Acanthisitta chloris*), helpers provide additive care, but this has no effect on nestling body mass at fledging (Preston et al., 2016). Indeed, studies have shown that food *quality* is more important than the rate of food delivery when it comes to nestling mass (Schwagmeyer and Mock, 2008). If helpers provide lower quality food items, this could explain why helpers have no beneficial effect on any of the fitness metrics measured here, despite providing additional food resources. Unfortunately, in the Seychelles warbler, it is not possible to assess prey quality as nests are often high in the canopy.

If male offspring with natal helpers have a lower LRS, the amount of genetic material contributed by dominant breeders to future generations is reduced. This then poses the question: why would a dominant breeder allow a subordinate to help when the fitness of their male offspring is negatively affected? Similarly, if helpers are related to the offspring that they help, a reduction in offspring LRS will reduce their indirect fitness (Hamilton, 1964); why, then, would a subordinate *choose* to help? One explanation that is supported by previous research on the Seychelles warbler is that helpers are enabling dominant breeders to produce more offspring (Komdeur, 1994, Hammers et al., 2015). When helpers are present, dominant breeders can reduce their own investment and, instead, reallocate resources to self-maintenance and future broods (Crick, 1992). By 'lightening the load' of dominant breeders, helpers can extend the reproductive lifespans of dominant breeders (Hammers et al., 2019, van Boheemen et al., 2019) or increase their rate of reproduction (Komdeur, 1994, Richardson et al., 2002), allowing them to produce more offspring over their lifetime. So, whilst the quality of individual male offspring may be reduced, the quantity of offspring is increased. This finding echoes research on the long-tailed tit; helpers increase the reproductive output of dominant breeders (Hatchwell et al., 2004) yet have a negative effect on the future breeding performance of the offspring they help (MacColl and Hatchwell, 2004).

Another explanation is that dominant breeders are prioritising their investment in helpers who are usually their offspring from a previous breeding attempt (Komdeur et al., 2016). If helping experience improves a subordinate's future reproductive success as a breeder (Komdeur, 1996), allowing subordinates to help could increase the indirect fitness of dominant breeders. As helpers have already reached reproductive age and demonstrated their survivability and physiological quality, allowing subordinates to help may be a good fitness strategy for dominant breeders. However, in chapter 2, we showed no positive effect of helping on reproductive success or life-history traits often associated with fitness (dominant breeder position acquisition, length of breeding tenure, number of offspring produced as a dominant breeder, or LRS). We did, however, find that co-breeding females produce more offspring as dominant breeders and have a greater LRS than females that do not co-breed. It is not yet known whether females must first help before they can co-breed in the Seychelles warbler.

In addition, we do not know what the fitness outcomes of helped offspring would have been had they not received help. For instance, Seychelles warbler helpers are more likely to be present when dominant females are older; older dominant females have a lower provisioning rate, and helpers compensate for this reduction (Hammers et al., 2021). If natal helpers were not present, the offspring of older dominant females may have suffered a reduction in fitness. The negative effects of helpers on male offspring likelihood of dominance and LRS could then arise due to density-dependent competition. However, we found no interaction between natal helper presence and maternal age (Table S3).

Furthermore, studies on other taxa have shown that, in the presence of helpers, breeding females sometimes reduce their investment in egg production, producing smaller eggs with a lower nutritional content, resulting in smaller hatchlings (Smith et al., 1995, Hatchwell, 1999, Krist, 2011, Russell et al., 2007b), although this is not the case in all taxa (Santos & Nakagawa 2013; Lejeune et al. 2016) . The additive care that helpers provide may then improve offspring growth rates, resulting in offspring of similar mass to offspring born to breeders that did not reduce their egg investment (Krist et al., 2004). The beneficial effects of helpers are therefore concealed by the breeders reduced investment (Hatchwell, 1999, Russell et al., 2007b, Canestrari et al., 2011, Santos and Macedo, 2011, Taborsky et al., 2007, Paquet et al., 2013) see Dixit et al. (2017) for meta-analysis). In this way, helpers may provide a fitness benefit by preventing a detrimental outcome rather than promoting a fitness advantage over non-helped offspring.

Egg investment is difficult to measure in our population as nests high in the canopy are difficult to access. In a limited dataset of 86 eggs from 69 nests measured across two years (1997 and 2003), no relationship between helper presence and egg size or volume was found, which suggests that breeding females do not alter their egg investment when helpers are present (Hein et al., 2019 unpublished report). However, this analysis lacked power due to sample size, and so conclusions drawn from these data are limited. Nonetheless, it is indeed possible that no relationship exists between helper presence and egg size, and this could be due to the offspring life-history stages in which Seychelles warbler helpers typically help. As is the case for many avian cooperative breeders, helpers typically provide help *after* an egg has been laid (Komdeur, 1992, Richardson et al., 2002). As such, breeding females cannot be certain that subordinates within the group will provide help to their offspring. Adjusting egg size on the assumption that a subordinate will provide help could be a risky strategy for a breeding female, as it could result in offspring of lower quality if subordinates do not then compensate for their reduction in egg investment.

Despite this, whether or not egg size is an appropriate proxy for the nutritional content of eggs remains uncertain. Whilst egg size has been shown to be a predictor of nestling mass in a number of species (Smith et al., 1995, Hatchwell, 1999, Krist, 2011, Russell et al., 2007b), egg size is not necessarily correlated with yolk size, immunoglobulin, or hormone content (Hargitai, Prechl & Torok 2006; Ojanen 1983; Paquet et al 2013). In species where egg size has not been correlated with helper presence, it is indeed possible that female breeders are adjusting the nutritional content of eggs in the presence of helpers without affecting egg mass or size. Analyses considering the relationship between egg size and nutritional content are yet to be conducted on the Seychelles warbler. In addition, there are a number of additional factors that influence egg size; for instance, studies on other species have shown egg mass and volume to decline with lay order (Reynolds et a., 2003). Egg size differences may therefore vary at different points of sampling depending on whether or not a breeder has previously laid, and this could confound any relationship between helper presence and egg size.

3.6. CONCLUSION

Whilst previous studies have shown that helping can increase offspring fitness in early-life e.g., by improving nestling mass, survival to independence and first-year survival, here, we show that natal helpers have no beneficial effect on four longer-term measures of offspring breeding performance and reproductive success (acquisition of a dominant breeding position, dominance tenure, offspring produced as a dominant, and LRS). For male offspring, the presence of a natal helper resulted in a decreased likelihood of obtaining dominance and reduced LRS. The negative effects of helping, in this instance, could be due to an association between the existence of helpers and high local population density, thus increasing competition for dominant breeding vacancies. Our results highlight the importance of considering the costs and benefits of helping to all individuals at various life-history stages, as short-term benefits of having a natal helper may not translate into longer-term fitness benefits.

3.7. SUPPLEMENT

Table S3. Output from models including quadratic variables and interactions that were not included in final analyses (Tables 6-9) due to lack of significance. The name of the corresponding model is included as the subheading, with each consecutively numbered model of the same name-type displaying model output after the variable of least significance was removed. Male and female models are presented side-by-side, however, in situations where males and females differed in variable of least significance, model output is presented on separate lines. No quadratic variables or interactions were significant after non-significant terms were sequentially removed, and so were not included in the final models.

	Males					**Females**				
	Estimate	SE	z	p	n	Estimate	SE	z	p	n
Acquisition of dominance (full models)										
Maternal age^2	0.55	3.22	0.17	0.865	506	-3.88	2.33	-1.67	0.095	504
Natal helper x maternal age	7.81	5.63	1.39	0.167		-7.56	4.13	-1.83	0.067	
Natal helper x maternal age^2	-12.22	7.31	-1.67	0.095		7.85	4.63	1.69	0.091	
Acquisition of dominance 2 (males)										
Maternal age^2	-1.33	2.84	-0.47	0.641		/	/	/	/	
Natal helper x maternal age^2	-2.60	1.80	-1.44	0.150		/	/	/	/	
Acquisition of dominance 2 (females)										
Maternal age^2	/	/	/	/		-2.15	2.01	-1.07	0.285	
Natal helper x maternal age	/	/	/	/		-0.77	1.18	-0.65	0.514	
Acquisition of dominance 3										
Maternal age^2	-2.26	2.68	-0.84	0.399		-2.23	2.00	-1.12	0.264	

Age at first breeding attempt (full models)										
Maternal age^2	0.09	0.62	0.14	0.899	333	1.09	0.67	1.64	0.101	327
Natal helper x maternal age	-0.39	1.24	-0.32	0.750		1.72	1.34	1.28	0.201	
Natal helper x maternal age^2	0.21	1.55	0.14	0.894		-1.92	1.61	-1.19	0.235	
Age at first breeding attempt 2										
Maternal age^2	0.12	0.57	0.21	0.833		0.78	0.61	1.29	0.196	
Natal helper x maternal age	-0.24	0.36	-0.66	0.507		0.18	0.36	0.50	0.617	
Age at first breeding attempt 3 (males)										
Natal helper x maternal age	-0.24	0.36	-0.66	0.509		/	/	/	/	
Age at first breeding attempt 3 (females)										
Maternal age^2	/	/	/	/		0.77	0.61	1.27	0.204	
Lifetime reproductive success (full models)										
Maternal age^2	3.69	1.81	2.04	0.042	506	-1.77	1.79	-0.99	0.322	504
Natal helper x maternal age	7.76	5.05	1.53	0.125		-4.28	3.16	-1.35	0.176	
Natal helper x maternal age^2	-11.02	6.70	-1.65	0.100		5.36	3.73	1.44	0.150	
Lifetime reproductive success 2										
Maternal age^2	2.71	1.75	1.55	0.122		-0.79	1.57	-0.50	0.614	
Natal helper x maternal age^2	-1.28	1.54	-0.84	0.403		0.50	1.12	0.45	0.654	
Lifetime reproductive success 3										

Maternal age^2	2.67	1.76	1.52	0.129		-0.66	1.53	-0.43	0.664	
Lifespan (full models)										
Maternal age^2	1.70	1.17	1.45	0.146	506	-0.53	0.92	-0.57	0.566	504
Natal helper x maternal age	1.42	2.05	0.69	0.488		-1.66	1.85	-0.90	0.369	
Natal helper x maternal age^2	-3.07	2.52	-1.22	0.223		1.45	2.13	0.68	0.496	
Lifespan 2 (males)										
Maternal age^2	1.37	1.06	1.29	0.196		/	/	/	/	
Natal helper x maternal age^2	-1.39	0.69	-2.00	0.045		/	/	/	/	
Lifespan 2 (females)										
Maternal age^2	/	/	/	/		-0.24	0.83	-0.29	0.770	
Natal helper x maternal age	/	/	/	/		-0.44	0.49	-0.91	0.360	
Lifespan 3 (males)										
Maternal age^2	1.09	1.04	1.05	0.294		/	/	/	/	
Lifespan 3 (females)										
Natal helper x maternal age	/	/	/	/		-0.44	0.49	-0.91	0.364	

Table S4. Natal socio-ecological predictors of lifetime reproductive success in the Seychelles warbler, estimated using a zero-inflated GLMM with quasi-Poisson distributions (nbinom1). The model is identical to Table 8, except that it includes an additional fixed effect of whether or not the male ever acquired dominance. Total number of males: 506 (males with helpers: 94, males that acquired dominance: 327). The estimate, standard error (SE), z-value, and p-values are given for each fixed effect. Conditional r^2 values are provided for each model. Significant results are shown in bold. Reference level for natal helper/nestmates = absent; reference level for dominant ever = no.

		Males (*n*=506)				
Fixed effect	**Levels**	**Estimate**	**SE**	**z**	**p**	**r^2**
(Intercept)		**-3.70**	**0.54**	**-6.81**	**<0.001**	0.763
Group size		0.21	0.52	0.40	0.688	
Natal helper	Present	-0.29	0.23	-1.25	0.211	
Maternal age		0.53	0.40	1.33	0.184	
Nestmates	Present	0.39	0.20	1.95	0.051	
Territory quality		**2.10**	**0.93**	**2.25**	**0.024**	
Dominant ever	Yes	**3.69**	**0.51**	**7.25**	**<0.001**	
Zero-inflated model						
(Intercept)		-23.71	48942.68	-0.00	1.000	
Random effect		**Levels**	**Variance**	**p**		
Mother ID		290	0.08	0.378		
Social father ID		278	0.00	1.000		
Cohort		**22**	**0.14**	**0.003**		

Chapter 4

Single-generation fitness proxies as predictors of long-term genetic contributions in a cooperatively breeding bird

4.1. ABSTRACT

Single-generation fitness proxies are often used to estimate individual fitness. How well these proxies predict long-term genetic contributions to future populations, however, is poorly understood. Here, we use the long-term Seychelles warbler dataset to consider how the acquisition of a dominant breeding position, the age at first breeding attempt, length of dominant breeding tenure, lifespan, and lifetime reproductive success predict individual genetic contributions to a population 15 years (~3 generations) in the future, as well as the likelihood of lineage extinction. We found that the acquisition of a dominant breeding position and the age at first breeding attempt had no effect on individual genetic contributions, or the likelihood of lineage extinction. The length of dominant breeding tenure had a positive effect on the individual genetic contributions of male ancestors, but not females. Longer lifespans and a higher lifetime reproductive success were positively associated with individual genetic contributions and a reduced likelihood of lineage extinction in both sexes. Lifetime reproductive success explained more of the variance in individual genetic contributions than any single-generation fitness metric. Future studies should carefully consider the relationship between life-history metrics and reproductive success, as the relationship between life-history measures and individual genetic contribution is likely contingent upon the relationship between life-history and reproductive success.

Key words: fitness, individual genetic contributions, cooperative breeding, lifetime reproductive success

4.2. INTRODUCTION

Fitness is a relative concept: an individual's fitness is determined by their ability to survive and reproduce compared to conspecifics (Darwin, 1859). The "fittest" individuals, or fittest alleles, are those that leave the most descendant copies of themselves to future generations (Darwin, 1859). Ideally, to measure fitness, we would consider the actual, realised amount of genetic material that an individual contributes to a future population (Leimar, 1996, McNamara and Houston, 1996). However, even in long-term projects, data are only available for a snapshot of evolutionary time and complete, comprehensive genomic pedigrees are rarely available. As such, the long-term genetic contributions of individuals are difficult to measure directly, and so single-generation proxies are often used to estimate individual fitness and selection gradients. How well these single-generation fitness proxies predict long-term genetic contributions to future populations, however, is poorly understood.

To estimate fitness, researchers often consider how individuals vary in their reproductive success (Grafen, 1988, Clutton-Brock and Sheldon, 2010). Variation in reproductive success can be calculated in a number of different ways; for instance, by calculating the number of offspring an individual produces in their first breeding season (Komdeur, 1994, Dickinson et al., 1996, Meade and Hatchwell, 2010), annually (Zanette et al., 2006, Stracey and Robinson, 2012), or over their lifetime (LRS; Kruuk et al., 1999, McLoughlin et al., 2006, Le Boeuf et al., 2019) compared to others within the population. However, these different measures are not always consistent with one another, and so fitness estimates may vary depending on the method (Murray, 2000).

An additional complication of quantifying reproductive success is that offspring are often censused at different life-history stages (Alif et al., 2022). For example, in avian species, reproductive success has been quantified as the number of eggs (Marzal et al., 2005, Mumme, 1992), nestlings (Bart and Tornes, 1989, Safina and Burger, 1983), fledglings (Gates and Gysel, 1978, Stevenson and Bryant, 2000, Safina and Burger, 1983), or adult/breeding offspring (Meierhofer et al., 1999, von Holst et al., 2002, Araki et al., 2007) produced by an individual. The life-history stage at which offspring are censused is likely to affect how the measure of reproductive success predicts longer-term, multi-generational fitness (Catton and Michener, 2016, Refsnider and Janzen, 2010, Alif et al., 2022). For instance, eggs may fail to hatch, and nestlings and fledglings may perish before they reach sexual maturity, preventing them from entering the breeding population and propagating the lineage. It is largely agreed, therefore, that performing a census on offspring at a later stage e.g., offspring that survive to adulthood or are recruited into the breeding population, is a better estimate of long-term fitness (Alif et al., 2022).

When reproductive success information is unavailable or incomplete, fitness is sometimes estimated based on information about individual life-history traits and strategies (Jakob et al., 1996, McGraw and Caswell, 1996, Lailvaux et al., 2010, Thompson et al., 2011, Powers et al., 2020). For instance, researchers might consider how a particular trait affects the likelihood of an individual acquiring dominance. In many socially-hierarchical species, dominant individuals are responsible for the majority of within-group reproduction, so if a particular trait is a significant predictor of dominance, it is presumed that individuals possessing that trait will have a higher reproductive success (Alados and Escós, 1992, Hirotani, 1994, Hodge, 2005, Jennings et al., 2006, van de Crommenacker et al., 2011). Other studies use life-history traits such as lifespan to estimate reproductive success, as lifespan is a reasonable predictor of reproductive success in a number of taxa (Wauters and Dhondt, 1995, Grant and Grant, 2000, Krüger and Lindström, 2001, Lahdenperä et al., 2011, Costanzo et al., 2017). However, as the relationship between life-history traits and Darwinian fitness is believed to be contingent upon an *expected* intermediary relationship between the life-history trait and reproductive success, there is likely to be error when using life-history traits as fitness proxies. Indeed, acquiring dominance or having a long life does not guarantee that an individual will breed successfully, or that any offspring produced will survive and reproduce themselves (Stearns, 1992). Direct measures of reproductive success, such as LRS, should be more informative fitness proxies, as they quantify the genetic information that an individual contributes to the F_1 progeny with fewer assumptions (Wilder et al., 2016). However, whilst single-generation measures of reproductive success can predict genetic contributions to F_1, they may not be accurate predictors of contributions to generations beyond that, as the reproductive success of an ancestor does not guarantee the survival and reproductive success of their descendants (Sæther and Engen, 2015, Snyder and Ellner, 2018, Emery Thompson et al., 2016).

There are a number of potential explanations for why reproductive output may not accurately predict long-term genetic contributions. Firstly, there may be a quality-quantity trade-off in reproduction; individuals that produce a larger quantity of offspring may invest less in each, resulting in offspring of lower quality (Einum and Fleming, 2000, Gillespie et al., 2008, Emery Thompson et al., 2016, Mishra and Kumar, 2019). As such, the amount of genetic information passed on to the F_2 progeny (and beyond) may be less than expected given the reproductive success of the ancestral breeder (Chen et al., 2019, Reid et al., 2019b, Alif et al., 2022). In addition, density-, frequency-, and environmentally-dependent variables can all affect how the genetic contributions of breeders are represented in future populations (Hunt et al., 2004, Roff, 2008, Sæther and Engen, 2015). Fitness measured over multiple generations, e.g., number of grand-offspring produced, is likely to correlate more strongly with individual genetic contributions as it incorporates stochastic forces and potential trade-offs in offspring quality (Sæther and Engen, 2015, Snyder and Ellner, 2018). If we wish to draw meaningful conclusions about the evolutionary past and evolutionary potential of particular traits using fitness proxies, we therefore need to understand how much variance in individual genetic contributions can be explained by these metrics.

Here, we use the long-term Seychelles warbler dataset to estimate how much variance in future genetic contributions can be explained by single-generation life-history traits and fitness proxies. To do this, we estimate an individual's genetic contribution (IGC) to a population 15 years (~3 generations) in the future and consider how the acquisition of a dominant breeding position, age at first breeding attempt, tenure as a dominant breeder, lifespan, and LRS (measured as both the number of independent (3 months+) and adult (1 year+) offspring produced over an individual's lifetime) predict IGCs. As IGCs are a measure of the amount of genetic information that an individual has contributed to a population, they provide an estimate of Darwinian fitness that is closer to its theoretical definition. Using this method, we can then determine how well single generation estimates of fitness predict longer-term genetic fitness.

Recently, a handful of studies have considered the relationship between single-generation fitness proxies and the amount of genetic information that is contributed to future generations (Chen et al., 2019, Reid et al., 2019b, Alif et al., 2022, Young et al., 2022). For example, Reid et al (2019) showed that, in song-sparrows (*Melospiza melodia*), the reproductive output of an ancestor explained <50% of the variance in their genetic contribution to a population 15 years in the future. Similarly, Young et al. (2022) found that, in humans (*Homo sapiens*), LRS explained only 29% of the variance in estimated genetic contributions to a population ~16 generations in the future. These examples illustrate the limitations of using single-generation fitness proxies, as the reproductive output of an individual does not necessarily predict longer term genetic contributions. However, to our knowledge, no previous studies have sought to quantify the relationship between life-history traits (often used as proxies for reproductive success) and IGCs, nor have they attempted to perform these analyses on a cooperative breeder. In cooperatively breeding species, the relationship between these metrics and future IGCs could differ to non-cooperatively breeding species, as the reproductive success of breeders and the success of their offspring may be influenced by the addition of helping subordinates.

4.3. METHODS

4.3.1. Study system and data collection

The Seychelles warbler is a facultative cooperative breeding passerine endemic to the Seychelles archipelago (Komdeur et al., 2016). The closed population on Cousin Island (0.29 km^2; 4°20'S, 55°40'E) consists of approximately 320 adult individuals, and has been studied since 1985, with intensive monitoring from 1997 onwards (Richardson et al., 2002, Davies et al., 2021). Each year, the population is usually monitored over two breeding seasons: the major breeding season (June–September) and the minor breeding season (January–March; (Richardson et al., 2002). There are ~115 Seychelles warbler territories on Cousin (Komdeur, 2003), each of which is occupied by a breed group consisting of a dominant breeding pair and 0-5 helping and non-helping subordinates (Komdeur, 1992, Richardson et al., 2002). The statuses of individuals are determined through behavioural observations during the breeding seasons. Dominant breeders are determined by observations of mate guarding and contact calls (Richardson et al., 2002). Subordinates are defined as all other sexually mature adults within a territory.

During the breeding seasons, as many Seychelles warblers as possible are captured in the nest as nestlings or in mist nets. The majority of birds (96%; Richardson et al., 2001) have been ringed with a unique colour combination of three ultraviolet-resistant rings and a British Trust for Ornithology metal ring. Blood samples (*ca.* 25 µl) are taken using brachial venepuncture and stored in 100% ethanol at room temperature. 1–3 biomarkers are used to perform molecular sexing, and 30 microsatellites are used to genotype individuals and determine genetic parentage (Sparks et al., 2021). The package MASTERBAYES 2.52 (Hadfield et al., 2006) was used to assign parentage to 1853 birds hatched between 1992 and the minor breeding season in 2018, with 89% of fathers and 86% of mothers assigned at ≥80% accuracy (Sparks et al., 2021). Importantly, the microsatellites used are under neutral selection (Supplementary methods 1 & Fig S1). From these parentage data, a pedigree spanning 12 generations was created (Sparks et al., 2021, Raj Pant et al., 2022), from which accurate information about reproductive success could be extracted.

4.3.2. Single-generation life-history traits and fitness metrics

The fitness estimates from the Seychelles warbler are, unusually for a wild population, very accurate. This is because the whole island population is studied, the resighting probability of Seychelles warblers is high (0.92 ± 0.02 for <2-year-olds and 0.98 ± 0.01 for older birds; (Brouwer et al., 2010) and inter-dispersal between islands is rare (<0.1% of all individuals studied, (Komdeur et al., 2004). Therefore, if a warbler is not seen for ≥2 consecutive field seasons, we can confidently assume that it is dead (Brouwer et al., 2006). The separation of dispersal and death allows lifetime fitness estimates, such as lifespan and LRS, to be accurately calculated.

We considered how acquiring dominance, the age at first breeding attempt, dominance tenure, lifespan, and LRS (measured as both the number of independent (≥3 months) and adult (≥1 year) offspring) predict estimated IGCs to a population 15 years (~3 generations) in the future (see Table 10 for full definitions of life-history traits and fitness metrics, and their predicted relationship with IGCs). The number of independent and adult offspring were both considered to assess whether censoring offspring at later stages provides a better estimate of IGCs, as has previously been found in three other systems (Reid et al., 2019b, Alif et al., 2022, Young et al., 2022). Our dataset included individuals hatched over 6 years (1997–2002) during both the major and minor breeding seasons. Only individuals hatched from 1997 onwards were included as this is when intensive monitoring began, a greater majority of individuals within cohorts were genotyped, and parentage assignment rates increased (Sparks et al., 2021). Removing individuals hatched prior to 1997 reduces the likelihood of LRS being underestimated. Because the Seychelles warbler have overlapping generations, analyses focused on yearly cohorts rather than discrete generations. Only deceased individuals were included in the analyses, as the long-term fitness measures of living individuals are subject to change. In addition, only individuals that survived to independence (≥3 months) were included to remove potential bias in the dataset; nests located high in the canopy are hard to find and access so individuals hatched in high nests may not be sampled until after fledging, and catching effort varies across years such that offspring are caught at different ages (Raj Pant et al., 2022). Our final dataset consisted of 224 males and 194 females.

4.3.3. Estimation of individual genetic contributions

Individual genetic contributions (IGCs) to a future population were calculated using a pedigree-based method following Hunter et al. (2019). The principle of random segregation of Mendelian inheritance dictates that an individual will contribute ~50% of their alleles to their genetic offspring. Based on this assumption, pedigrees can be used to estimate the genetic contribution of an individual to a future population by quantifying the number of direct descendants present at a specific point in time. An individual that produces 3 offspring, for example, will have a relatedness coefficient of ~0.5 with each offspring, resulting in an absolute genetic contribution of 1.5 to the population in which the offspring exist (assuming the focal ancestor is deceased). We can establish the estimated IGC of an ancestor to a future population by dividing their absolute genetic contribution by the total number of individuals present within the population at that time. This provides us with the proportion of genetic information in the future population that can be directly attributed to the focal ancestor.

IGCs are expected to stabilise within a population after log2(*N*) generations, where *N* is the adult population size (Chang, 1999). Genetic contributions are said to have "stabilised" because, at a certain point, the contributions of an ancestor to descendant populations change minimally from one cohort to the next (Barton and Etheridge, 2011). Therefore, once stabilisation has occurred, ancestral contributions to one generation tightly predict contributions to the generations beyond (Chang, 1999). The adult population size on Cousin is ~320 individuals, which provides an estimated stabilisation time of ~8.3 generations. Generation time was calculated as the mean parental age at hatch for each sex (females: 4.7 years, males: 5.1 years), resulting in an estimated time to stabilisation of 39 years for females and 42 years for males. However, this calculation assumes conditions such as non-overlapping generations and random mating (Chang, 1999), which may not reflect natural conditions.

Although our dataset is one of the largest genetic pedigrees for cooperative breeders in the world, it covers only 21 years with high rates of parentage assignment (1997-2017; (Raj Pant et al., 2022, Sparks et al., 2021). To confirm that stabilisation does not occur within the timeframe of our dataset, the correlation coefficient between the IGCs at 17-years post-hatch and each year preceding were calculated for 4 cohorts (1997–2000; Fig. S2), as detailed in (Reid et al., 2019b) and also applied in Young et al. (2022). For the correlation coefficient analysis, IGCs at 17-years post-hatch were used to account for the fact that later cohorts will have a high correlation coefficient with the cohorts directly before, allowing us to confirm with a higher degree of certainty that stabilisation does not occur within a 15-year timeframe. A consistent correlation coefficient of ≥0.95 indicates stabilisation; correlation coefficients of <0.95 indicate a high degree of variability in IGCs between cohorts. In addition, the IGCs of 6 cohorts (1997–2002) to a population 15-years post-hatch were extracted (i.e. maximum 2017). We then plotted the IGCs of individuals to each cohort post-hatch and visually inspected the degree of variability in IGCs over time (Fig. S3) as detailed in Hunter (2019). As expected, we do not have the data to analyse the accuracy of single-generation fitness proxies in predicting IGCs at the point of stabilisation (Figs S2 & S3). We can still, nonetheless, assess the value of life-history traits and fitness metrics in predicting longer-term, multi-generational IGCs.

4.3.4. Statistical analyses

To test how well single-generation life-history traits and fitness metrics predict future IGCs, we ran sex-specific generalised additive models with zero-inflated beta distributions using the GAMLSS 5.4–3 package (Rigby and Stasinopoulos, 2005) in R Studio 2022.07.1 (RStudio Team, 2022). Models were run for each sex separately as males have more variable reproductive success than females. Each model included a single-generation life-history trait or fitness proxy as a fixed effect, and the estimated IGC to the population 15 years post-hatch as the response. Cohort was included as a random effect to control for temporal variation in mean IGC. The beta distributed portion of the model considers the relationship between the given life-history trait or fitness metric and the IGCs of individuals that had non-zero IGCs 15 years in the future. The zero-inflated portion of the models consider the relationship between the fitness metric and the probability of an individual having an IGC of 0 to the future population (i.e., their lineage became extinct). Model fit was checked by visually analysing Q-Q plots, and the r^2 of each model was calculated to determine how much variance in future IGCs can be explained by the models using the GAMLSS package (Rigby and Stasinopoulos, 2005).

Table 10. Descriptions of single-generation life-history traits and fitness proxies, how they were calculated, and their predicted effect on future individual genetic contributions (IGCs) to a population 15 years in the future.

Fitness metric	Description and calculation of metric	Predicted effect on future IGCs
Acquisition of dominance	Binary metric of whether an individual acquired a dominant breeding position at any point throughout their lifetime.	Acquiring a dominant breeding position will be positively associated with higher IGCs, as dominant breeders account for the majority of reproduction (Raj Pant et al., 2019). The effect is likely to be stronger in males than in females as subordinate females often co-breed (Richardson et al., 2001).
Age at first breeding attempt	The length of time between an individual's estimated hatch date and the birth date of their first genetic offspring or the midpoint of the first breeding season that they were assigned a dominant breeding status, whichever came first.	Age at first breeding attempt will be negatively associated with IGCs because age at first dominance is negatively associated with lifetime reproductive success (Paj Pant et al 2022).
Dominant breeding tenure	The total length of time that an individual spends as a dominant breeder throughout their lifetime.	Length of dominant breeding tenure will be positively associated with IGCs, as dominant breeders account for the majority of reproduction (Raj Pant et al., 2019). The effect is likely to be stronger in males than in females, as females can reproduce through co-breeding (Richardson et al., 2001).
Lifespan	The length of time between an individual's estimated hatch date and the midpoint of the final breeding season that they were assigned a status or the last date that they were observed or caught in the field, whichever came last.	Lifespan will be positively associated with future IGCs, as lifespan is positively correlated with lifetime reproductive success in Seychelles warblers (Sparks et al 2021).
LRS (independent offspring)	The total number of offspring produced by an individual that made it to independence (≥3 months old), assigned using the genetic pedigree.	Number of independent and adult offspring will be positively correlated with future IGCs, as individuals that produce more offspring will likely have more descendants alive at the point of sampling. Number of adult offspring will provide a better estimate of IGCs than number of independent offspring, as it provides a better measure of the number of offspring that are recruited to the breeding population. LRS is expected to outperform all life-history measures, as it accounts for trade-offs in survival and reproduction.
LRS (adult offspring)	The total number of offspring produced by an individual that made it to adulthood (≥1 year old), assigned using the genetic pedigree.	

4.4. RESULTS

For both sexes, the models containing the number of adult (≥1 year old) offspring explained the most variation in IGCs (males: 55.0% of the variance, females: 46.8%), followed by independent (≥3 months old) offspring (males: 53.8%, females: 46.5%), lifespan (males: 32.1%, females: 29.8%), dominant breeding tenure (males: 21.7%, females: 19.6%), age at first breeding attempt (males: 7.7%, females: 3.7%), and, finally, the acquisition of dominant breeding position (males: 7.1%, females: 0.9%).

Dominance acquisition

The acquisition of a dominant breeding position had no effect on non-zero future IGCs in males or females (Table 11). Within our analyses, 160/224 males (71%) and 141/194 females (72%) obtained a dominant breeding position at some point during their lifetime. Dominant males and females had mean non-zero IGCs of 6.5e-3 (±8.7e-4, *n*=83) and 5.4e-3 (±9.4e-4, *n*=72), respectively; males that never acquired dominance had a mean non-zero IGC of 4.2e-3 (±7.4e-3, *n*=3), and females that never acquired dominance had a mean non-zero IGC of 3.5e-3 (±1.7e-3, *n*=5). However, acquiring a dominant breeding position significantly reduced the likelihood of lineage extinction in both sexes (Table 11). Dominant males and females had lineage extinction probabilities of 48.1% (*n*=160) and 48.9% (*n*=141), respectively, compared to 95.7% of males (*n*=69) and 90.6% of females (*n*=53) that never acquired dominance.

Age at first breeding attempt

The age at first breeding attempt had no effect, in either sex, on future non-zero IGCs or on the probability of lineage extinction (Table 12). The mean age at first breeding attempt for males and females whose lineage went extinct was 1.7 (±0.15, *n*=79) and 1.6 years (±0.18, *n*=73), respectively. The mean age at first breeding attempt for males and females whose lineage persisted (i.e., they had a non-zero IGC) was 1.7 (±0.15, *n*=86) and 1.5 years (±0.13, *n*=77), respectively.

Lifespan

Lifespan had a significant, positive relationship to non-zero future IGCs in both males and females (Table 13; Fig. 7); individuals that lived longer contributed more genetic information to a population 15 years in the future than individuals that had shorter lifespans. In addition, a longer lifespan was associated with a reduced likelihood of lineage extinction in both sexes (Table 13). The mean lifespan of male or female Seychelles warblers whose lineage went extinct was 3.19 (±0.53, *n*=138) and 2.97 (±0.55, *n*=117) years, respectively. However, the mean lifespan of a male or female Seychelles warbler whose lineage persisted (i.e., they had a non-zero IGC) was 6.93 (±0.85, *n*=86) and 7.17 (±0.91, *n*=77) years, respectively.

Dominant breeding tenure

The length of a male's dominant breeding tenure had a significant, positive association to future IGCs in males, but not females (Table 14; Fig. 8); males with longer breeding tenures had higher IGCs than males with shorter breeding tenures. In addition, a longer dominant breeding tenure was associated with a reduced likelihood of lineage extinction in both sexes (Table 14; Fig. 8). The mean length of dominant breeding tenure of males and females whose lineage went extinct were 2.73 (±0.52, *n*=77) and 2.81 (±0.55, *n*=69) years, respectively. However, the mean tenure of males and females whose lineage persisted (i.e., they had a non-zero IGC) were 5.32 (±0.68, *n*=83) and 5.56 (±0.70, *n*=72) years, respectively.

Lifetime reproductive success

The number of independent offspring (≥3 months old) that an individual produced over their lifetime had a significant, positive association with future IGCs in both male and female Seychelles warblers (Table 15; Fig. 9). The number of independent offspring produced was also associated with a significant reduction in the probability of lineage extinction in both sexes (Table 15). The mean number of independent offspring produced by males and females whose lineage went extinct was 0.77 (±0.22 *n*=138) and 0.90 (±0.22, *n*=117), respectively. However, the mean number of independent offspring produced by males and females whose lineage persisted (i.e., they had a non-zero IGC) was 4.82 (±0.58, *n*=86) and 4.44 (±0.50, *n*=77), respectively.

The number of adult offspring (≥1 year old) produced by an individual over their lifetime also had a significant, positive association with future IGCs in both male and female Seychelles warblers (Table 16; Fig. 10). The number of adult offspring also significantly reduced the likelihood of lineage extinction in both sexes (Table 16). The mean number of adult offspring produced by males and females whose lineage went extinct was 0.58 (±0.17

n=138) and 0.68 (±0.19, *n*=117), respectively. However, the mean number of adult offspring produced by males and females whose lineage persisted (i.e., they had a non-zero IGC) was 3.76 (±0.42, *n*=86) and 3.53 (±0.37, *n*=77), respectively. Whilst the models containing the number of adult offspring explained more of the variance in IGCs than the models containing the number of independent offspring (Table 15; Table 16), the difference in r^2 was small (<0.02).

Table 11. The relationship between dominance acquisition and the estimated individual genetic contribution (IGC) to a population 15 years (~3 generations) in the future. Sex-specific generalised additive models were run with zero-inflated beta distributions using the package GAMLSS 5.4–3 (Rigby and Stasinopoulos, 2005). The beta distribution of the model assesses how dominance acquisition influences future IGCs for individuals with non-zero IGCs; the zero-inflated portion of the model assesses how dominance acquisition influences the probability of an individual having an IGC of zero (indicating lineage extinction). The estimate, standard error (SE), t-value, and p-values are given. Model r^2 is provided. Reference level for dominance= no. Significant effects are shown in bold.

		Males (*n*=224)					**Females (*n*=194)**				
Fixed effect	Levels	Estimate	SE	t	p	r^2	Estimate	SE	t	p	r^2
Beta distribution						0.071					0.009
(Intercept)		**-5.80**	**0.45**	**-13.04**	**<0.001**		**-5.34**	**0.32**	**-16.46**	**<0.001**	
Dominance	Yes	0.72	0.45	1.61	0.109		0.14	0.33	0.42	0.677	
Zero-inflated											
(Intercept)		**3.01**	**0.59**	**5.09**	**<0.001**		**2.26**	**0.47**	**4.82**	**<0.001**	
Dominance	Yes	**-3.09**	**0.61**	**-5.04**	**<0.001**		**-2.31**	**0.50**	**-4.62**	**<0.001**	
Random effect	Levels	Variance					Variance				
Cohort	7	0.22					0.08				

Table 12. The relationship between age at first breeding attempt and the estimated genetic contribution of an individual (IGC) to a population 15 years (~3 generations) in the future. Sex-specific generalised additive models were run with zero-inflated beta distributions using the package GAMLSS 5.4–3 (Rigby and Stasinopoulos, 2005). The beta distribution of the model assesses how the age at first breeding attempt influences future IGCs for individuals with non-zero IGCs; the zero-inflated portion of the model assesses how age at first breeding attempt influences the probability of an individual having an IGC of zero (indicating lineage extinction). The estimate, standard error (SE), t-value, and p-values are given. Model r^2 is provided. Significant effects are shown in bold.

		Males (*n*=165)					**Females (*n*=150)**				
Fixed effect	Levels	Estimate	SE	t	p	r^2	Estimate	SE	t	p	r^2
Beta distribution						0.077					0.037
(Intercept)		**-5.10**	**0.15**	**-35.13**	**<0.001**		**-5.37**	**0.18**	**-30.69**	**<0.001**	
Age at first breeding		0.03	0.49	0.07	0.949		0.69	0.57	1.18	0.240	
Zero-inflated model											
(Intercept)		-0.11	0.33	-0.32	0.749		-0.30	0.32	-0.95	0.342	
Age at first breeding		0.08	1.11	0.07	0.942		0.98	1.06	0.92	0.358	
Random effect	Levels	Variance					Variance				
Cohort	7	0.23					0.09				

Table 13. The relationship between lifespan and the estimated genetic contribution of an individual (IGC) to a population 15 years (~3 generations) in the future. Sex-specific generalised additive models were run with zero-inflated beta distributions using the package GAMLSS 5.4–3 (Rigby and Stasinopoulos, 2005). The beta distribution of the model assesses how lifespan influences future IGCs for individuals with non-zero IGCs; the zero-inflated portion of the model assesses how lifespan influences the probability of an individual having an IGC of zero (indicating lineage extinction). The estimate, standard error (SE), t-value, and p-values are given. Model r^2 is provided. Significant effects are shown in bold.

		Males (*n*=224)					**Females (*n*=194)**				
Fixed effect	Levels	Estimate	SE	t	p	r^2	Estimate	SE	t	p	r^2
Beta distribution						0.321					0.298
(Intercept)		**-5.58**	**0.14**	**-41.14**	**<0.001**		**-5.62**	**0.16**	**-35.61**	**<0.001**	
Lifespan		**1.13**	**0.25**	**4.56**	**<0.001**		**1.08**	**0.35**	**3.05**	**0.003**	
Zero-inflated model											
(Intercept)		**1.76**	**0.26**	**6.83**	**<0.001**		**1.90**	**0.29**	**6.60**	**<0.001**	
Lifespan		**-4.70**	**0.75**	**-6.30**	**<0.001**		**-6.28**	**0.99**	**-6.32**	**<0.001**	
Random effect	Levels	Variance					Variance				
Cohort	7	0.26					0.14				

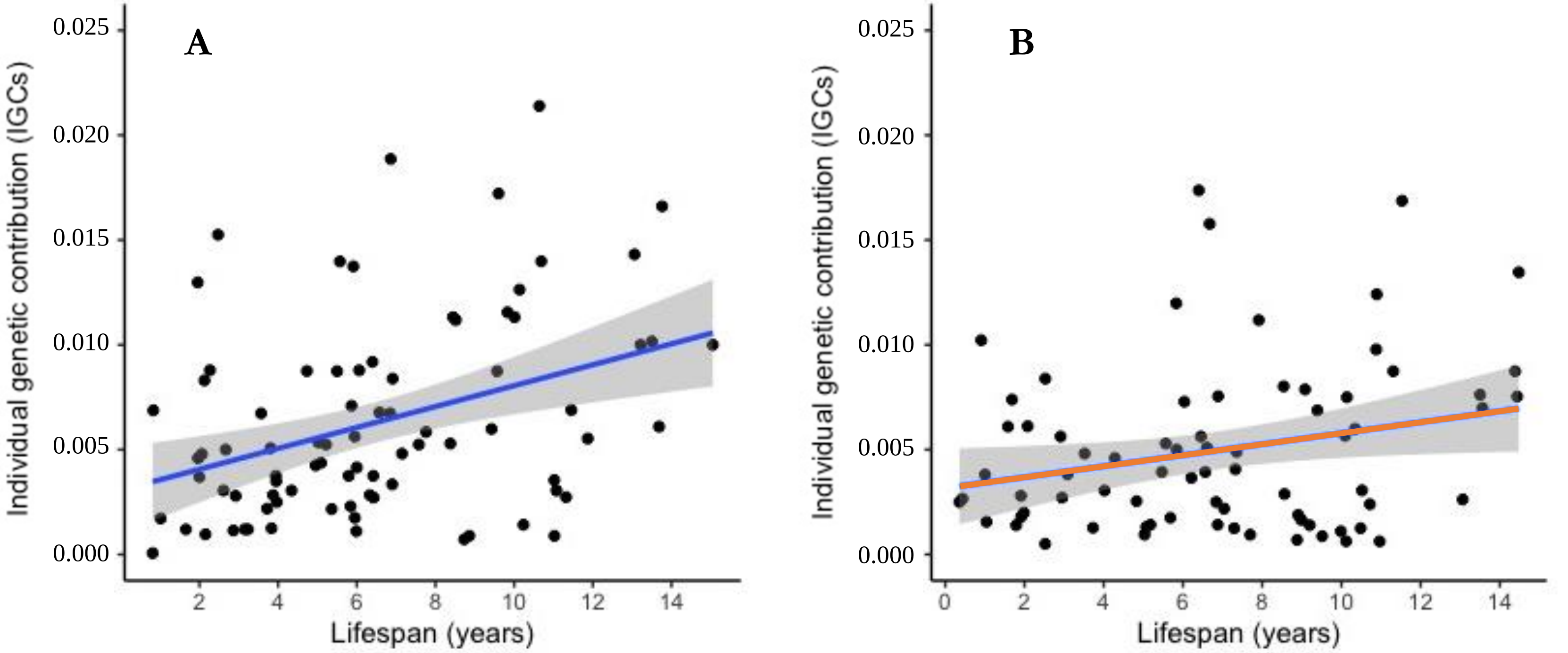


Figure 7. The relationship between lifespan (years) and the estimated non-zero individual genetic contribution (IGC) of a male (**A**; *n*=224) or female (**B**; *n*=194) Seychelles warbler to a population 15 years in the future. Estimated IGC's were calculated by considering the amount of genetic information that an individual shares with all of their living, direct descendants (i.e., the summed *r* coefficient), divided by the total number of individuals alive in the sample cohort 15 years in the future. Individual values (dots) are presented, along with the fitted regression line. The grey shading around the fitted regression line shows the corresponding 95% confidence interval.

Table 14. The relationship between length of dominant breeding tenure and the estimated genetic contribution of an individual (IGC) to a population 15 years (~3 generations) in the future. Sex-specific generalised additive models were run with zero-inflated beta distributions using the package GAMLSS 5.4–3 (Rigby and Stasinopoulos, 2005). The beta distribution of the model assesses how lifespan influences future IGCs for individuals with non-zero IGCs; the zero-inflated portion of the model assesses how length of the dominant breeding tenure influences the probability of an individual having an IGC of zero (indicating lineage extinction). The estimate, standard error (SE), t-value, and p-values are given. Model r^2 is provided. Significant effects are shown in bold.

		Males (*n*=160)					**Females (*n*=141)**				
Fixed effect	Levels	Estimate	SE	t	p	r^2	Estimate	SE	t	p	r^2
Beta distribution						0.217					0.198
(Intercept)		**-5.36**	**0.12**	**-44.42**	**<0.001**		**-5.42**	**0.18**	**-30.67**	**<0.001**	
Tenure		**0.73**	**0.23**	**3.13**	**0.002**		0.51	0.34	1.50	0.135	
Zero-inflated model											
(Intercept)		**0.86**	**0.26**	**3.27**	**0.001**		**1.07**	**0.30**	**3.59**	**<0.001**	
Tenure		**-3.33**	**0.77**	**-4.31**	**<0.001**		**-3.73**	**0.83**	**-4.49**	**<0.001**	
Random effect	Levels	Variance					Variance				
Cohort	7	0.15					0.00				

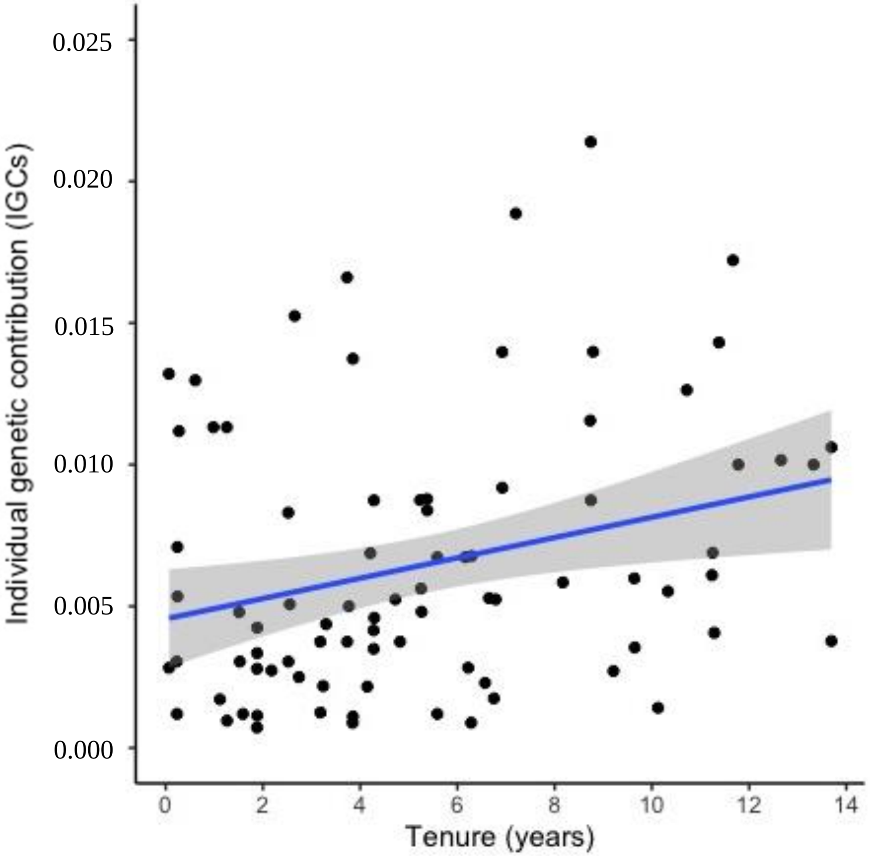


Figure 8. The relationship between dominant breeding tenure (years) and the estimated non-zero individual genetic contribution (IGC) of a male Seychelles warbler to a population 15 years in the future (*n*=160). Estimated IGC's were calculated by considering the amount of genetic information that an individual shares with all of their living, direct descendants (i.e., the summed *r* coefficient), divided by the total number of individuals alive in the sample cohort 15 years in the future. Individual values (dots) are presented, along with the fitted regression line. The grey shading around the fitted regression line shows the corresponding 95% confidence interval.

Table 15. The relationship between the number of independent offspring (3 months+) produced over an individual's lifetime (LRS) and the estimated genetic contribution of an individual (IGC) to a population 15 years (~3 generations) in the future. Sex-specific generalised additive models were run with zero-inflated beta distributions using the package GAMLSS 5.4–3 (Rigby and Stasinopoulos, 2005). The beta distribution of the model assesses how LRS influences future IGCs for individuals with non-zero IGCs; the zero-inflated portion of the model assesses how LRS influences the probability of an individual having an IGC of zero (indicating lineage extinction). The estimate, standard error (SE), t-value, and p-values are given. Model r^2 is provided. Significant effects are shown in bold.

		Males (*n*=224)					**Females (*n*=194)**				
Fixed effect	Levels	Estimate	SE	t	p	r^2	Estimate	SE	t	p	r^2
Beta distribution						0.538					0.465
(Intercept)		**-5.74**	**0.11**	**-52.36**	**<0.001**		**-5.77**	**0.17**	**-34.83**	**<0.001**	
Independent offspring		**0.12**	**0.02**	**7.69**	**<0.001**		**0.11**	**0.03**	**4.27**	**<0.001**	
Zero-inflated model											
(Intercept)		**2.16**	**0.27**	**7.89**	**<0.001**		**-5.77**	**0.17**	**-34.83**	**<0.001**	
Independent offspring		**-0.78**	**0.10**	**-7.70**	**<0.001**		**-0.11**	**0.03**	**4.27**	**<0.001**	
Random effect	Levels	Variance					Variance				
Cohort	7	0.25					0.14				

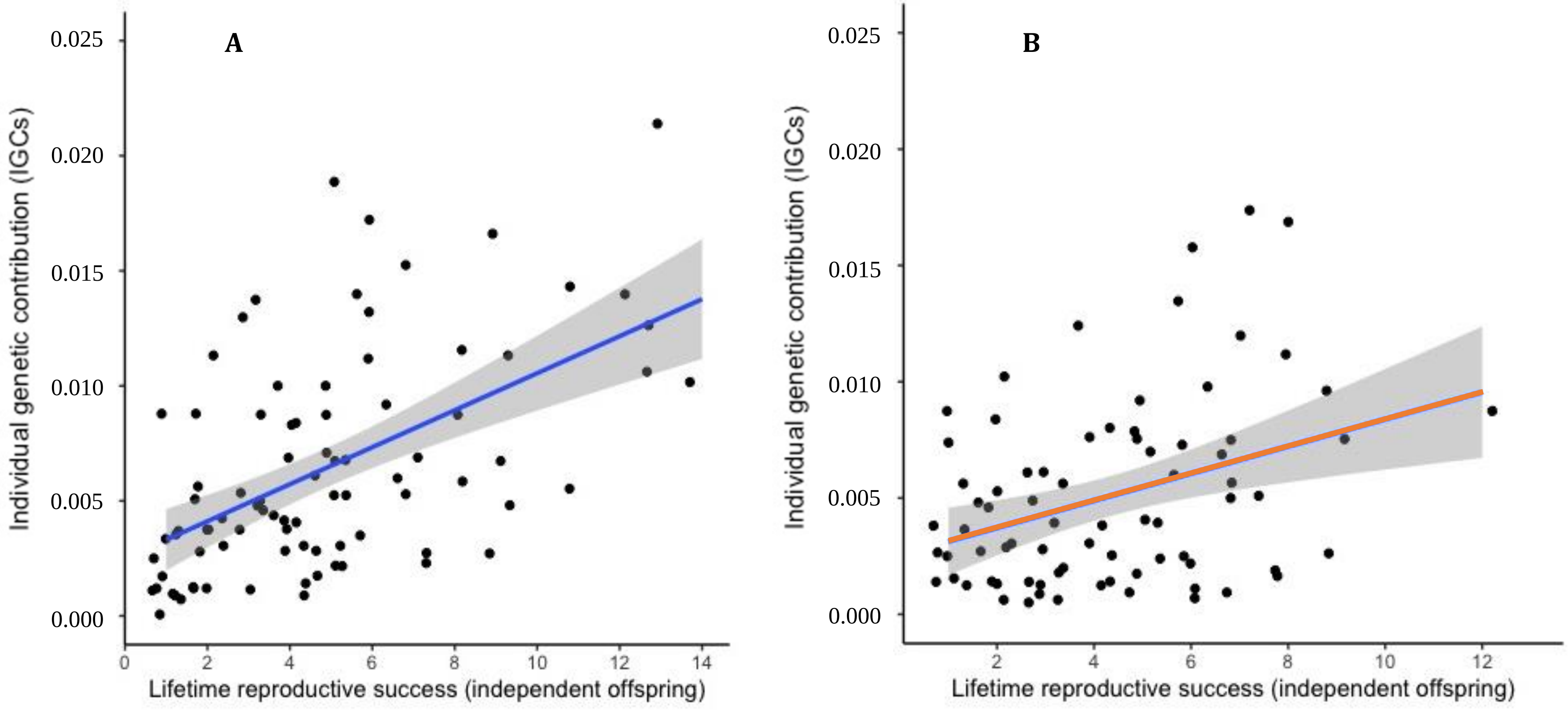


Figure 9. The relationship between the number of independent offspring (3 months+) produced over a male (**A**; *n*=224) or female (**B**; *n*=194) Seychelles warbler's lifetime and the estimated non-zero individual genetic contribution (IGC) to a population 15 years in the future. Estimated IGC's were calculated by considering the amount of genetic information that an individual shares with all of their living, direct descendants (i.e., the summed *r* coefficient), divided by the total number of individuals alive in the sample cohort 15 years in the future. Individual values (dots) are presented, along with the fitted regression line. The grey shading around the fitted regression line shows the corresponding 95% confidence interval.

Table 16. The relationship between the number of adult offspring (1 year+) produced over an individual's lifetime (LRS) and the estimated genetic contribution of an individual (IGC) to a population 15 years (~3 generations) in the future. Sex-specific generalised additive models were run with zero-inflated beta distributions using the package GAMLSS 5.4–3 (Rigby and Stasinopoulos, 2005). The beta distribution of the model assesses how LRS influences future IGCs for individuals with non-zero IGCs; the zero-inflated portion of the model assesses how LRS_A influences the probability of an individual having an IGC of zero (indicating lineage extinction). The estimate, standard error (SE), t-value, and p-values are given. Model r^2 is provided. Significant effects are shown in bold.

		Males (*n*=224)					**Females (*n*=194)**				
Fixed effect	Levels	Estimate	SE	t	p	r^2	Estimate	SE	t	p	r^2
Beta distribution						0.550					0.468
(Intercept)		**-5.80**	**0.12**	**-49.74**	**<0.001**		**2.30**	**0.17**	**-33.88**	**<0.001**	
Recruited offspring		**0.17**	**0.023**	**7.73**	**<0.001**		**0.14**	**0.04**	**3.93**	**<0.001**	
Zero-inflated model											
(Intercept)		**2.30**	**0.29**	**7.96**	**<0.001**		**2.40**	**0.33**	**7.29**	**<0.001**	
Recruited offspring		**-1.07**	**0.14**	**-7.68**	**<0.001**		**-1.12**	**0.15**	**-7.26**	**<0.001**	
Random effect	Levels	Variance					Variance				
Cohort	7	0.24					0.13				

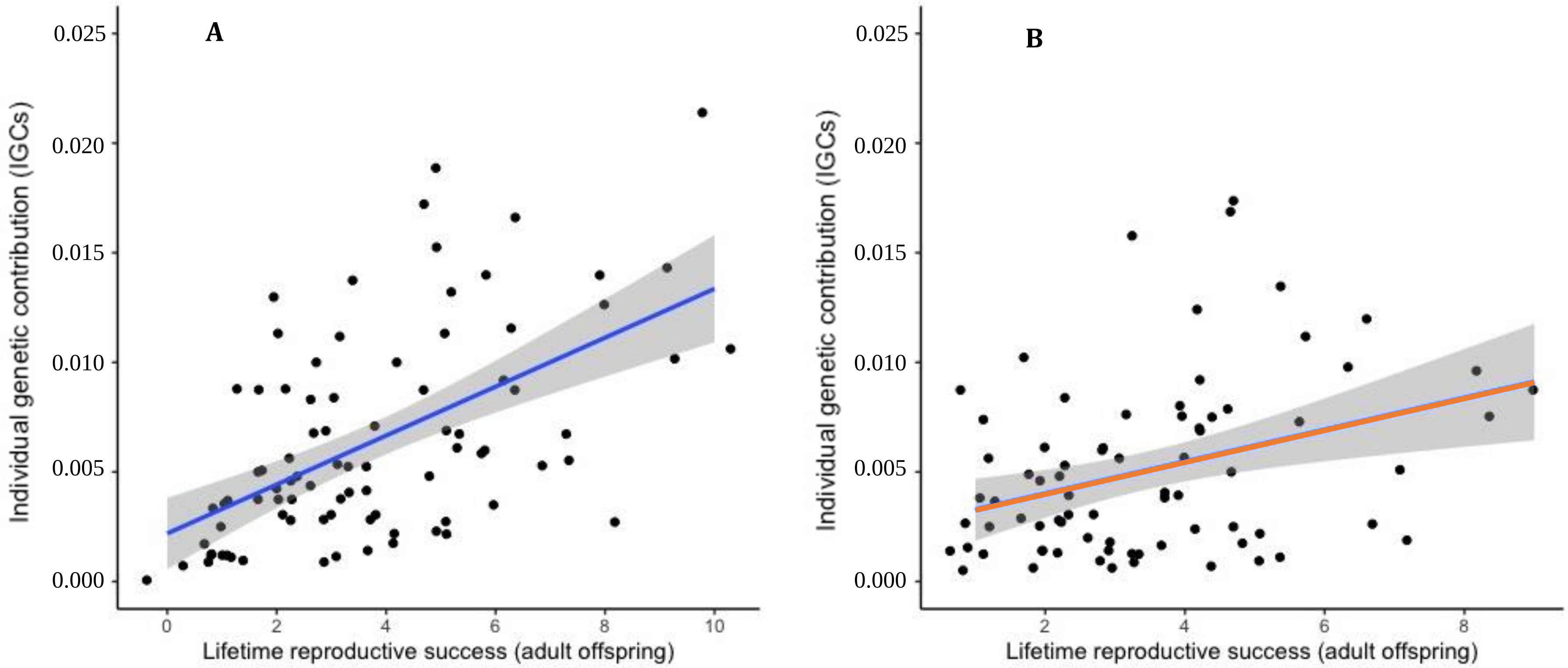


Figure 10. The relationship between the number of adult offspring (1 year+) produced over a male (**A**; *n*=224) or female (**B**; *n*=194) Seychelles warbler's lifetime and the estimated non-zero individual genetic contribution (IGC) to a population 15 years in the future. Estimated IGC's were calculated by considering the amount of genetic information that an individual shares with all of their living, direct descendants (i.e., the summed *r* coefficient), divided by the total number of individuals alive in the sample cohort 15 years in the future. Individual values (dots) are presented, along with the fitted regression line. The grey shading around the fitted regression line shows the corresponding 95% confidence interval.

4.5. DISCUSSION

Here, we estimated the ability of single-generation life-history traits and fitness proxies to predict lineage extinction and non-zero IGCs three generations into the future, in a natural population of a cooperatively breeding bird. We found that single-generation life-history traits and fitness proxies explained between 8-56% of the variation in IGCs, with the most variation explained using the number of offspring counted at older offspring life-history stages.

Lifetime reproductive success and IGCs

LRS (measured as both the number of independent and adult offspring) had a significant, positive association with future non-zero IGCs in both males and females, as expected. In addition, a higher LRS was associated with a significant reduction in the likelihood of lineage extinction three generations in the future. Producing multiple offspring may buffer the risk of lineage extinction, as there are more offspring that could potentially breed even if some fail. Although survival is lower in the first year than later-life (Brouwer et al., 2006), there was little difference in r^2 between the models containing the number of independent offspring at 3 months of age (males = 0.54, females = 0.47) and the number of adult offspring at 1 year of age (males = 0.55, females = 0.47). This indicates that LRS counts at these two offspring life-history stages has minimal effect on the ability to predict future IGCs. This finding conflicts with previous studies on other taxa which found that censusing offspring at later life-history stages results in a higher correlation to future IGCs (Alif et al., 2022, Young et al., 2022).

LRS explained more variance in IGCs than any of the life-history traits considered. Similarly, LRS was found to be a better predictor than lifespan in song sparrows (Reid et al., 2019b) and humans (Young et al., 2022), likely because LRS accounts for trade-offs in survival and reproduction (Day and Otto, 2001, Brommer et al., 2002, Hunt et al., 2004). Whilst LRS explained more variance in IGCs than any of the life-history traits, there was still a large amount of variation that was not explained (range: 44-53%). Indeed, some Seychelles warblers that produced many offspring had lower IGCs than would be expected given their LRS (Fig 9 & 10), and there were some significant rank order changes between individuals in terms of their IGCs from one cohort to the next (Fig. S3). Unexplained variation in IGCs is to be expected, as offspring are not exposed to the same environmental conditions as their ancestors (Reid et al., 2019b, Alif et al., 2022), which may influence their survival and subsequent reproduction. For instance, change in local population density is likely to affect an individual's likelihood of obtaining a dominant breeding position. The population of Seychelles warblers on Cousin Island is at carrying capacity (Komdeur et al., 2016), and all available territories are occupied (Komdeur, 1992). If local population density increases, then this may decrease the likelihood of any one individual obtaining a dominant breeding position. Dominant breeders account for the majority of offspring produced (Richardson et al., 2001, Raj Pant et al., 2019, Sparks et al., 2021), and so failing to obtain a breeding position is likely to have a significant effect on reproductive success. In addition, heritability of LRS in wild populations is low (<10%; Merilä and Sheldon, 2000, Burt, 1995) and so the reproductive success of an ancestor does not necessitate that their offspring, too, will be successful breeders. Additionally, there is often a quality-quantity trade off in reproduction; individuals that produce many offspring may produce offspring of lower quality (Einum and Fleming, 2000, Gillespie et al., 2008, Emery Thompson et al., 2016, Mishra and Kumar, 2019) that may be less successful breeders. Indeed, in other taxa, such as the long-tailed tit (*Aegithalos caudatus*), LRS explains only one-third of the observed variation in the number of grand-offspring fledged (MacColl and Hatchwell, 2004).

Life-history traits and IGCs

Out of all life-history traits, lifespan explained the most variance in IGCs (<33%), followed by dominant breeding tenure (<22%), and the age at first breeding attempt and acquisition of dominant breeding position (both <8%).

The acquisition of dominance had no effect on non-zero IGCs three generations in the future in either male or female Seychelles warblers. This result was surprising, especially for males; initially, we hypothesised that males acquiring dominance would lead to higher IGCs, as dominant breeders are responsible for the vast majority of the reproduction within the population (Richardson et al., 2001, Raj Pant et al., 2019, Sparks et al., 2021). This result, however, can likely be explained by the fact that very few life-long subordinate males (4.7%; *n*=3) and females (9.5%; *n*=5) had non-zero IGCs, which may have reduced power in the beta distributed portions of these models. In addition, we found that the acquisition of a dominant breeding position significantly reduced the likelihood of lineage extinction three generations in the future in both sexes. Many life-long subordinates never produced offspring (males: 93.8%, *n*=64; females: 84.9%, *n*=53), whereas comparatively few dominant breeders had an LRS of 0 (males: 25.6%, *n*=160, females: 23.4%, *n*=141), which would explain this effect.

Here, we found that the age at which an individual made their first breeding attempt had no effect on the non-zero IGCs or the likelihood of lineage extinction in either sex, which was unexpected. Trade-offs between early reproduction, longevity and late-life reproductive success have been well documented both theoretically (Stearns, 1992, Williams, 1957) and empirically in a variety of taxa (*see* Lemaître et al. (2015) for review). Individuals that reproduce at an early age may have more opportunities to produce offspring, but they may also have a shorter lifespan due to the energetic demands of reproduction (Stearns, 1992, Williams, 1957). Indeed, in the Seychelles warbler, an earlier age at first breeding is negatively associated with both late-life survival (Hammers et al., 2013) and male LRS (Raj Pant et al., 2022). As such, we hypothesised that an earlier age at first breeding would be negatively associated with IGCs. Whilst an earlier age at first breeding is associated with the production of fewer offspring (Raj Pant et al., 2022), parental age has also been linked to differences in offspring quality. In the Seychelles warbler, female offspring produced by younger mothers have higher LRS than when their mother is older (Sparks et al., 2021). Age at first breeding could therefore have implications for the IGCs of breeders beyond the number of offspring produced, which could explain why we found no effect of age at first breeding on future non-zero IGCs or likelihood of lineage extinction.

Lifespan had a significant, positive association with non-zero IGCs and a reduced likelihood of lineage extinction in both males and females. This result was expected, as lifespan predicts LRS in the Seychelles warbler, likely due to the fact that long-lived individuals have more opportunity to reproduce compared to individuals with shorter lifespans (Sparks et al., 2022). Indeed, lifespan has been positively correlated with lifetime reproductive success in a variety of species (Wauters and Dhondt, 1995, Grant and Grant, 2000, Krüger and Lindström, 2001, Lahdenperä et al., 2011, Costanzo et al., 2017). Our findings are consistent with those in other taxa, such as those on the song sparrow (Reid et al., 2019a) and in humans (Young et al., 2022), which also found lifespan to be a positive predictor of future non-zero IGCs.

A longer dominant breeding tenure was associated with higher non-zero IGCs in males, but not females. Males only tend to sire offspring as dominant breeders (Raj Pant et al., 2019); it follows, therefore, that length of male breeding tenure would have a positive effect on non-zero IGCs, as males that breed for longer will have more opportunity to produce offspring over the course of their tenures. Females, on the other hand, can co-breed as subordinates (Richardson et al., 2001), allowing them to produce offspring that contribute to their future IGCs irrespective of their length of dominant breeding tenure. In addition, in both sexes, individuals with longer breeding tenures had a significantly reduced probability of lineage extinction over three generations compared to individuals with shorter dominant breeding tenures. This was expected, as virtually all males only reproduce during their dominant breeding tenure (0.6% of offspring have a subordinate father) and only 11% of offspring have a subordinate mother (Sparks et al., 2022).

Often, when studies use life-history traits as a way of estimating fitness, they do so because of an expected intermediary relationship between the life-history trait and reproductive success. However, the relationships between life-history traits and LRS are not direct (Snyder and Ellner, 2018), nor is the relationship between reproductive success and long-term genetic contributions, evidenced by the large amount of unexplained variation between LRS and IGCs found in the Seychelles warbler (this study) and other taxa (Reid et al., 2019; Young et al., 2022). The variance that arises at each of these levels contributes to the overall association between life-history traits and IGCs and explains why life-history traits explain significantly less variance in IGCs than LRS. Regardless of the cause of unexplained variation, the nature of its existence may lead to erroneous conclusions about the evolutionary past and potential of particular traits, with researchers overestimating their multi-generational fitness benefit.

Considering cooperative breeding

We calculated IGCs based on direct reproduction. However, the Seychelles warbler is a cooperative breeder and non-breeding subordinates gain indirect fitness benefits from helping to raise relatives (Richardson et al., 2002). As such, the amount of actual, realised genetic contributions to future populations may vary from the expected genetic contributions calculated based on direct reproduction alone. For instance, whilst we found age at first breeding to have no effect on IGCs to a population 15 years in the future, individuals that start breeding at an older age may have helped to raise relatives prior to independent reproduction (chapter 2). By helping to raise relatives, they may increase their genetic representation in future populations without direct breeding (Hamilton, 1964).

Additionally, helpers have been shown to increase the lifespan (Hammers et al., 2019) and reproductive success of dominant breeders (Komdeur, 1994, Richardson et al., 2007, Hammers et al., 2021). If helpers are present during an individual's dominant breeding tenure, this may mask the effect of certain life-history traits on future IGCs. For instance, breeding at an earlier age has been shown to reduce late-life survival (Hammers et al., 2013) and male LRS (Raj Pant et al., 2022), with shorter lifespans and a lower LRS being linked to reduced IGCs (this study). However, with the addition of helpers, this negative effect may be mitigated against. Whilst not considered here, assessing how helpers influence these relationships could be an important avenue for future study.

4.6. CONCLUSION

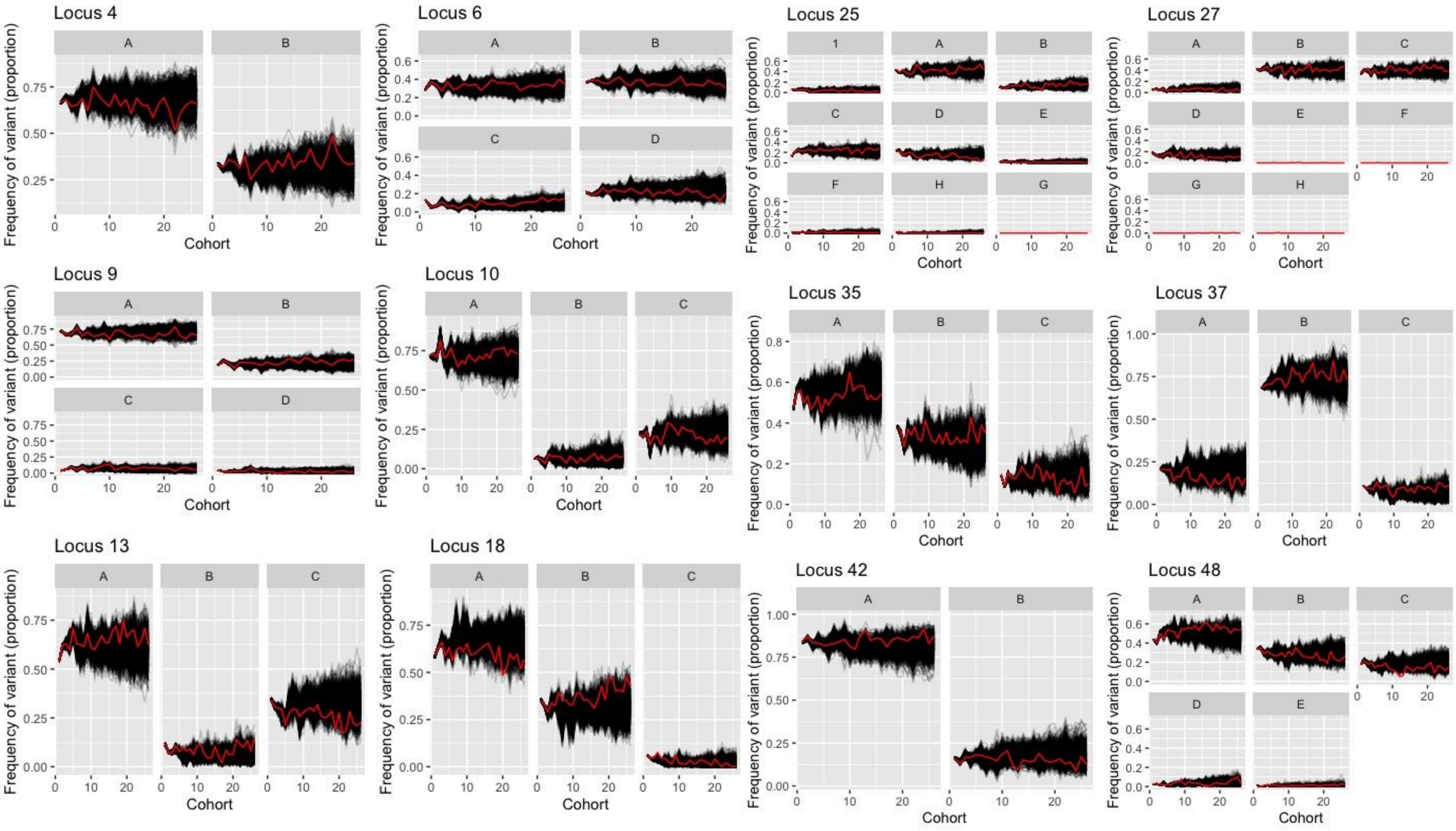
Life-history traits such as dominance acquisition, age at first breeding, and dominant breeding tenure had no relationship with IGCs to a population 15 years in the future. However, longer-term fitness measures such as lifespan and LRS were found to have a positive association, although there was still a large amount of variation in IGCs that could not be explained by these metrics, which could potentially lead to erroneous evolutionary inferences. The age at which offspring were censused to calculate LRS had little effect on the explanatory power of the LRS models. The relationship between LRS and IGCs is likely to be both species and context specific, as social, demographic, spatial and temporal variables may affect offspring survival and reproductive success. Our study sheds light on how different life-history traits and fitness proxies relate to longer-term genetic contributions.

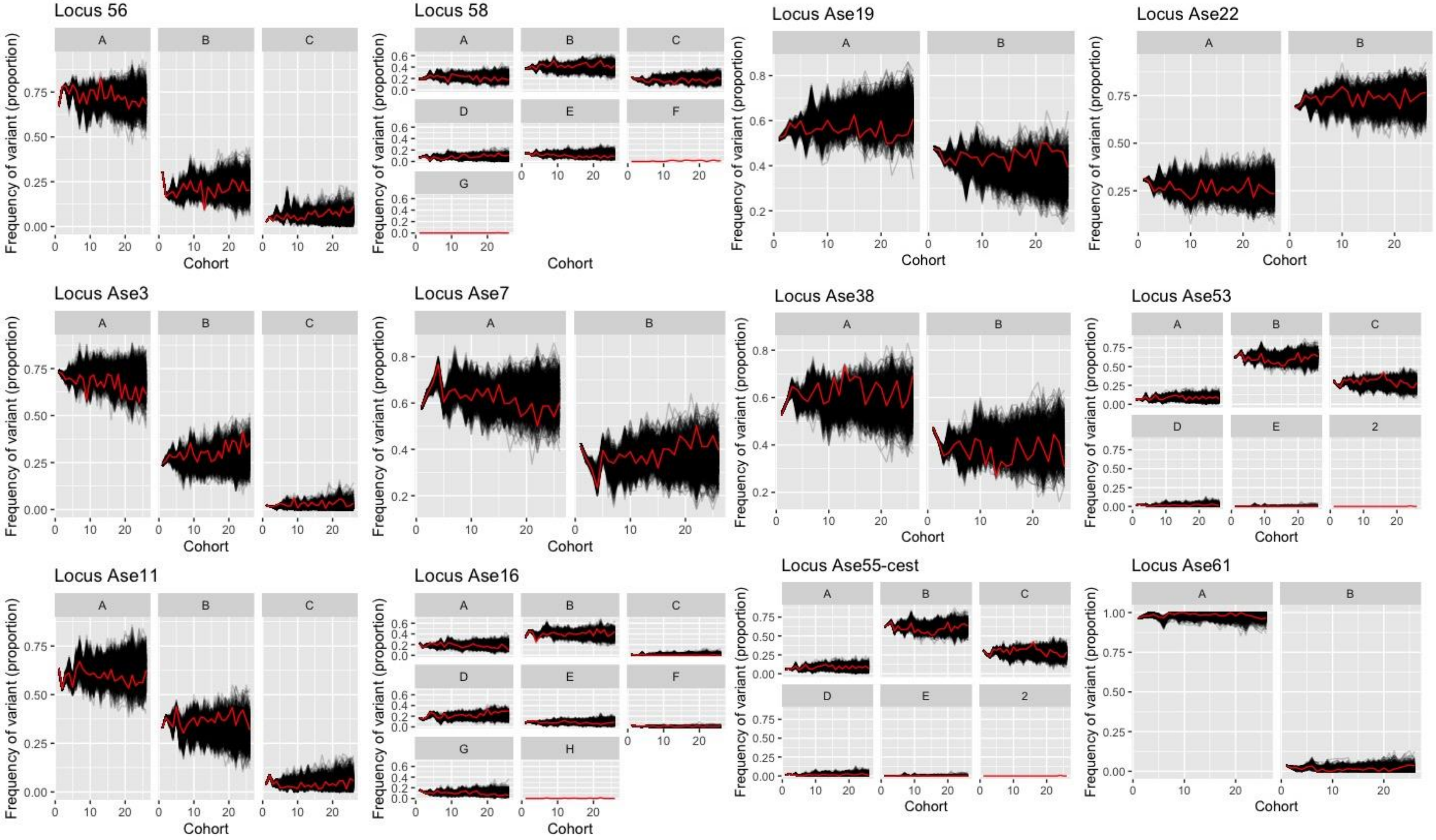
4.7. SUPPLEMENT

Supplementary methods 1: Gene-drop analyses to confirm that the microsatellites used to determine parentage are under neutral selection.

The probability of a particular descendant having the same allele as the focal ancestor was estimated based on Mendelian principles. An offspring inherits one chromosome from each parent; if a heterozygous ancestor produces an offspring, there is a 50% chance of their offspring inheriting a particular allelic variant from them. From this, we can calculate the probability of a particular descendant within a lineage having an allelic variant, based on the variants of their ancestors. We used microsatellite data to test whether allelic variants are inherited at the rate we would expect if inheritance was random (i.e., the locus is under neutral selection). If a locus is not under neutral selection and confers a fitness advantage, we would expect the allelic variant to be present in the future population at a higher frequency. In contrast, if a variant confers a fitness disadvantage, we expect a reduced representation of the allelic variant in future generations. To test whether a particular locus is under neutral selection, gene-drop analyses were performed using the *R* package gendroppeR (RStudio Team, 2022) on each of the 30 microsatellite loci used to determine parentage in the Seychelles warbler. All individuals within the pedigree (*n*=1853, cohorts: 1992–2018) were included within the analyses. 1000 simulations were run for each locus in order to estimate the confidence intervals. For all loci considered, the frequency of each allelic variant fell within the 95% confidence interval of what we would expect given random inheritance, indicating that all 30 loci are under neutral selection.

Figure S1. Results from the gene-drop analysis for each microsatellite used to determine genetic parentage, to confirm that each allele is under neutral selection using methodology detailed in **Supplementary methods 1**.




Locus 56
A
B
C
Frequency of variant (proportion)
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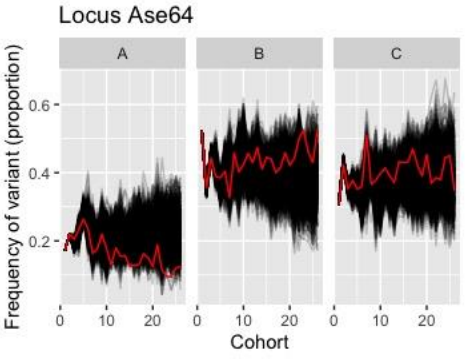
0.25
0.50
0.75
0
10
20
Cohort
Locus 58
A
B
C
D
E
F
G
0.0
0.2
0.4
0.6
Locus Ase19
A
B
0.2
0.4
0.6
0.8
Locus Ase22
A
B
0.25
0.50
0.75
Locus Ase3
A
B
C
Locus Ase7
A
B
Locus Ase38
A
B
Locus Ase53
A
B
C
D
E
2
Locus Ase11
A
B
C
Locus Ase16
A
B
C
D
E
F
G
H
Locus Ase55-cest
A
B
C
D
E
2
Locus Ase61
A
B
1.00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B
C
Frequency of variant (proportion)
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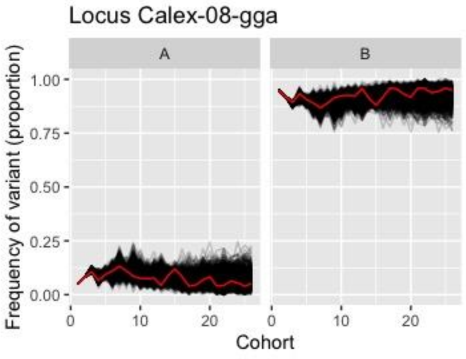
0.4
0.2
0
10
20
Cohort


Locus Calex-08-gga
A
B
Frequency of variant (proportion)
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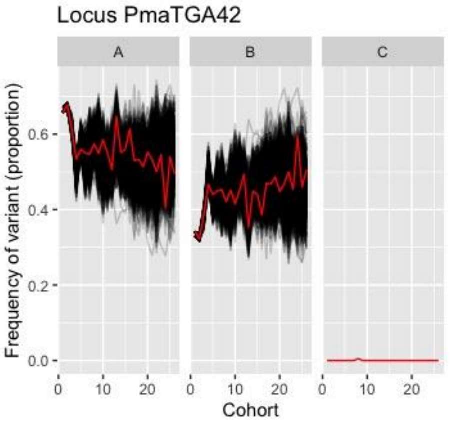
0.75
0.50
0.25
0.00
0
10
20
Cohort


Locus PmaTGA42
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B
C
Frequency of variant (proportion)
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0.2
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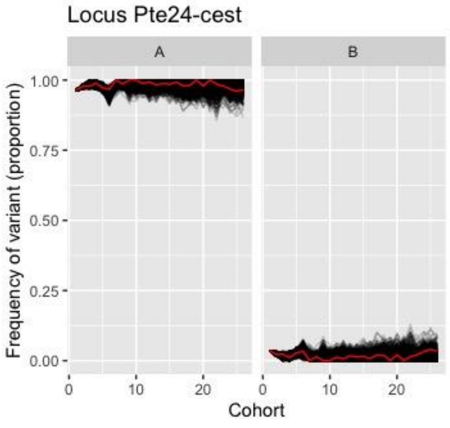
0
10
20
Cohort


Locus Pte24-cest
A
B
Frequency of variant (proportion)
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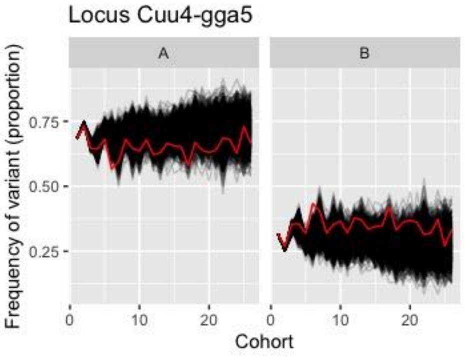
0.75
0.50
0.25
0.00
0
10
20
Cohort


Locus Cuu4-gga5
A
B
Frequency of variant (proportion)
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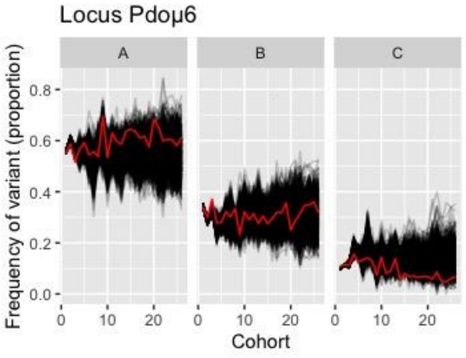
0.50
0.25
0
10
20
Cohort


Locus Pdoμ6
A
B
C
Frequency of variant (proportion)
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0.6
0.4
0.2
0.0
0
10
20
Cohort

Figure S2. Correlation coefficients of IGCs measured 17 years post-hatch and each year preceding for 4 cohorts (1997–2000) of male (**A**) and female (**B**) Seychelles warblers, using methodology detailed in Reid et al., (2019). Correlation coefficients of ≥0.95 indicate stabilisation. The horizontal dotted lines indicate the 0.95 correlation coefficient requirement for stabilisation, and the vertical dotted lines indicate the correlation coefficient at 15-years post hatch. IGCs did not stabilise in males (3/4 cohorts) or females (2/4 cohorts), indicating that IGCs do not reliably stabilise in the Seychelles warbler within a 15-year timeframe.

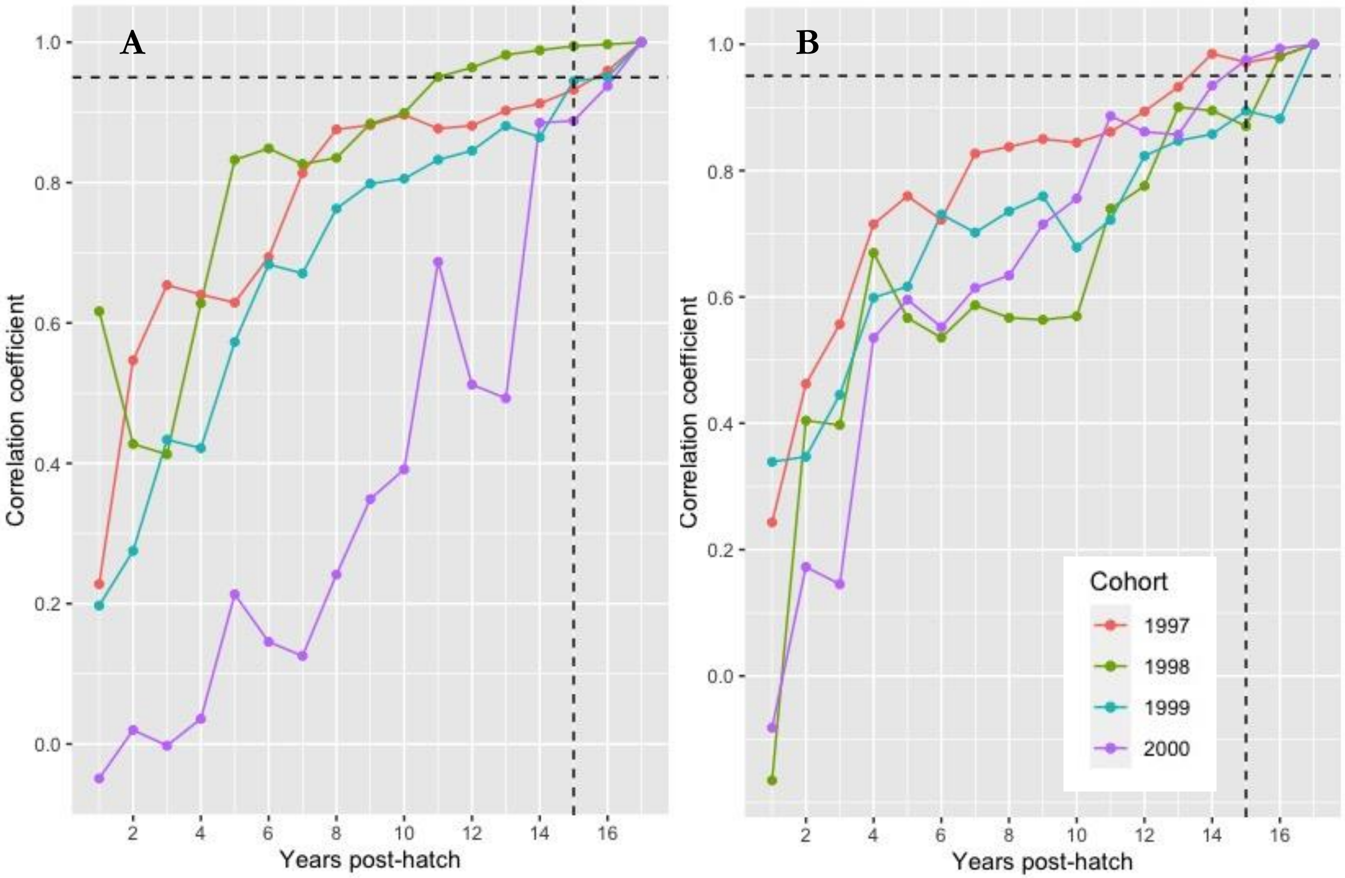
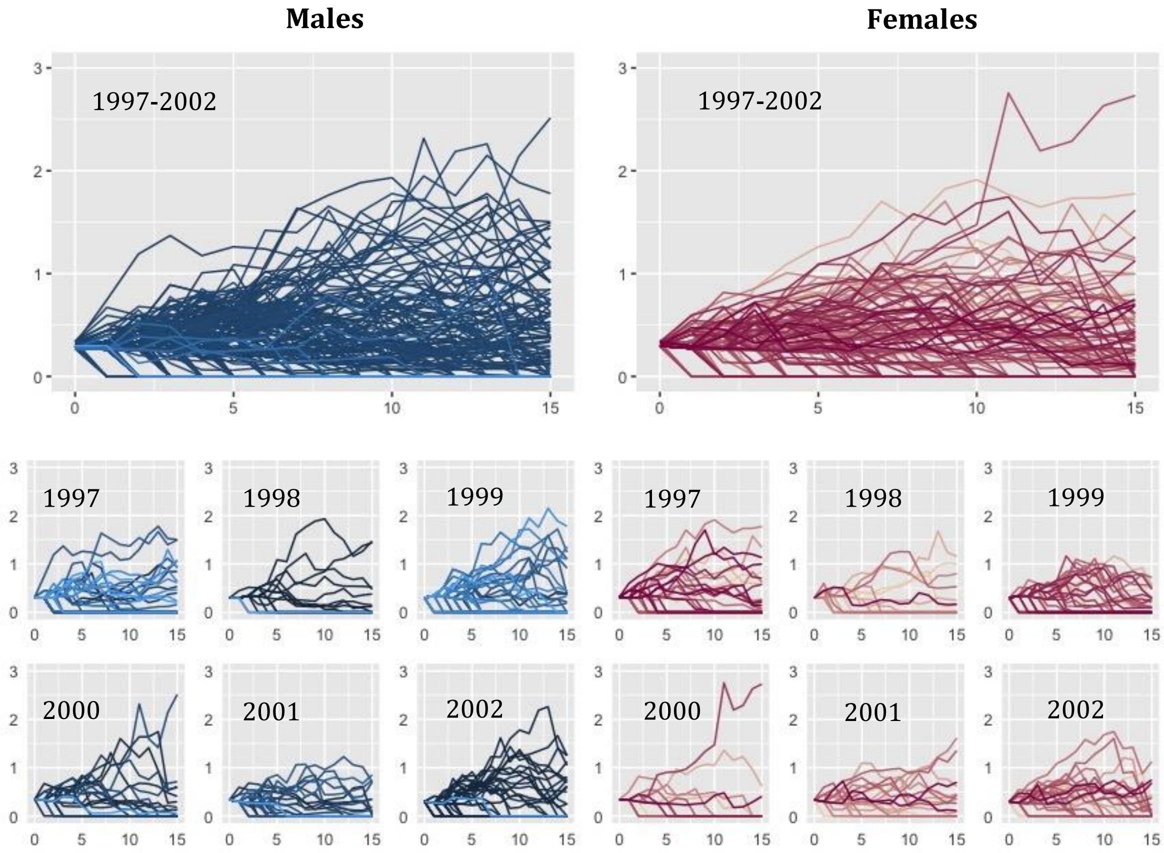


Figure S3. Change in IGCs over time. The blue graphs show the variation in IGCs of males, and the pink graphs show the IGCs of females over a 15-year timeframe for 6 cohorts (1997-2002), using methodology detailed in Hunter (2019). The two larger graphs show the IGCs of all males (blue) and females (pink) included within the analyses across all cohorts. The smaller graphs show the IGCs of all individuals broken down by cohort to aid visualisation. IGCs do not appear to visually stabilise, evidenced by significant rank order changes between individuals in terms of their contributions, which indicates a lack of stabilisation.



Chapter 5

General discussion

5.1. RESEARCH SUMMARY

The aim of my thesis was to further the scientific understanding of reproductive variation in a natural population. I chose to address this question from a cooperative breeding standpoint by considering how cooperative behaviours influence key breeding and fitness-related parameters. To achieve this aim, the studies that I conducted within this thesis have: quantified some of the potential fitness benefits of helping to helpers (chapter 2) and helped offspring (chapter 3) and assessed the relationship between single-generation fitness metrics, including reproductive success, on long-term genetic contributions (chapter 4) in the Seychelles warbler. In this general discussion, I first summarise the main findings of these chapters, I then outline the limitations of my thesis and provide ideas for future studies.

5.1.1. Overview of chapters

Chapter 2

Helping is energetically costly (Heinsohn and Legge, 1999), and helpers often forego their own reproduction, at least temporarily, to help (Sherman et al., 1995). Why an individual would choose to sacrifice their energetic resources and reproductive opportunities to help raise non-descendant offspring has been a topic of great interest to evolutionary biologists. In chapter 2, I considered how helping behaviour affects key breeding and fitness-related parameters of Seychelles warbler helpers. Within this chapter, I directly tested the skills hypothesis, which predicts that helping provides helpers with important caregiving experience that allows them to be more successful breeders once they acquire a dominant breeding position (Selander, 1965). I found that helping had no effect on any of the metrics considered, except that male and female subordinates with helping experience gained dominance at an older age compared to those without helping experience. This effect was likely due to helpers spending time helping, whilst non-helper subordinates can move directly into a dominant breeding position. Importantly, I separated helpers from co-breeders, which had not been done before in Seychelles warblers, and found that females with co-breeding experience produced more offspring as dominant breeders and had a higher lifetime reproductive success than those without co-breeding experience. In addition to demonstrating that helping has no positive effect on future reproductive success or life-history traits considered, this chapter also highlights the importance of separating helpers from co-breeders. Short-term reproductive benefits of helping were identified in a previous study on the Seychelles warbler (Komdeur, 1994); however, helpers and co-breeders were not separated, and the long-term fitness benefits were not investigated. My findings suggest that short-term beneficial effects of 'helping' may have actually been due to the fact that helpers also had previous experience with direct reproduction (i.e., co-breeding).

Chapter 3

Many studies have identified benefits of having a natal helper on short-term offspring fitness measures, such as juvenile growth and survival (Solomon, 1991, Hatchwell et al., 1999, Dickinson et al., 1996, Koenig and Dickinson, 2004, Hodge, 2005, Salomon and Lubin, 2007, Kingma et al., 2010). However, comparatively few studies have considered the long-term fitness consequences of having a natal helper (*see* Sparkman et al., 2011, Vitikainen et al., 2019, Sparks et al., 2022). In chapter 3, I assessed the effect of having a natal helper on a number of short and long-term fitness metrics. I found no positive effect of helping on any of the metrics considered; in fact, the presence of a natal helper decreased the likelihood of male offspring acquiring dominance and their future lifetime reproductive success. I hypothesised that the reduction in the likelihood of acquiring dominance was due to increased competition for dominant breeding positions, and reduced lifetime reproductive success was a consequence of helped males failing to acquire a dominant breeding position. This study highlights the importance of quantifying fitness at different life-history stages, as short-term fitness benefits may not translate into increased lifetime fitness.

Chapter 4

When estimating fitness (i.e., the number of descendant copies an individual, or allele, contributes to future generations), studies often use single-generation fitness proxies. Even within long-term study systems, data only exist for a snapshot of evolutionary time, and so studies estimate fitness using these single-generation proxies as they are expected to correlate with an individual's genetic contribution to future populations. Studies often use life-history traits (e.g., body size, age at first breeding attempt, or the likelihood of becoming a dominant breeder) to estimate fitness, as these traits are frequently associated with the production of a larger number of offspring (Jakob et al., 1996, McGraw and Caswell, 1996, Lailvaux et al., 2010, Thompson et al., 2011, Powers et al., 2020). Less often, studies use LRS to estimate fitness (Grafen, 1988, Clutton-Brock and Sheldon, 2010) as it provides a direct measure of the genetic information an individual contributes to the F_1 generation; however, lifetime data are hard to acquire in most species due to systems ecology. In chapter 4, I assessed the relationship between life-history traits, single-generation fitness proxies (including LRS), and an individual's genetic contribution (IGC) to a population 15 years in the future. Whilst a handful of other studies on other taxa have considered the relationship between lifespan, lifetime reproductive success and IGCs (Reid et al., 2019; Alif et al., 2022; Young et al., 2022), this is the first study of its kind to assess the relationship between life-history traits linked to breeding performance and future genetic contributions. Lifetime reproductive success explained more variation in IGCs than any other metric considered (≤56%), however, there was still a large amount of variance that could not be explained by this metric. Indeed, the reproductive success of an individual does not guarantee the reproductive success of their descendants; offspring are exposed to different environmental conditions (spatially and temporally) which will affect their survival and reproduction (Reid et al., 2019b, Alif et al., 2022). This study highlights the limitations of using single-generation life-history traits and fitness proxies to predict the genetic representation of breeders in future populations.

5.2. WHY DOES HELPING OCCUR?

I identified no positive fitness benefit of helping, to either helpers or individual helped offspring in any of the metrics considered within chapters 2 and 3, which poses the question of why helping occurs. Previous research on the Seychelles warbler has shown that dominant breeders with helpers produce more offspring (Komdeur, 1994, Hammers et al., 2015), either by extending their reproductive lifespan (Hammers et al., 2019, van Boheemen et al., 2019) or increasing their rate of reproduction (Komdeur, 1994, Richardson et al., 2002). As helpers tend to be the older offspring of at least one of the dominant breeders that they help (Richardson et al., 2002), helping can also increase the indirect fitness of helpers (Hamilton, 1964). If helpers are able to increase the amount of shared genetic material that is passed onto the next generation in this way, this could provide an important basis for the evolution of alloparental care, even in the absence of personal reproduction (Hamilton, 1964). Inclusive fitness benefits could be calculated in future analyses, as most individuals (98%; Sparks et al., 2021) have been genotyped, and information on helper status is available. Unfortunately, indirect fitness benefits associated with helping were not explored here, primarily due to time constraints for the production of the thesis.

In the Seychelles warbler, it has been estimated that the potential direct reproductive benefits of being a subordinate (not accounting for helping status), primarily through female co-breeding, are six times greater than the indirect fitness benefits (Richardson et al 2002). Although, I did not investigate the number of helped offspring raised as a result of helping, either through increased offspring production per season or increased dominant survival resulting in greater offspring production over the reproductive lifespan, as part of this thesis. The reason I did not consider the number of offspring produced by dominant breeders as a result of helping was due to the fact that this has been studied previously, and recently, in the Seychelles warbler (Komdeur, 1994; Hammers et al., 2015; Hammers et al., 2019; Hammers et al., 2021), and the aim of chapter 3 was to explore the benefits of helping from a novel perspective – that is, how helpers affect individual offspring *quality*.

Additionally, there may be other fitness benefits to helpers that I did not consider within chapter 2. For example, the pay-to-stay hypothesis proposes that helping behaviour is used as a form of "rent", paid by subordinates in exchange for group membership (Gaston, 1978). The hypothesis argues that subordinates provide care for non-descendant offspring so that dominant breeders allow them to remain on the territory, enabling helpers to retain group benefits (Bergmüller and Taborsky, 2005), such as resource/territory access, mating opportunities (Hellmann et al., 2015) and reduced mortality rates (Groenewoud et al., 2016). Dominant breeders benefit from the help that subordinates provide, and subordinates obtain benefits from group membership. In the Seychelles warbler, helping behaviour is not thought to be physically enforced and subordinate-directed aggression is rarely observed (Komdeur and Edelaar, 2001). Whilst the lack of subordinate-directed aggression could be interpreted as evidence opposing the pay-to-stay hypothesis, it is possible that the *threat* of eviction provides enough of an incentive for subordinates to provide care (Quinones et al., 2016). If premature eviction from a particular territory reduces a subordinate's lifetime reproductive success or increases their mortality risk (Eikenaar et al., 2007), it could be that subordinates help to raise offspring as a way of preventing this.

In chapter 3, I found that individual helped offspring experience no fitness benefit in any of the metrics considered. In fact, male offspring with a natal helper had a reduced likelihood of acquiring dominance and a reduced LRS compared to males without a natal helper. My study only included offspring that had made it to 3 months of age (independence), to exclude potential biases in the dataset as many offspring are not caught until after independence (Raj Pant et al., 2022). However, previous studies on the Seychelles warbler have highlighted fitness benefits of having a natal helper to helped offspring prior to my point of censusing. For instance, Seychelles warbler helpers increase the likelihood of an offspring fledging and reaching independence (Komdeur, 1994), as well as first year survival (Brouwer et al., 2006). So, whilst I identified no fitness benefit to being helped beyond independence, helpers could have enabled them to reach this particular life-history stage. The reason I did not consider the benefits to helped offspring prior to independence is due to the fact that this would have resulted in a sampling bias. For an individual to be included within the analyses present within this thesis, they must have been caught and genotyped to accurately determine parentage (for both for maternal ID to be included within the analyses, and for the offspring's future reproductive success to be quantified; Sparks et al., 2022). Therefore, studying how helpers affect nestling survival and rate of fledging will inevitably bias the dataset towards nests located in low-level vegetation that can be physically accessed by researchers. Unfortunately, this would not provide a representative sample of how helpers affect offspring fitness across the wider Seychelles warbler population.

5.3. LIMITATIONS

5.3.1. The definition of helping

Whilst I found no positive effect of helping on helper or helped offspring fitness on any of the fitness metrics considered (chapters 2 and 3), one factor that may be influencing these findings is my definition of helping. Like many cooperative breeding systems, I define helping as the incubation or provisioning of non-descendant offspring (Heinsohn and Legge, 1999, Woxvold et al., 2006, Eguchi et al., 2007). However, in the Seychelles warbler, helping can also occur in the form of helping to build nests (mainly females, Komdeur et al., 1994) and nest defence (Komdeur and Kats, 1999, Veen et al., 2000), although I do not consider these behaviours when determining helper status due to insufficient data. Such behaviours are hard to measure in a reliable and consistent way, and much of the data that is available is only so because of opportunistic observations. It is possible, therefore, that many 'non-helping' subordinates are, in fact, helping, but in ways that are not being routinely documented. As males are more likely to perform defence behaviours (Komdeur, 1996), my definition of helping could especially be a problem when determining the helper status of males. In chapter two, it is possible that males were erroneously identified as non-helpers and, in chapter three, offspring may have been recorded as having no natal-nest helper when they may have, in fact, received help that could have influenced their future reproductive success.

In addition, a study by van Boheemen et al. (2019) on 449 nests between 1996 and 2015 found that, whilst the majority of nests were observed only once during the nestling provisioning stage, 99 (22%) of nests were observed more than once. Of the 99 nests visited by researchers more than once, 12 (13%) identified a natal helper in one visit that was not identified in the other watch. It is possible, therefore, that some helpers may be misidentified as non-helpers if single nest-watches fail to fully capture the behaviours of individuals within a breed group.

5.3.2. Helper traits that were not considered

In the Seychelles warbler, subordinates of both sexes provide help. However, females are more likely to be helpers than males; roughly 42% of female subordinates help compared to only 20% of male subordinates (Hammers et al., 2019). Female helpers are the only sex to incubate (Komdeur, 1996) and provision at a higher rate than male helpers (van Boheemen et al., 2019); it is possible, therefore, that there are sex-dependent helper effects on helped offspring fitness. Indeed, studies on other taxa, such as the apostlebird (*Struthidea cinerea*) have identified sex differences in helper effort; male helpers provision at a higher rate than female helpers and dominant breeders (Woxvold et al., 2006). In the grey-crowned babbler (*Pomastostomus temporalis*), male, but not female, helpers increase the number of offspring fledged (Blackmore and Heinsohn, 2007). And, in a review by Green et al. (2016), helper effort was found to be negatively associated with a higher proportion of male helpers within a breed group across 36 bird species. Combining male and female helpers into one variable in chapter 3 addressing the impact of helpers on offspring fitness may have, consequently, affected my results. Initially, I included helper sex within my models in chapter 3, however, few offspring had a male helper and so I did not have the power to test for sex-specific helper effects. In retrospect, it would have been beneficial to have run additional analyses by excluding offspring with male helpers and considering offspring with female helpers only.

In chapters 2 and 3, I assigned an individual a helper status if they incubated or provisioned non-descendant offspring. However, I did not differentiate between helpers in terms of their effort (e.g., their time spent helping, or whether they incubated or provisioned at a higher rate than other helpers). Whilst I found no positive effect of helping to helpers or helped offspring in any of the measures of fitness considered, it is possible that variation in fitness could arise if I were to consider differences in helper effort. Offspring that have more attentive helpers may receive food at a higher rate than offspring with less attentive helpers, which could impact offspring fitness and future breeding success. Additionally, helpers that help over multiple breeding seasons may have better future reproductive success than helpers that helped over one breeding season, for example, as they have more experience with caregiving. Future studies on the Seychelles warbler could assess whether the hour-long nest watches provide sufficient resolution data to precisely quantify helping provisioning rates (rather than just helper per se). If so, then these data could be used to assess whether helper effort affects helper and/or helped offspring performance. If so, then future studies could delve deeper into the factors that determine helper effort.

Helper effort has been correlated with a number of factors such as genetic relatedness to offspring, as well as helper sex, age, and quality. In noisy miners (*Manorina melanocephala*), helper effort is correlated with the genetic relatedness between helpers and helped offspring, with a higher relatedness coefficient predicting a higher rate of helping (Barati et al., 2018). In the Seychelles warbler, females sometimes disperse to non-natal territories and provide alloparental care to offspring that they are not genetically related to (Groenewould et al., 2018), which may lead to variation in helper effort. Future studies on the Seychelles warbler could consider how genetic relatedness influences helper effort, and whether this has any effect on offspring performance. Helper age can be a predictor of helper effort; in the superb fairy-wren (*Malurus cyaneus*), the average age of helpers within a breeding group is positively associated with helper effort which, in turn, has a positive effect on offspring performance (Cooper et al., 2020). Similarly, in the apostle bird (*Struthidea cinerea*), younger helpers provision at a lower rate than older helpers (Woxvold et al., 2006). In addition, in the Seychelles warbler, individuals of higher body condition are more likely to help (van de Crommenacker et al., 2011). It has not yet been tested whether Seychelles warbler helpers of different 'quality' have different levels of helping effort. However, in other cooperative species, such as the cichlid (*Neolamprologus pulcher*), larger helpers put more effort into digging and territory defence than smaller helpers (Bruintjes and Taborsky, 2008).

In addition, in chapter 2, it was found that co-breeding, as opposed to helping, increases the fitness of female helpers in terms of the number of offspring that they produce as a dominant breeder (if dominance is acquired) and their subsequent lifetime reproductive success. In chapter two, I provided a number of potential explanations for this finding, including the hypothesis that co-breeding provides subordinates with important breeding experience which may make them more successful in their future breeding attempts. However, it was also noted that this finding could be due to differences in female body condition; better quality females may be more likely to co-breed and then be more successful breeders due to their better quality, rather than their co-breeding experience *per se* (van de Crommenacker et al. (2011). This alternative hypothesis would be difficult to test, as body condition in the Seychelles warbler cannot be measured in a consistent way – body condition changes throughout the breeding season (van de Crommenacker et al., 2011) and not all birds are captured to collect this variable data. In addition, even if the data were available, this chapter focuses on the long-term fitness consequences of helping by utilising *lifetime* data. If we were to include body condition as a variable, we would have to select a specific timepoint from which the data is to be taken. Not only would this dramatically reduce our sample size as not all birds are captured at the same life-history stage or at the same time throughout a breeding season, but we do not yet have a deep enough understanding of body condition to be able to select a biologically meaningful timepoint.

5.3.3. The socio-ecological context

In chapter 2, I assigned a helper status to individuals that had been observed provisioning or incubating non-descendant offspring and found that helping does not improve the future reproductive success of helpers. However, there are different social and environmental variables that may have influenced my findings. For instance, helping does not increase the likelihood of acquiring dominance on the natal territory (Komdeur and Edelaar, 2001); however, another study conducted by Groenewould et al., (2018) found that subordinate females that help on non-natal territories have an increased likelihood of inheriting the territory compared to immigrant subordinate females that do not help. If helping is beneficial to helper fitness under some conditions, but not others, this may affect the significance of my results. Future studies might wish to consider the long-term fitness consequences of helping under different socio-ecological contexts.

In addition, helpers are more likely to be present under certain conditions e.g., when the dominant breeding pair are unlikely to successfully raise offspring alone (Covas et al., 2008, Canário et al., 2004). This may explain why older dominant females with a reduced provisioning capacity are more likely to have helpers than younger dominant females in the Seychelles warbler (Hammers et al., 2019). In this way, the presence of a helper prevents offspring suffering a decrease in fitness rather than promoting a fitness advantage over non-helped offspring. As such, comparing the fitness of all helped to all non-helped offspring, without considering the socio-ecological context, may lead to erroneous conclusions about the benefits helping provides. This issue could potentially be investigated with helper removal experiments – comparing the fitness of helped offspring to offspring that *would* have been helped. This would control for the fact that helpers may be more likely to help under certain circumstances than others and allow comparison of the effect of helpers in situations where they choose to help (Brown et al., 1982, Mumme, 1992). However, experimental removals have the potential to significantly disrupt social relationships within the group, which could impact findings (Dunn and Cockburn, 1996, Jamieson and Quinn, 1997, Cockburn, 1998). Regardless, experimental removals would not be possible on Cousin; Cousin Island is a nature reserve, and experimental studies of this nature are not permitted. I acknowledge that this is a potential limitation to my study.

5.3.4. Applicability to other systems

It is likely that there are between-species differences in the fitness benefits driving the evolution of helping behaviour. As such, the ability to extract fundamental principles and generalise findings across study systems poses a challenge. It has been suggested that there are potentially no common drivers of cooperation that span across taxa other than kinship (McDonald, 2014). Whilst there are many studies and models that address the different hypotheses of helping behaviour, it is perhaps more likely that the combined effect of any number of hypotheses drive cooperative behaviour in different systems (Kingma et al., 2011). The difficultly lies in disentangling them and quantifying their importance (Taborsky et al., 2016).

5.3.5. Unsuccessful analyses

In chapter 3, I was initially going to consider how helper number, in addition to helper presence, affects offspring life-history and reproductive success. However, an earlier study by Komdeur (1994) found the relationship between helper number and nestling survival and rate of fledging to be non-linear and dependent upon particular environmental conditions (Komdeur, 1994). As such, helper number would need to be incorporated into the models as a factor (helper number: 1, 2), rather than as a linear variable. After the data had been subset to include individuals that had datapoints for all of the model variables of interest, this greatly reduced the sample size for individuals that had two helpers (<8). Due to the small sample size, the models lacked statistical power, and a number of models failed to converge, so it was decided that the analyses in chapter 3 would focus exclusively on the presence of one helper (yes/no) as opposed to considering the number of natal-nest helpers. In addition, helper sex and helper age were also included in our helper presence models, however, multiple models failed to converge due to over-parametrisation.

For chapter 4, I attempted to analyse how the number of breeding offspring (i.e., the number of F_1 offspring that produced at least one F_2 offspring) and total number of grand offspring produced by a focal individual correlated with their future individual genetic contributions.

However, in order to accurately determine these variables, not only do all focal individuals need to be deceased, but all of their F_1 offspring also need to be deceased. If any of the F_1 offspring are still alive, it is possible that they could become breeders at some point in the future and/or the number of grand offspring that could be attributed to the focal individual could change. As chapter 4 analyses the relationship between focal individuals and their descendants 15 years in the future, and the maximum lifespan of a Seychelles warbler is 19 years (Hammers and Brouwer, 2017), analysing the number of breeding offspring or grand offspring would bias the analyses towards focal individuals and/or F_1 offspring that had comparatively short lives. As such, it was decided that this analysis should be reserved for the future when the dataset has expanded.

5.4. FUTURE DIRECTIONS

As discussed within the **limitations** section of this general discussion, there are a number of variables that I did not consider within my analyses. Whilst these factors provide bases for future study, there are a number of additional avenues that could be explored in future study:

5.4.1. The heritability of fitness

Heritability is typically defined as the proportion of phenotypic variance that can be owed to genomic variation (Falconer et al., 1996). According to Fisher's fundamental theorem of natural selection, traits associated with reproductive success will have little-to-no additive genetic variation (Fisher, 1930). This is because fitness is under such strong directional selection that any alleles conferring higher fitness will rapidly arrive at fixation, reducing genetic variance as a consequence (Fisher, 1930). A number of studies have found evidence supporting Fisher's theorem when considering fitness-associated traits (Garant et al., 2003, Teplitsky et al., 2009), with the heritability of lifetime reproductive success expected to be low in wild populations (<10%; Merilä and Sheldon, 2000, Burt, 1995, Bonnet et al., 2022). The fact that fitness generally has low-level heritability may partially explain my findings in chapter 3 – that lifetime reproductive success only explains ≤56% of the variance in genetic contributions to a population 15 years in the future. Quantifying the heritability of lifetime reproductive success and other fitness-related traits would further our understanding of this variance and is a possible avenue for future study.

If reproductive success is heritable in the Seychelles warbler, then a regional heritability analysis could be performed using whole genome resequencing data to partition genomic variation across genomic regions, and this identify genomic regions associated with fitness (Robinson et al., 2013). Traits closely associated with fitness are expected to be conferred by many genes with low-level additive variation (Fisher, 1930), and regional heritability analyses will allow loci that have small contributions to fitness variance to be identified (Nagamine et al., 2012).

5.4.2. Indirect and inclusive fitness benefits

In chapter 2, I identified no fitness benefit of helping in any of the measures included within my study. Whilst there may be other direct fitness benefits of helping that I did not consider; it is also possible that indirect fitness benefits accrued from helping to raise relatives may drive helping behaviour. A previous study on the Seychelles warbler sought to quantify the indirect fitness benefits associated with helping using data taken from 1997–1999 (*n*=~340; Richardson et al., 2002). The level of relatedness between helpers and non-descendant offspring was relatively low due to high levels of extra-pair paternity (0.13 ± 0.23 and 0.08 ± 0.25 for male and female subordinates, respectively; Richardson et al., 2002), leading the authors to conclude that direct fitness benefits are greater drivers of helping behaviour than indirect fitness benefits (by up to six times). However, since the analysis by Richardson et al. (2002), the sample size has increased considerably, with lifetime data and parentage assignments being available for more than 2,000 individuals spanning more than 11 generations (Komdeur et al., 2016). With the expanded dataset, researchers could recalculate the importance of indirect fitness to a greater degree of accuracy, and estimate the inclusive fitness benefits (*e.g.,* see methods in Oli, 2003) of helping and not helping. Once indirect fitness benefits are accurately quantified, inclusive fitness can then be calculated in the Seychelles warbler.

5.4.3. Individual genetic contributions at the point of stabilisation

In chapter 4, I did not have the data to analyse the relationship between life-history traits, fitness metrics, and IGCs at the point of stabilisation. IGCs are expected to stabilise within log2(*N*) generations, where *N* is the adult population size (Chang, 1999; Barton and Etheridge, 2011). There are approximately 320 adult Seychelles warblers on Cousin Island (Richardson et al., 2002), with an average generation time of 4.7 years for females and 5.1 years for males (chapter 4). With this information, I expect stabilisation to occur within 39 years for females and 42 years for males. Unfortunately, whilst I have one of the longest and most comprehensive pedigrees of all cooperative breeding systems, my dataset spans only 21 years (Raj Pant et al., 2022, Sparks et al., 2021). Whilst my data allowed me to consider the relationship between life-history traits, fitness metrics and long-term, multigenerational IGCs, which is informative and relatively novel (Van de Walle et al., 2022), I did not have sufficient data to consider the relationship between IGCs at the point of stabilisation. It is likely, therefore, that the IGCs of individuals will continue to change until stabilisation is achieved (Chang, 1999). Indeed, in my supplementary analyses, I showed that there were some significant rank order changes in the contributions of individuals from one cohort to the next. I acknowledge that this is a potentially significant limitation to my study and recommend that future researchers revisit this analysis when the data are available.

5.4.4. Realised genetic contributions

In chapter 3, my study considered the relationship between single-generation fitness metrics and future genetic contributions to a population 15 years in the future. However, genetic contributions were estimated based on the average, expected relatedness between individuals and their descendants. However, due to the principles of Mendelian inheritance, the realised amount of shared genetic information could vary, but can only be calculated by analysing individual genomes. Now that Seychelles warbler genomic data have been generated, future studies could estimate the actual, realised genetic contributions of ancestors to future populations and gain a greater insight into allele frequency dynamics (see Chen et al., 2019).

5.6. FINAL CONCLUSIONS

My study population of the cooperatively breeding Seychelles warbler exists within a closed system on Cousin Island; migration to and from the island is rare, and individuals are closely monitored from birth to death, allowing lifetime fitness measures to be accurately calculated which is rare in natural populations. Systems such as this are instrumental in furthering our understanding of the evolutionary processes shaping cooperative breeding behaviour. Using the Seychelles warbler dataset, I demonstrated that helping has no positive fitness benefit to helpers or helped offspring in a number of key breeding and fitness-related parameters. These findings provide an important contribution to the literature, furthering our understanding of the traits that do, or, rather, do not, affect variation in breeding performance and reproductive success. I also discovered that single-generation fitness estimates explained only 8-56% of the variation in individual genetic contributions – which are closer to the theoretical definition of Darwinian fitness. Taken together, these results emphasise the fact that 'fitness' is hard to estimate. Even when single-generation fitness measures are accurate, there is a large amount of variance in how these measures relate to the amount of genetic material an individual leaves to descendant populations. Overall, my thesis highlights the importance of assessing both the short and long-term fitness effects of helping, to all individuals involved, to improve our understanding of the evolution of cooperative breeding.

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The long-lasting legacy of reproduction: lifetime reproductive success shapes expected genetic contributions of humans after ten generations

Author names, ORCID ID
Euan A. Young[1*], 0000-0001-9370-9681
Ellie Chesterton[2]
Virpi Lummaa[3],
Erik Postma[4,^], 0000-0003-0856-1294
Hannah L. Dugdale[1,2,^], 0000-0001-8769-0099

Keywords: fitness proxies, genetic contribution, lifetime reproductive success, human, human life-history, pedigree data

1 - Groningen Institute for Evolutionary Life Sciences, University of Groningen, Groningen, The Netherlands
2 - Faculty of Biological Sciences, School of Biology, University of Leeds, Leeds, United Kingdom.
3 - Department of Biology, University of Turku, Turku, Finland
4 - Centre for Ecology and Conservation, University of Exeter, Penryn, United Kingdom
^ equal last-authorship
*Corresponding author email: e.a.young@rug.nl

ABSTRACT

An individual's lifetime reproductive success (LRS) measures its realised genetic contributions to the next generation, but how well does it predict these over longer periods? Here we use human genealogical data to estimate expected individual genetic contributions (IGC) and quantify the degree to which LRS, relative to other fitness proxies, predicts IGC over longer periods in natural populations. This allows an identification of the life-history stages that are most important in shaping variation in IGC. We use historical genealogical data from two non-isolated local populations in Switzerland to estimate the stabilised IGC for 2,230 individuals ~10 generations after they were born. We find that LRS explains 30% less variation in IGC than the best predictor of IGC, the number of grandoffspring. However, albeit less precise than the number of grandoffspring, we show that LRS does provide an unbiased prediction of IGC and overall predicts IGC better than lifespan and similarly when accounting for offspring survival to adulthood. Overall, our findings demonstrate the value of human genealogy data to evolutionary biology and showing that reproduction - more than lifespan or offspring survival - impacts the long-term genetic contributions of historic humans, even in a population with appreciable migration.

INTRODUCTION

Fitness is a fundamental concept in evolutionary biology (1). On the individual level, lifetime reproductive success (LRS) - the total number of offspring an individual produces over the course of its lifetime (2)- provides a useful approximation of fitness because it captures the realised ability to contribute genes to the next generation, relative to conspecifics. LRS's strength stems from, in theory, 1) not confounding selection acting on parents and offspring (3–5) and 2) requiring tracking of only one generation of individuals. LRS is therefore one of the most widely used fitness proxies for the estimation of the strength and direction of natural selection in both free-living and captive populations (6). However, we have little understanding of the extent to which LRS influences the genetic contributions of individuals beyond initial generations (7) and how this compares to other fitness proxies (but see Brommer *et al.* (8)), or in other words, which part(s) of an individual's life-history are the key determinants of IGC.

An individual's expected genetic contributions (IGC) – the proportional contribution of an individual to the gene pool at a specific point in time – is expected to stabilise over generations, enabling the estimation of the genetic contributions over far longer periods (7,9,10). Assuming, among others, random mating, non-overlapping generations, negligible inbreeding and stable population size, stabilisation is predicted to occur after approximately 10 generations in a population of 1000 individuals, but longer in larger populations or if any of these assumptions are violated (7,9,11). Largely in line with these theoretical predictions, three studies of wild vertebrate populations found IGC to be relatively stable after around 8 generations (7,10,12) (though other studies have measured expected genetic contributions over shorter periods, e.g. Walle *et al.* (13)). They also found that LRS may predict variation in IGC, but the amount of variation explained varied greatly among studies (<1-48%, Supplementary Table 1) (7,12,14). The latter is expected as an individual's realised genetic contributions is the ultimate outcome of many factors (e.g. selection, migration, environmental stochasticity and genetic drift), all of which we expect to vary among study systems. For example, we expect LRS to be a poor predictor of IGC if long-term stochastic processes override an initial adaptive response to selection.

The degree to which LRS predicts IGC may also vary with aspects of a species' or population's life-history. For example, we could expect the correlation between LRS and IGC to be lower in species – given a similar number of generations – that are long-lived and reproduce over longer time periods, as due to the longer time span there is a greater likelihood that they are exposed to either stochastic mortality events (e.g. a disease outbreak) or changes in selection pressures (e.g. the appearance of a new predator as in Alif *et al.* (12)). However, thus far only species with relatively short generation times (e.g. ~2-4 years (7,10,12,14)) have been examined. This is at least partly for practical reasons: estimating IGC and demonstrating their stabilisation is more difficult in longer-lived species because it requires data across greater periods of time.

Human genealogical data, which typically spans centuries rather than decades, provides a powerful opportunity to examine the extent to which LRS predicts long-term genetic contributions in a long-lived species with relatively long generation times. Furthermore, by comparing the predictive power of LRS to other fitness proxies, such as lifespan and the number of grandchildren, we can identify key determinants of variation in IGC. For example, annual survival is considered to be a particularly important driver of within-generation changes to the gene pool (e.g. (15)) in humans. Furthermore, lifespan is associated with increased reproductive success (16). Hence we would expect lifespan to predict IGC, albeit probably with less accuracy than LRS as it does not directly measure reproductive output. The predictive power of LRS is also likely to vary depending on if it is conditioned on offspring survival until a certain age: In pre-demographic transition humans, infant mortality was high (17,18). Therefore, measuring LRS as the number of offspring surviving to adulthood and not only the number born, should better predict IGC. Finally, variation in both the survival and reproduction of an individual and their offspring are ultimately captured by an individual's number of grandoffspring (19), which is expected to provide a more precise predictor of IGC than LRS. Quantifying the differences in the predictive power of lifespan, number of (surviving) offspring, and the number of grandoffspring will give insight into the relative importance of parental and offspring survival and reproduction in shaping IGC in humans.

The number of grandoffspring is not only expected to explain more variation in IGC (i.e. to be a more precise predictor), but it may also be less biased than LRS (i.e. more accurate). For example, LRS may overestimate IGC if there is an offspring quality versus quantity trade-off or sibling competition, causing offspring from larger families to have lower fitness (20). Conversely, sibling cooperation (e.g. (21) could cause LRS to underestimate IGC if individuals with many siblings have improved fitness. A first step towards identifying the underlying causes of any bias is testing if LRS systematically over- or underestimates IGC. We can do this by quantifying the relationship between an individual's LRS and the average IGC of their offspring (i.e. of siblings). If this relationship is negative, LRS overestimates the IGC of individuals with high LRS (e.g. due to quality-quantity trade-off or sibling competition), whereas a positive relationship is suggestive of LRS underestimating IGC. This may be the result of e.g. sibling cooperation or parental quality effects (e.g. mediated by socio-economic status) that positively affect both parental reproduction and offspring survival/reproduction (21).

Here, we quantify the degree to which LRS shapes pedigree-derived estimates of stabilised IGC measured after at least 8 generations (10) using data from a genealogical archive containing the life-histories of humans from two parishes in the canton of Glarus, Switzerland. This dataset spans up to 16 generations, containing individuals born in the 16th to the 20th century. We estimate IGC and infer the number of generations required to reach stabilisation. We then use generalised linear mixed models (GLMMs) to examine the degree to which IGCs are predicted by four fitness proxies: lifespan, lifetime reproductive success measured at birth (LRS), LRS counting only offspring surviving to adulthood (LRS_{SA}), and the number of grandoffspring. We then compare the predictive power of these four proxies to elucidate the importance of parental and offspring survival and reproduction in shaping IGC, and compare these results to those of previously studied bird species. Finally, we test if LRS provides a biased prediction of IGC by estimating the relationship between an individual's LRS and the average IGC of their offspring.

METHODS

Dataset

We use life-history information, including an individual's year of birth, marriage and death, and the identity of its children, for individuals born or married in two parishes in the canton of Glarus, Switzerland: Linthal (46°55'N, 9°E) and Elm (46°55'N, 9°10'E). The genealogical archive from which these data were extracted includes records for unmarried adults, children dying before reaching adulthood, and illegitimate children (22) (although these are rare, in line with expectations of historical European populations (23,24)).

The data span over four centuries, containing individuals born from 1562 to 1996. The pedigree reconstructed from these records contained 44,967 individuals, 35,882 maternities, 35,973 paternities and 89,904 full-sibling relationships. The mean maternal and paternal sibship sizes were 4.01 and 4.42, respectively. There were 8,667 founders (individuals with unknown parents), and the mean and maximum pedigree depth was 6.9 and 16 generations, respectively.

During the 18th-20th century, population sizes of Linthal and Elm varied between 994-2,645 and 516-1,051, respectively (25,26). The household and family structures are representative of Central Europe as a whole (nuclear and patriarchal), with new households being formed after couples had accumulated enough wealth to get married (27). As such, the median age-at-first reproduction for females was 25, and for 95% of individuals occurred after 19 years of age. For individuals who reproduced, the median number of offspring born was 4 (range = 1-24). Families were largely sustained through the farming of sheep and cattle, with additional earning through weaving and spinning becoming possible in the 18th century (28), particularly in Linthal. Over the course of the entire study period and across all individuals, the median lifespan was 49 years and 74% of individuals lived beyond age 5.

Estimation of individual genetic contributions

We estimated individual genetic contributions (IGC) following Hunter *et al.* (10), which uses pedigree information to estimate *expected* genetic contributions to future generations, under the *expectation* of random Mendelian segregation of alleles (e.g., each parent contributes 50% of an offspring's alleles). Hence, IGC provides an estimate of the allele copies given to descendants, and the realised contribution will vary around this expectation. The relatedness matrix, containing the relatedness coefficients between all pairs of individuals (e.g. for a parent and offspring, the relatedness coefficient is 0.5), was created in R 4.1.1 (29) using the package *nadiv* 2.17.1 (30). These relatedness coefficients become expected genetic contributions when directionality is considered: An individual *gives* its offspring 50% of their alleles, and therefore the absolute expected genetic contribution an individual makes to its offspring is 0.5. We will henceforth refer to the individual making the expected genetic contributions as the *focal* individual and to the individual receiving the genetic contribution as the *descendant*.

IGC are equal to the expected genetic contributions proportional to the total gene pool for a given population at a given time point (i.e. all individuals alive and located in the study population). We used birth and marriage locations along with birth and death years to determine if individuals were present in the population (Linthal and Elm were analysed separately) for all individuals with a known birth year (Linthal, N=19558, 98%; Elm, N=16,484, 97%; Supplementary Material 1). To estimate IGC, for each individual in each year, we subset the relationship matrix to include only the focal individual (row) and all individuals present in the specific population at that point (columns), starting at the focal individual's birth year (or arrival year if an immigrant, see Supplementary Material 1). The total expected genetic contribution of a focal individual to the gene pool in a given year is the sum of this subset of relatedness coefficients. This was done for all the following years until 1990. Following previous studies (7,10,12,14), we did not consider IGC through non-direct descent (e.g., kin genetic contributions) by temporarily removing parental IDs of the focal individuals from the pedigree before creating the relatedness matrix. Genetic contributions were converted into IGC by dividing them by the total number of individuals present in the population in that year.

Stabilisation of IGC

Although IGCs fluctuate, they are expected to stabilise over time and become representative of longer term genetic contributions (9,11,31). Following previous work (7,12), we evaluated stabilisation of IGC by grouping individuals into 10-year birth cohorts and quantifying the Pearson correlation coefficient between IGC to each subsequent year and the final year considered (1990). 10-year cohorts were used to ensure each cohort had at least 2 focal individuals, as correlation coefficients could not be calculated using one individual When the correlation remained above a 0.95 threshold for a period of 2 generations, IGC were considered to have stabilised. We defined a generation as the mean (± SE) parental age at offspring birth, which were 32.2±0.04 and 32.1±0.05 yr for Linthal and Elm, respectively. According to this criterion, IGC had stabilised in 1990 for individuals born before 1718 in Linthal (or after 8.5 generations) and before 1734 in Elm (after 8 generations; Figure 1, and see Supplementary Figure 2 for a comparison to non-stabilised IGC). Hence, IGC to the year 1990 from 3475 focal individuals (1,605 from Linthal and 1,870 from Elm) were used for further analyses. The length over which IGC were estimated was at least 274 and 257 yr, and on average 10.1 and 9.9 generations (324.81(±0.86) and 319.26 (±0.93) yr, for Linthal and Elm, respectively), with the birth years of focal individuals ranging between 1575-1734 (Supplementary Figure 3).

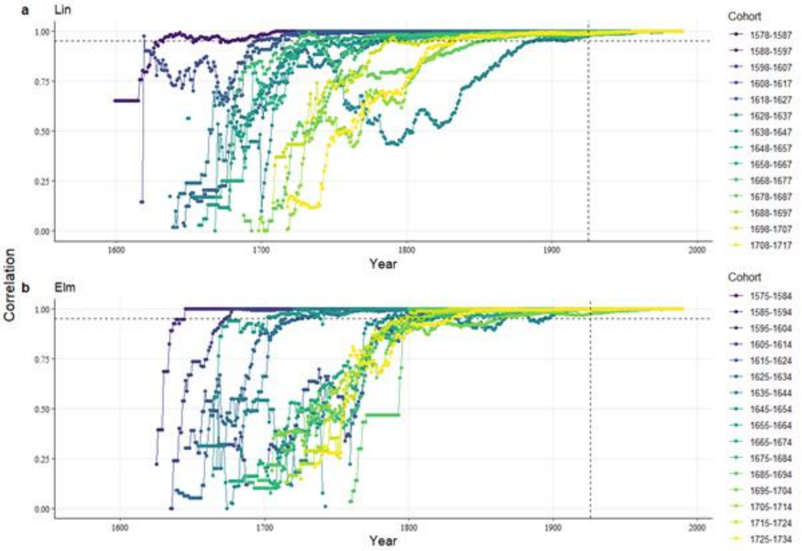

Figure 1: Stabilised IGC. Pearson correlation coefficients between the genetic contribution of individuals grouped into 10-year birth cohort in each year and their final year IGC. Stabilisation is defined as the correlations exceeding 0.95 (horizontal dotted line) for at least two generations pre-1990 (vertical dotted line) (4). Plots are shown for the parishes (**a**) Linthal and (**b**) Elm. Only stabilised cohorts are shown here (born before 1718 for Linthal and 1735 for Elm) but see Supplementary Figure 2.

Migration

Despite having fulfilled our criterion for stabilisation, IGC will continue to change in populations with a non-zero migration rate (Supplementary Figure 4). This is because immigration decreases IGC by adding to the gene pool but not to the IGC of focal individuals, thereby diluting their contribution to the gene pool. Emigration also decreases IGC and can lead to lineage extinction if emigrating offspring do not contribute to the *local* gene pool. In addition, migration will introduce variation in IGC not captured by any fitness proxies, and hence weakening their correlation with IGC.

To quantify the potential effect of migration on IGC, we classified individuals born and married in the population as residents, individuals born outside but married in the population as immigrants, and individuals born in the population but married outside as emigrants. In Linthal and Elm the vast majority of individuals were residents (62.9% and 61.5%, respectively), but both populations had a substantial proportion of immigrants (16.5% and 15.8%, respectively) and emigrants (20.6% and 22.7%). There was also a very small percentage of individuals who moved between the two parishes (from Linthal to Elm, 0.17%, and Elm to Linthal, 0.22%, see Supplementary Figure 1).

To quantify how often lineage extinction was the result of descendants dispersing versus dying before reproduction, we calculated for each focal individual the percentages of now deceased descendants (traced using the *visPedigree* (32) package) that successfully continued the lineage (i.e. reproduced in the population), did not reproduce in the population, and dispersed (emigrated) out of the population.

Fitness proxies

We considered the following fitness proxies: lifespan (the difference between the death date and birth date), LRS (lifetime number of offspring produced), LRS_{SA} (lifetime number of offspring surviving to adulthood), and the number of grandoffspring (total number of offspring of an individual's offspring). Adulthood was defined as the sex-specific 5th percentile of age-at-first reproduction for the whole dataset (females: 19.1 yr, males: 21.2 yr). We estimated lifespan, LRS, and LRS_{SA} for all individuals for which we had an estimated IGC and with known birth and death dates; N=2358), including individuals that died before adulthood. For the number of grandoffspring, we additionally required that the individual's offspring also had their complete life-history recorded (N=2358).

Statistical analyses

We used generalised linear mixed models (GLMMs) to examine the relationship between IGC and the four fitness proxies. We used a zero-inflated beta model in which the zero-inflated part of the model modelled the probability of an individual's IGC to the present-day gene pool being equal to zero (i.e. the probability of lineage extinction) using a logit-link function. The distribution of the non-zero proportional genetic contributions was modelled using a beta distribution.

We controlled for differences in mean IGC, for example due to differences in population size, between both parishes (Linthal or Elm), and the sexes (female or male) by including these as categorical fixed effects. An individual's 10-year parish-specific birth cohort was fitted as a random intercept to control for temporal variation in mean IGC. We furthermore included a random slope for the effect of each of the fitness proxies to allow their relationship with IGC to vary among parish-specific birth cohorts. Initially a two-way interaction between sex and parish was included, but this was removed if non-significant to aid the interpretation of first-order effects. Model structures were the same for the zero-inflated and beta parts of the model. Counting only individuals that were informative for all predictors, the sample size for these models was 2,230.

To quantify how much variation in IGC each fitness proxy explained, we estimated the Bayesian R-squared for each of our models (33). The significance of the differences in Bayesian R-squared values were evaluated through finding the mode and 95% credible intervals of the difference between the R-squared values of the models being compared (ΔR^2) and seeing if these 95% credible intervals overlapped 0.

We quantify the bias in LRS in predicting IGC by examining the slope of the relationship between the LRS of an individual and the mean IGC of their offspring. Here we used the same individuals as before, but excluding non-reproducing individuals, leaving 1256 individuals. For this model, we performed a beta regression (with no zero-inflated distribution included) controlling for the same confounding fixed and random effects structures as above. Beta regressions require response variables to non-zero values and we therefore added 10^{-10} to all mean offspring genetic contributions. Here, no relationship would indicate LRS is an unbiased predictor of IGC. We additionally examined if the lifespan of parents was an important covariate, as offspring whose parents died younger might receive less parental care, potentially impacting their IGC.

Both zero-inflated beta and beta models were implemented in the R package *brms* (2.16.1 (34)) using the Markov chain Monte Carlo (MCMC) sampler Rstan (2.21.2 (35)) using R (4.0.2 (29)). For each model, we ran four runs of 6,000 iterations across four cores, sampling every 10 iterations, after a warm-up of 2000 iterations. We set the delta parameter to 0.95 to aid convergence. Default priors were used: flat for all fixed effects and a student's t distribution for random effects. Convergence of models was confirmed based on R hat parameters and Monte Carlo standard errors being approximately 1 and 0, respectively. The *pp_check* function was used to check that simulated data from the model matched the original data well. We used the probability of Direction (*pd*) (36) (the percentage of the posterior distribution that has the same sign as the median) to infer statistical significance. In line with Makowski *et al.* (36), we classified *pd* values as follows: 0.95-0.975=trend effect; 0.975-0.99 =

significant; > 0.99 = highly significant. For random effects, *pd* is not applicable and no significance criteria were used. Figures were created using the packages *brms, ggplot2* (3.3.5, (37)) and *ggpubr* (0.4.0 (38)).

RESULTS

Individual genetic contributions (IGC)

We estimated the IGC for 3475 individuals (1,605 from Linthal and 1,870 from Elm), born between 1575-1735, to the individuals making up the gene pool of the parishes of Linthal and Elm in 1990. The probability of an individual's lineage going extinct was high, with 73% of individuals having an IGC of zero to the 1990 population (Supplementary Figure 5a) (although the extinction rate of specific genes will vary). The majority of extinctions are because an individual did not survive to reproductive age (23.4%), survived until reproductive age but had no offspring (43.5%), had offspring but none survived to adulthood (45.3%), or had surviving offspring but no grandoffspring (52.7%) (Supplementary Figure 5). This leaves approximately 20% of the individual lineage extinctions, which occurred after individuals had at least one grandchild. Over all individuals included in the analysis, a median of 15.9% of their descendants reproduced and thereby continued the lineage, and 14.6% of the descendants had not yet reproduced but were still alive. This leaves 69.7% of the descendants who failed to continue the lineage, of these, a median of 40.3%, due to emigration rather than death without reproducing. Individuals whose lineages did not go extinct on average contributed 0.1% of the genetic material present in the population in 1990 (Supplementary Figure 5a), although one male contributed 0.6% of the Linthal gene pool.

Lifespan, LRS, LRS_{SA}, and the number of grandoffspring were positively associated with IGC (Beta distribution, *pd* > 0.975, Table 1, Figure 2). We also found a negative effect of any of the fitness proxies on the probability of an individuals' lineage going extinct (zero-inflated distribution, *pd* > 0.975, Table 1).

IGC (distribution and extinction probability) were dependent upon several other factors. First, individuals born in Linthal had lower IGC, probably because of its larger population size (all models, beta distribution, *pd* > 0.975, Table 1) and in line with this showed no difference in probability of lineage extinction (zero-inflated distribution, *pd* < 0.975, Table 1). There were no interactions between these effects and sex (*pd* < 0.975, Supplementary Table 2) and no differences between males and females were found (beta and zero-inflated distribution, *pd* < 0.975, Table 1). Further, we found that IGC of individuals varied among birth cohorts (both in their extinction probability and in the non-zero IGC values; see random effects, Table 1). There was also variation among birth cohorts in the slope of the relationship between each fitness proxy and IGC, but except for the slope of the relationship between probability of lineage extinction and LRS, LRS_{SA} and the number of grandoffspring, this variation was small. Finally, a supplementary analysis showed that the proportion of offspring migrating was associated with lower IGC and higher extinction probabilities but this did not substantially change the predictive power of the models (Supplementary Material 2 and Supplementary Table 3).

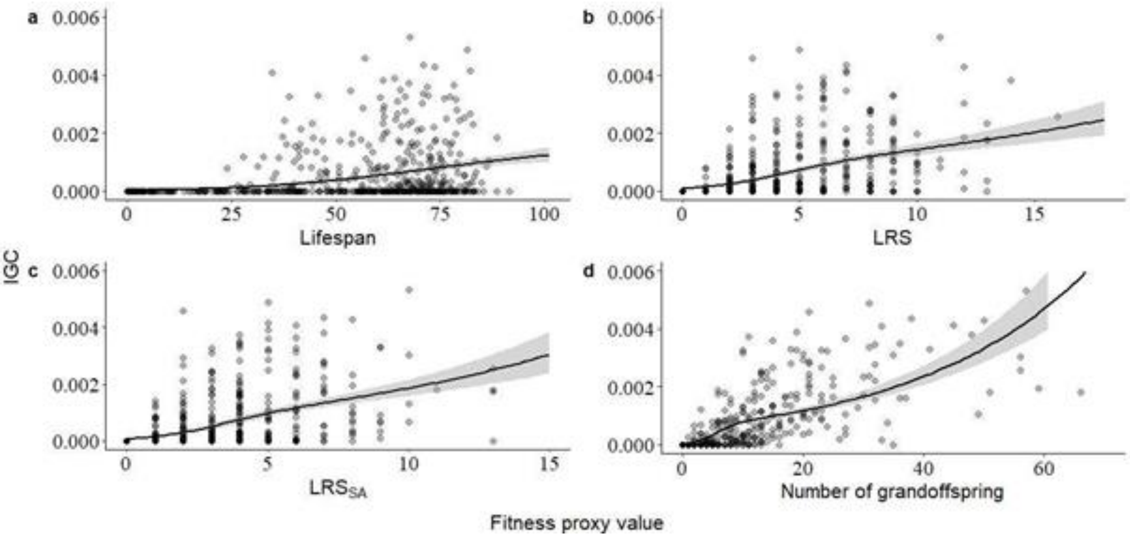

Figure 2: The relationship between IGC and four fitness proxies: (a) lifespan, (b) LRS, (c) LRS_{SA}, and (d) the number of grandoffspring. The plots were produced using the *conditional_effects()* function from the R package *brms* to standardise points across values for covariates. Shaded areas indicate 95% credible intervals of the model estimate. Data is conditioned on the mean values of the other predictors (birth cohort, parish and sex). Data points too far away from the values conditioned upon were removed from the plot. Symbols are partially transparent to aid visualisation.

Team, 2022) on each of the 30 microsatellite loci used to determine parentage in the Seychelles warbler. All individuals within the pedigree (*n*=1853, cohorts: 1992–2018) were included within the analyses. 1000 simulations were run for each locus in order to estimate the confidence intervals. For all loci considered, the frequency of each allelic variant fell within the 95% confidence interval of what we would expect given random inheritance, indicating that all 30 loci are under neutral selection.

Table 1: Output from four beta zero-inflated models of IGC with different fitness proxies included: Lifespan, LRS, LRS$_{SA}$, and the number of grandoffspring. Fixed and random effect estimates (posterior distribution median [95% credible intervals] are provided for both the zero-inflated and beta distributions. Significant effects (probability of Direction > 0.975) are in bold. Non-significant two-way interactions were removed from the models. Model results with non-significant interactions included are shown in Supplementary Table 2.

	Lifespan		LRS		LRS$_{SA}$		Number of grandoffspring	
	Zero inflated	Beta	Zero inflated	Beta	Zero inflated	Beta	Zero inflated	Beta
Fixed effects								
Intercept	**3.248 [2.882 - 3.628]**	**-7.171 [-7.468 - -6.880]**	**2.145 [1.880 - 2.427]**	**-7.177 [-7.328 - -7.022]**	**2.219 [1.926 - 2.521]**	**-7.264 [-7.418 - -7.118]**	**3.032 [2.623 - 3.415]**	**-7.442 [-7.564 - -7.322]**
[Fitness proxy]	**-0.054 [-0.059 - -0.048]**	**0.006 [0.002 - 0.010]**	**-0.587 [-0.659 - -0.515]**	**0.065 [0.047 - 0.082]**	**-0.796 [-0.922 - -0.684]**	**0.098 [0.075 - 0.119]**	**-0.591 [-0.711 - -0.475]**	**0.035 [0.031 - 0.039]**
Birth Parish (Linthal)	-0.037 [-0.351 - 0.297]	**-0.312 [-0.448 - -0.162]**	0.319 [-0.053 - 0.718]	**-0.403 [-0.535 - -0.263]**	0.255 [-0.101 - 0.631]	**-0.396 [-0.533 - -0.260]**	0.220 [-0.323 - 0.781]	**-0.489 [-0.63 - -0.349]**
Sex (Male)	-0.154 [-0.371 - 0.049]	0.079 [-0.029 - 0.188]	0.138 [-0.111 - 0.389]	0.050 [-0.057 - 0.157]	0.115 [-0.125 - 0.362]	0.063 [-0.045 - 0.169]	0.141 [-0.241 - 0.493]	0.057 [-0.047 - 0.158]
Random effects								
Parish-specific birth cohort (random intercept)	0.217 [0.009 - 0.626]	0.110 [0.004 – 0.371]	0.153 [0.006 – 0.415]	0.069 [0.002 – 0.212]	0.170 [0.008 – 0.465]	0.066 [0.002 – 0.187]	0.281 [0.014 – 0.759]	0.061 [0.003 – 0.165]
Parish-specific birth cohort × fitness proxy (random slope)	0.006 [0.001 – 0.014]	0.002 [0.000 - 0.006]	0.138 [0.069 - 0.223]	0.011 [0.001 - 0.031]	0.268 [0.172 - 0.402]	0.014 [0.001 - 0.034]	0.269 [0.173 - 0.402]	0.004 [0 - 0.009]

How well do fitness proxies predict IGC?

Although all fitness proxies predicted IGC, we found that they significantly varied in their predictive power. As expected, the number of grandoffspring explained most variation in IGC (R^2=57.3%, Table 2), explaining 44.3 percentage points more variation than lifespan, 29.8 percentage points more than LRS and 25.2 percentage points more than LRS$_{SA}$ (Table 2). Contrary to expectations, the difference in predictability between LRS and LRS$_{SA}$ was very small (ΔR^2=2.7%, Δ95% Credible Intervals (CrI)=-1.8% – 9.2%, Table 2). A null model containing no fitness proxy but all other first-order fixed and effects and random effects explained only 1.4% (95% CrI= 0.9% – 2.2%) of the variation in IGC.

Table 2: On the diagonal, Bayesian R^2 values (R^2 and 95% credible intervals) for models containing either lifespan, LRS, LRS$_{SA}$, or the number of grandoffspring and any other significant covariates retained in the model. Pairwise Pearson correlation coefficients (ϱ) between fitness proxies are shown above the diagonal (also see Supplementary Figure 6) and the difference in Bayesian R^2 values are shown below the diagonal (ΔR^2 and Δ95% credible intervals). Δ95% credible intervals that do not overlap with zero are in bold.

	Lifespan	LRS	LRS$_{SA}$	The number of grandoffspring
Lifespan	R^2 = 13.2% [10.8 - 15.8]	r = 0.55	r = 0.54	r = 0.43
LRS	**ΔR^2 = 14.8% [10.5 - 19.1**	R^2 = 27.9% [24.2 - 31.6]	r = 0.94	r = 0.71
LRS$_{SA}$	**ΔR^2 = 19.2% [14.5 – 23.7]**	ΔR^2 = 2.7% [-1.8 – 9.2]	R^2 = 32% [27.8 – 36.0]	r = 0.74
Number of grandoffspring	**ΔR^2 = 44.3% [39.5 – 48.2]**	**ΔR^2 = 29.8% [24.2 - 34.8]**	**ΔR^2 = 25.2% [19.9 – 31.0]**	R^2 = 57.3% [53.5 - 60.8]

Is LRS an unbiased estimate of IGC?

The per-capita IGC of an individual's offspring increased with LRS, but the slope of this relationship was very shallow (*pd* > 0.975, posterior mode=0.070, 95% CrI=0.052 - 0.089, Figure 3). This finding suggests that LRS slightly underestimates IGC in larger family sizes. Furthermore, individuals who lived longer had offspring with higher IGC (*pd* > 0.975, posterior mode=0.010, 95% CrI=0.006 - 0.014). As before, and likely due to population size differences, mean IGC of offspring was lower for individuals born in Linthal (*pd* > 0.975, posterior mode= -0.162, 95% CrI=-0.339 - 0.011) but sex differences showed only trend effects and the offspring of males did not have lower mean IGC (*pd* = 0.962, posterior mode=-0.066, 95% CrI=-0.173 - 0.04). No interactions were significant (*pd* < 0.975, Supplementary Table 4).

Finally, we found that variance in the mean IGC of offspring was explained by their parents' birth cohort (posterior mode=0.163, 95% CrI=0.032 - 0.306). The parent's birth cohort also affected the slope of relationship between LRS and mean offspring IGC but this variation was relatively small (posterior mode= 0.014, 95% CrI=0.001 - 0.038).

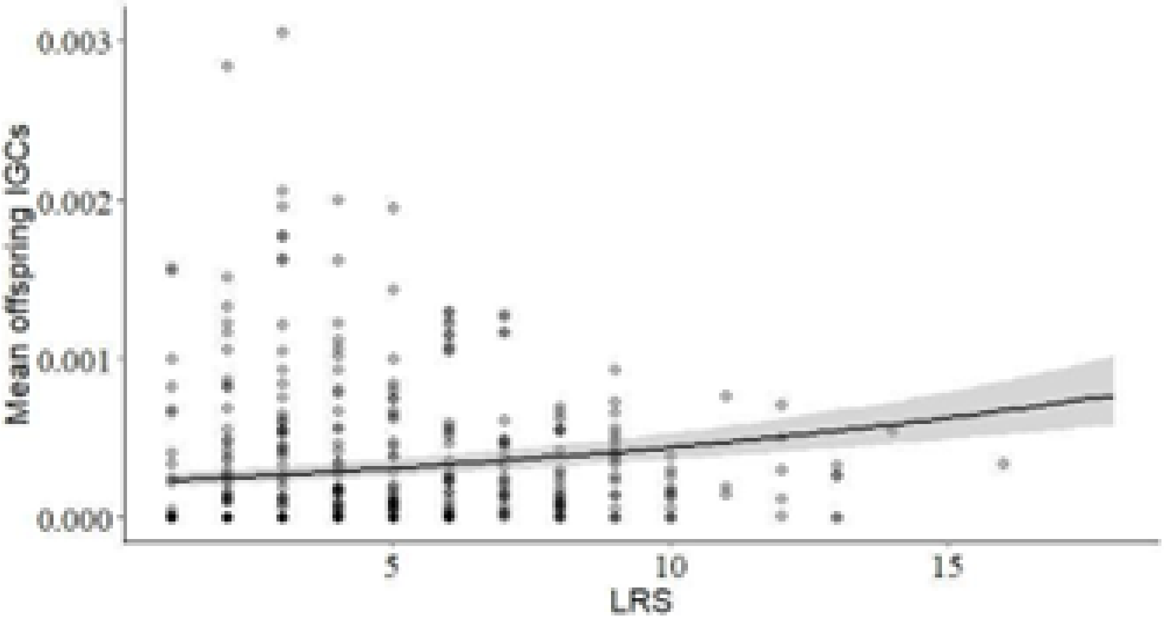

Figure 3: The relationship between mean offspring IGC and LRS. The plots were produced using the *conditional_effects()* function from the R package *brms* to standardise points across values for covariates. Shaded areas indicate 95% credible intervals. Data points too far away from the values specified were removed from the plot and data points included are partially transparent to aid visualisation.

DISCUSSION

We quantified the extent to which LRS and other fitness proxies predict stabilised IGC of individuals measured after ca 10 generations (321 years), in historical humans from the Swiss Canton of Glarus. We found that LRS predicted 28% of the variation in IGC, showing that reproductive success shapes the long-term genetic contributions of individuals even in a population of a long-lived species with appreciable migration that has experienced large and rapid changes in its environment.

We have shown that fitness proxies varied in their predictive power of IGC (Table 2), allowing us to identify the components of an individuals' life-history that are most important in determining IGC. Overall, the model containing the number of grandoffspring explained 57% of variation in IGC, whereas the next best fitness proxy (LRS_{SA}) explained only 32%, followed by LRS (28%) and lifespan (13%). This is broadly in line with results based on genetic contributions estimated over 4 generations in 19th century Sweden (39). That the number of grandoffspring explained the most variation was expected, as the number of grandoffspring incorporates the most information about the life-history of an individual. However, together with our finding that LRS_{SA} and LRS explain a similar amount of variation in IGC (28% vs 32%) and that lifespan explains only 13% of the variation in IGC, this suggests that offspring mating and reproduction is a much greater determinant of IGC than survival (of both offspring and the individual themselves), even in a population with substantial childhood mortality (Supplementary Figure 1). Finally, we showed no difference between the sexes although the highest IGCs were multiple-marrying males who's first wives died around the age of menopause, allowing the widowers to remarry a younger female and achieve a lifetime reproductive success (and IGC) greater than males who did not remarry.

Although the number of grandoffspring explains the most variation in IGC, the number of grandoffspring is not necessarily the most useful fitness proxy. First, although statistically significant, we found a weak relationship between LRS and the average IGC of their offspring, showing that LRS is a relatively unbiased measure of IGC. The positive association suggests that the increase in predictive power between LRS and number of grandoffspring is not due to LRS being a biased predictor. The number of grandoffspring will naturally be a more precise predictor of IGC than LRS because it is closer in time to IGC and therefore incorporates more of the stochasticity that influences IGC. Albeit small, the positive relationship between LRS and per-capita IGC argues against the existence of an offspring quality-quantity trade off, which has been previously found in humans (40–42). Instead it is somewhat suggestive of positive sibling effects, perhaps due to alloparenting (21), or an overriding effect of parental quality (e.g. socio-economic status) (e.g. (43,44)). Second, there are practical reasons that limit the utility of the number of grandoffspring as a fitness proxy: Not only is it more sampling intensive, reliably counting the number of grandoffspring may not be feasible if a significant proportion of the population disperses outside of the study site, or offspring cannot be linked to parents once they have reached independence. Third, the number of grandoffspring confounds the fitness of multiple individuals, which can be problematic when estimating the strength of phenotypic selection (3–5). All things considered, our results therefore strengthen the case for LRS as an evolutionary relevant and relatively unbiased fitness proxy when it comes to the study of selection in humans, assuming our findings are representative for other populations and time periods.

Although at first sight high, our finding that 70% of individual lineages went extinct over the study period is similar to that found in previous studies on pedigreed populations of birds, which reported extinction probabilities of 61-71% (Supplementary Table 1), and comparable with levels of lineage extinction in bighorn sheep (13) in humans after four generations in Sweden (45). The main difference between our results and those for the three bird studies (7,12,14) was that when we measured LRS at a later point in the offspring's life (i.e. LRS_{SA}) the ability of LRS to predict IGC did not increase greatly. This is in contrast to, for example (14), which found that offspring survival was a key determinant of reproductive success. Our results therefore suggest that despite substantial infant mortality, offspring survival to adulthood is a less important determinant of IGC than mating and reproductive success in humans.

The amount of variation in IGC explained by LRS measured close to birth (28%) in this study was close to previous findings for song sparrows and scrub-jays (37% and 32%, respectively), but higher than house sparrows (0-4%). This is somewhat surprising given the likely negligible role of migration in the latter island population but is potentially due to a bottleneck in the population that occurred between fitness proxies being measured and the estimation of IGC (12). This could have caused stochastic mortality resulting in low predictive power of fitness proxies. Another likely factor explaining different findings across populations is the role of stochasticity in driving variation in LRS itself. LRS is influenced by both environmental and genetic components with the environment contributing most of the variation (46), including in humans (47). In species where the environment determines less variation in LRS, LRS would be expected to be a greater predictor of IGC (7,8). Here, we showed that environmental effects were an important factor, with non-negligible variation in IGCs being explained by an individual's birth cohort (Table 1). Further, as mean LRS values decrease there is a greater likelihood of lineages going extinct due to stochasticity, drift or dispersal (7,48), which perhaps partially explains the relatively high rates of lineage extinction in this study (70% vs 61-71%, Supplementary Table 1). Future studies could examine if this phenomenon is detectable across the human fertility transition towards lower LRS. In summary, there are both similarities and differences across study systems, but the small number of species and the lack of different human populations (across cultures) studied limits broader extrapolation.

72% of the variation in IGC remained unexplained in the model containing LRS, with migration being a contributing factor to this unexplained variation: First, there were significant levels of both immigration and emigration (Supplementary Figure 1), and both are expected to decouple the relationship between LRS and IGC. Dispersal of descendants of ancestral individuals is a particularly important driver of lineage extinction. Although migration is also expected to reduce the stabilisation times relative to theoretical expectations, we observed stabilisation times lower than theory predicts (9). One explanation for this is that the effective population size (number of breeding individuals) is far lower than the total population size, for example because a significant proportion of individuals didn't reproduce (see Supplementary Figures 1 and 5). However, other explanations (e.g. non-random mating) are also possible and it is clear that we need to further our understanding of the drivers of the stabilisation of IGC in natural populations. Finally, the slopes of the relationships between fitness proxies are generally low (0.006 to 0.098); thus, discrepancies between LRS and fitness proxies generally arose because of individuals having high LRS but low or no IGC, and not vice-versa. Here, migration is a likely driver, although other evolutionary forces will be at play (e.g. drift and fluctuating selection). Enumerating the relative contributions of these factors across different systems (or using simulations, e.g. (49)) should be a target of future work.

Although still in its infancy, the use of pedigree data to estimate long-term genetic contributions opens a range of exciting avenues. Building on our work using human genealogical data, and the work on non-human animals by others (7,12,14), future work would benefit from further exploration of the similarities and differences among the different methodologies at our disposal. In particular between gene dropping methods (7,12,14) and expected genetic contributions (e.g. (10), this study), as the two will not necessarily equate. Furthermore, while our study has highlighted the ability of human genealogical data to provide insight into human evolution (50,51), and the estimation of fitness more broadly, applying these methods to similar data for an array of human populations (see (52), for a review) will allow us to quantify the degree to which these findings hold across cultures, environments and time.

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