THE EVOLUTION AND DYNAMICS OF INTERACTING POPULATIONS

Paul Marrow

Thesis submitted in accordance with the regulations for the degree of
Doctor of Philosophy.

University of York

Department of Biology

August 1992

ABSTRACT

The evolution of interacting species is investigated using mathematical models and computer simulation. Lotka-Volterra food web models are adapted to include genetic variation, and then used to model the coevolution of interspecific interactions. Due to the complexity of the population dynamics exhibited by multi-species community models, I concentrate upon the evolution of predator-prey interactions. The models so constructed can be solved either analytically, or numerically, to evaluate the evolutionary dynamics of phenotypes in predator and prey. The phenotypes that are considered have an effect on the interspecific interaction, and could represent predator and prey body size. These models show that a range of evolutionary dynamics can arise in simple predator-prey systems, including evolutionarily stable states, and continuous coevolutionary change, or Red Queen coevolution. They also show that the coexistence of predator and prey can be maintained under selection. Simulation models are developed in a similar fashion, where the population dynamics of genotypes are evaluated by numerical integration. One simulation model incorporates the evolution of body sizes, while in the other evolution acts directly upon the interspecific interaction coefficients. These models are used to investigate the build-up of invasion resistance to mutant invasion, the maintenance of polymorphism in predator-prey interactions, and the population dynamical consequences of predator-prey coevolution. It is unclear whether predator-prey interactions can maintain polymorphism, but evidence is obtained of the build-up of resistance to mutant invasions, implying approach to evolutionarily stable states. Evolution of predators and prey is seen to result in a range of dynamical behaviours: natural selection may lead to stable dynamics, but alternatively to cyclic behaviour or chaos.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

ACKNOWLEDGEMENTS

A work such as this could not have been completed without the assistance of many people. I would like to thank my supervisors, Richard Law and Chris Cannings, for their support and encouragement at every stage of this project, and for having the courage and imagination to propose such an unusual project and then watch it evolve into something completely different.

I would also like to thank the members of the Biology Department, for making it an agreeable place to work, despite the somewhat extreme microclimate engendered by acres of glass. Andy McLellan, James Merryweather, Kevin Newsham, Helen Peat, Duncan Reavey, Cathy Rowell, Andy Sedman, Alexia Stokes, and Julie Watson, among others, helped in numerous ways. Mark Williamson kindly provided a desk and computers on which to write up after Richard moved to Germany and surrendered his laboratory.

Individual acknowledgments sections were omitted from the chapters of this thesis in order to save space. So I would like to thank the people concerned here.

Chapter 2. I thank Vivian Hutson and Phil Warren for discussion, and Cathy Rowell, Mark Williamson, and an anonymous referee for comments on the manuscript.

Chapter 3. Most of this chapter was written while I was at the Arbeitsgruppe Theoretische Ökologie, Forschungszentrum Jülich. I thank Richard Law and Jaqueline McGlade for making my visit possible. The organisational help of Magret Spatzek, and assistance with computing from Steve Gaito are also gratefully acknowledged.

Chapters 4 and 5. The simulation models in these chapters could not have reached the form they have without the help of many members of the staff of the University of York Computing Service. Their services, in the face both of limited resources and my high demands upon their systems, are gratefully acknowledged.

ACKNOWLEDGEMENTS

Chapter 6. The development of the ideas in this chapter was assisted by discussions at the workshop on *Genetics and Demography of Interacting Populations*, held in Kraków in May 1992, as well as the follow-up meeting in Basel in July. I thank the organisers and participants of these meetings, and the European Science Foundation for supporting my attendance at both meetings.

I would also like to thank the following people, who provided reprints of papers in press or in preparation; H. R. Açkakaya, H. C. J. Godfray, J. H. Lawton, K. Lindgren, J. A. J. Metz, I. Scheuring, K. Schoenly, and H. G. Spencer.

My father, Jonathan Marrow, provided many sensible ideas and helped with data transfer. And I would like to thank the rest of my family, for their tolerance and support in many ways during my studentship. "Some day you'll understand what a Lotka-Volterra equation is!"

Finally, it is necessary to acknowledge the financial support of SERC, without whom this thesis might not have been.

AUTHOR'S DECLARATION

All material in this thesis was written by me. A number of parts of the thesis were the consequences of collaborative work, or are about to be presented elsewhere, and these are described below.

Chapter 2. This chapter arose from collaborative work involving R. Law, C. Cannings, and me. This chapter has been accepted for publication in the Journal of Theoretical Biology, as by P. Marrow and C. Cannings.

Chapter 3. This chapter is based upon collaborative work, involving R. Law and me, which arose in part as a consequence of the work described in Chapter 2. A paper based on this chapter, substantially revised, has been accepted for publication in the Proceedings of the Royal Society, Series B, under the title *The coevolution of predator-prey interactions: ESSs and Red Queen dynamics*, as by P. Marrow, R. Law, and C. Cannings.

Chapter 1. INTRODUCTION: MODELLING ECOLOGY AND EVOLUTION IN FOOD WEBS

> Nothing in biology makes sense except in the light of evolution.
>
> Theodosius Dobzhansky

1.1 SUMMARY

The topics investigated in this thesis are introduced. The basis for an investigation of the evolution of interacting species is presented. The observations of empirical regularities in food web structure has resulted in a great deal of theoretical attention, but the models that have resulted do not take into account the interaction of evolution and ecology in natural systems. Community assembly models have been used to understand trends in community structure, and these suggest some ways in which models of evolving interacting species might be constructed. Theoretical work on the evolution of interacting species has generated a wide range of predictions about the outcome of such evolution; will communities evolve to coevolutionarily stable states, or continue evolving in Red Queen coevolution? It is intended to investigate these problems by using mathematical and computational models of evolution in trophic webs. The aims of the research are presented; it is argued that a focus on predator-prey coevolution, rather than community coevolution in general, is necessary for a full understanding of the system being considered. Finally, the layout of succeeding chapters of the thesis is presented.

1.2 FOOD WEBS

Many advances have been made in recent years in classifying and explaining the patterns of ecological interactions in nature. One particular area of activity has been that of trophic interactions between predators and prey. Predators and prey interact in complicated ways in food webs. Food web theory is a flourishing area of theoretical ecology (Lawton & Warren 1988; Lawton 1989; Cohen *et al.* 1990a; Pimm *et al.* 1991), but studies of models of food webs have rarely considered any evolutionary component to ecological interactions. In order to examine this, one must first consider its ecological basis.

It was for a long time assumed that more complex communities would be more mature, more stable - and this seemed reasonable when one looked at the characteristics of a successional community from early succession until climax. However May (1972, 1973) showed that this was not necessarily the case: indeed with many models you would expect stability to decline with complexity. It was also shown (Gardner & Ashby 1970) that connectance, a measure of linkage within a food web, and thus complexity in a sense, declines with increased stability. But this was for a more general case of dynamical systems. When DeAngelis (1975) introduced some biologically reasonable assumptions into a randomly connected model he found the opposite: connectance was proportional to stability. Winemiller (1990a) looked at tropical freshwater communities and found connectance increases with species richness, thus implying connectance increases with stability.

These contradictory results highlight the difficulties of using such a general measure as connectance as a indicator of food web structure (see also Pimm 1984). In food web studies, as a consequence, the emphasis has shifted somewhat to detailed analyses of food web statistics across many real webs. These have been derived from a collection of food web matrices collated from many different sources (presented in Cohen 1977, 1978; Briand & Cohen 1987; Cohen *et al.* 1990a). Out of this mass of data a number of common patterns emerge (Table 1.1). A number of explanations have been put forward to account for this pattern: these must be taken into account in constructing an evolutionary model for food webs.

Patterns in food webs have been explained as being due to purely random assembly effects, selection for feeding at lower trophic levels (Hutchinson 1959), donor-controlled dynamics (DeAngelis 1975; Pimm 1982), and constraints imposed by inefficient energy flow through ecosystems (Hutchinson 1959; DeAngelis 1980; Yodzis 1981, 1984a, b). All these explanations have only limited validity either in terms of explicatory power, or in terms of the food webs to which they apply. Counter-examples to them can often be found.

More successful approaches to understanding patterns in food webs have taken one of two theoretical paths. Firstly, there are the static models, based upon the theory of random graphs, which seek to explain food webs purely in terms of structure. Secondly, dynamical models examine populations interacting in a food web and look for stable configurations as analogues of persistent structures in food webs.

The static models of Cohen and co-workers (Cohen & Newman 1985; Cohen *et al.* 1985, 1986; Newman & Cohen 1986; Cohen 1989, 1990; Cohen & Palka 1990; Cohen & Newman 1991; Cohen & Łuczak 1992; see also Cohen *et al.* 1990a) are based on the assumption that there exists a trophic hierarchy, such that any species can only feed on species below it in the hierarchy, and will only be preyed upon by species above it in the hierarchy. Such a hierarchy may seem unrealistically restrictive, but Warren and Lawton (1987) have suggested that it may be provided by the implicit constraints on body size in predators and prey (excluding parasites). This argument was put forward by Elton (1927) originally, and also mentioned by Hutchinson (1959).

Cohen and co-workers have shown that their cascade model explains a number of the patterns observed in real food webs. For example, constant proportions of species in different classes and links between these classes (Cohen *et al.* 1985), short food chains (Cohen *et al.* 1986; Newman & Cohen

---

1.Feeding loops are absent; this assumes such phenomena as cannibalism of juveniles are ignored.(Pimm 1982)

2.Trophic links between species are constant, i.e. there is a constant ratio of predators and prey. This also implies that connectance (Gardner & Ashby 1970) declines as the number of species in the web increases. (Macdonald 1979; Cohen & Briand 1984; Jeffries & Lawton 1984a,b).

3.Grouping species into top species, those at the highest trophic level, basal, those at the lowest trophic level, and intermediate those at all trophic levels in between, the proportion of species in top, intermediate and basal classes is constant. (Briand & Cohen 1984).

4.The proportion of links between any two of the above classes is also found to be constant. (Briand & Cohen 1984)

5.Omnivory (feeding at more than one trophic level) is rare. Exceptions are parasite and/or insect food webs. (Pimm & Lawton 1978).

6.Food webs in fluctuating and constant environments differ. (Briand & Cohen 1984; Cohen & Briand 1984; Cohen, Newman & Briand 1985).

7.Food chains are short: typically three trophic levels, rarely five or more. (Hutchinson 1959; Pimm & Lawton 1977; Pimm 1982; Briand 1983; Lawton 1989).

8.Food chains are shorter in two-dimensional as opposed to three-dimensional habitats. Just what defines a two- or three-dimensional habitat is more difficult to elucidate. (Briand & Cohen 1987; Briand & Cohen 1989 - but see Moore, Walter & Hunt 1989).

9.Webs are reticulate, rather than compartmentalised, within habitats, but compartmentalised between habitats. (Pimm & Lawton 1980; Pimm 1982).

10.Food webs are interval (i.e. the niche overlaps of predators at the same trophic level in terms of prey utilisation can be expressed in a one-dimensional classification). (Cohen 1978).

11.Certain properties of the predator and prey overlap graphs are common to many webs (Pimm *et al.* 1991; see Cohen 1978; Sugihara 1984).

(After Pimm 1982; Lawton & Warren 1988; Lawton 1989; Pimm *et al.* 1991; Polis 1991.)

Table 1.1. Observed patterns in food webs.

1986; Cohen & Łuczak 1992), and interval food webs (the latter unreliably however) are all produced. However these are at the cost of ignoring well-documented population processes occurring in ecological communities, and these are taken into account in dynamical models.

In order for us to observe them, food webs in the natural world must persist for some time, that is they must be ecologically stable. This in turn requires that their constituent populations should not fluctuate too widely about equilibrium values, for this would create the risk of either stochastic extinction of a small population, or extinction of the prey species by a large predator population, which would destabilise the web.

According to this view, ecological stability is somewhat akin to mathematical stability. Any food web that we see in nature must be stable otherwise we would not see it. This is the dynamical stability hypothesis (e.g. Pimm 1982; Lawton & Warren 1988). It explains most of the trends in Table 1.1, with the exception of differences in constant and fluctuating habitats, and shorter food chains in two-dimensional habitats (which may both be problems of definition), and also intervality and constant link-species scaling. The state of food web data is such (Paine 1988) that it is difficult to eliminate the possibility that the latter two patterns might be artifacts. In any case, the dynamical stability hypothesis looks promising- the main problems surrounding it concern the definition of stability. It is possible to model food webs through systems of Lotka-Volterra type differential equations (after Hofbauer *et al.* 1987);

$$\frac{dx_i}{dt}=x_i(r_i+\sum_{j=1}^{n}\alpha_{ij}x_j). \tag{1.1}$$

These equations are non-linear, but it is possible to linearize to an approximate solution, and look at stability around the equilibrium point, that is, local asymptotic stability. It is widely accepted that the equations are biologically unrealistic (e.g. May 1981a; Murray 1989), but they do show some fundamental characteristics of what are, in nature, much more complex systems. Also they are not entirely intractable!

The dynamical stability hypothesis and static models such as the cascade model might seem like opposite extremes in the study of food webs. In fact, a recent paper (Cohen *et al.* 1990b) presents a model which combines the two approaches- and one would suspect that such combinations of the techniques will become more important in the future.

It is possible that the emphasis on stability in the study of Lotka-Volterra models of food webs is misleading; after all, in the real world one might expect most species in most communities to spend a lot of their time away from equilibrium due to purely random environmental effects. Analysis about the equilibrium point may be discarding a lot of useful information about the non-equilibrium dynamics. Measures such as permanence (Hutson & Law 1985; Hofbauer *et al.* 1987; Hofbauer & Sigmund 1988, 1989), also referred to as ecological persistence (Maynard Smith 1969; Freeman & Waltman 1977) may be more illuminating. Permanence refers to the condition that the trajectory of n interacting species in an n-dimensional phase space does not pass on to an $n-1$ dimensional boundary of that space. This means that no species can go extinct. Ideal as though this might seem for community ecology, there are difficulties in applying the conditions for more than three species (Jansen 1987; Law & Blackford 1992). Since the community assembly models I shall construct have in effect much higher dimensions than three I shall not utilise such a measure.

The food web statistics approach to the analysis of trophic structure has additional problems. An increasing body of evidence from natural communities suggests that many trophic interactions are in fact very weak, or only occur rarely (Paine 1980, 1992; Rafaelli & Milne 1987; Warren 1988; Hall *et al.* 1990a, b; Juliano & Lawton 1990; Hall & Raffaelli 1991). This has implications for the theoretical representation of food web interactions by Lotka-Volterra equations; perhaps the α_{ij}, the interaction terms in the Lokta-Volterra equation should be given very low values most of the time. In addition, the presence of many weak interactions implies that many studies of natural food webs will have failed to identify these interactions. So real food webs may be even more complicated than previously thought.

More problems for this type of food web analysis may be posed by the large amount of spatial and temporal variation that can occur in a food web. Standard food web matrices are static and cumulative (Schoenly & Cohen 1991). They depict information gathered on many occasions. Cumulative webs will show many differences from time-dependent ones, such as predators switching their prey over the seasons, according to availability, or the change in prey niche of a predator as it ages (Werner & Gilliam 1984). Temporary components of food webs, 'opportunist' predators and 'tourist' (Moran & Southwood 1982) prey will not be distinguishable from more important components of the community.

A number of studies have shown considerable variation in space and time for food webs in particular habitats (Beaver 1985; Kitching 1987; Warren 1989). Several very detailed studies (Winemiller 1990b; Hall & Raffaelli 1991; Polis 1991) show departures from the expected patterns which have been found in broader comparisons. It is clear that generalizations about food web structure must be used with extreme care.

From the modelling point of view, observations and explanations of food web structure tell us that an adequate model of a food web must be very complicated, involving many species each with many interactions. Even if we disregard the evidence for weak interactions in food webs we are still left with systems of many species. It is difficult to justify a food web model of intermediate complexity. Since it is quite possible that a realistic food web model might exhaust any computational or analytical facilities available, perhaps a better approach would be to concentrate on pair-wise interactions between predators and prey within a food web.

The dynamical stability model has a good intuitive basis and excellent explanatory power: this does suggest that some element of dynamics should be incorporated in an evolutionary and ecological model. This would have the advantage that any results obtained could be linked to the large body of work on population ecology, specifically population dynamics, that already exists. That populations in the model should be dynamically stable in some sense is reasonable; what is not clear is in what sense stability is used.

By deciding to include some elements of population dynamics in the model, it becomes difficult to include the cascade model in an explicit sense, despite its obvious utility in explaining food web patterns. One crucial assumption the cascade model makes is that of a trophic hierarchy. Warren and Lawton (1987) have suggested that this could be caused by the effects of body size in structuring predator-prey interactions. This element of the static type of explanation will be reconsidered, noting the role of body size generally in ecological interactions (Calder 1983; Peters 1984), in connection with constraints on predator-prey coevolution.

The inclusion of population dynamics implies a dimension of ecological time in any model. Beyond ecological time, on a longer timescale, lies evolutionary time. This is not usually considered in any detail in food web models. If evolutionary processes are to be considered, some way of altering the characteristics of a model must be built in to it. One way to do this is via community assembly.

1.3 COMMUNITY ASSEMBLY

In order to look at the dynamics of food webs (especially in relation to changes leading to a stable state), a number of workers have simulated the process of invasion of an existing food web by new species, or successive invasion of species to create a food web (reviewed in Roughgarden 1989; Drake 1990a; Nee 1990; Pimm 1991).

A considerable amount of theoretical work in this area derives from the observations of Gardener and Ashby (1970) that randomly-constructed networks did not necessarily become more stable as their connectance increased, applied by May (1972, 1974) to overturn the then prevailing orthodoxy in community ecology that more complex communities would be more stable. Roberts and Tregonning (Roberts 1974; Roberts & Tregonning 1980; Tregonning & Roberts 1979) developed simple models of community assembly: they showed that, while randomly-assembled communities might exhibit the properties described by May, if selective elimination of populations without feasible equilibria was carried out, complex communities were more likely to be stable (but see Gilpin 1975a).

The selective criteria assumed by Tregonning and Roberts implied that populations had locally asymptotically stable equilibria. This arises automatically from the condition of the existence of feasible equilibria for certain types of simple community model, but does not necessarily occur in more complex systems. Nevertheless, this was followed by many other workers in related models of trophic or competitive communities (Gilpin & Case 1976; Lawlor 1978, 1980; Robinson & Valentine 1979; Drake 1983, 1985, 1990b; Post & Pimm 1983; Mithen & Lawton 1986; Shigeshada *et al.* 1988, 1989; Case 1990, 1991). Yodzis (1981, 1984b) took an alternative approach based on energy utilisation.

Post and Pimm (1983) modelled community assembly through a system of predator-prey Lotka-Volterra equations; they started with only autotrophic species then allowed heterotrophs successively to invade. The new community was then tested for equilibrium: invasions that did not result in equilibrium were rejected- as were invaders which completed trophic loops (a biologically implausible case). The invasion of a species could correspond to a new equilibrium with some negative populations: such populations were then deleted corresponding to extinction due to invasion. Post and Pimm showed with this model that turnover of species declines as does local stability as food web assembly proceeds. However the community never reached a stable state (i.e. one which was resistant to all further invasion). Although local stability declined, stability in terms of species turnover increased, so the conclusion we can draw from this model are not clear cut. One problem is that equilibrium was assumed for every step of the model- this may be a rather unrealistic assumption.

Nevertheless it was also assumed by Drake (1983, 1985, 1990b) in his Lotka-Volterra equation assembly models. Drake started with a three-species food web, and then invaded species, letting the system go to a feasible (all species populations non-negative) equilibrium after each invasion. Once again all non-equilibrium food webs were discarded. Drake found a decline in stability with increasing complexity (measured as numbers of species), but the usefulness of his model is once again limited by the assumption of equilibrium. Thus we have some implicit support for shorter food chains (more species implies less stable food webs; as more species are added, it is more difficult for others to invade).

The models of Nunney (1980) and Taylor (1985, 1988) are distinct from most previous assembly models of community construction in that they do not assume local asymptotic stability as a condition for inclusion of a new sub-system- the system is merely iterated until it reaches an equilibrium state or not. Such a "developmental" approach to community modelling (Taylor 1989) is an important way of approaching the development and evolution of ecological systems. It avoids the problems with defining stability engendered by the dynamical stability hypothesis.

In parallel with the construction of computer simulations, a large number of experimental studies of community assembly have been carried out, using mainly microbial communities (Dickinson & Robinson 1984, 1985, 1986; Robinson & Dickerson 1984, 1987; Robinson & Edgemon 1988; Drake 1985, 1991) but also water-filled tree holes (Pimm & Kitching 1987; Jenkins & Kitching 1990) and marine fouling communities (Sutherland 1974; Sutherland & Karlson 1977).

In addition a considerable number of studies of naturally occurring communities have detected phenomena consistent with community assembly processes occurring in diverse taxa; tropical (Connell 1978) and temperate (McCune & Allen 1985) forests, birds (Lack 1973), coral reefs (Connell 1978; Talbot *et al.* 1978; Buss & Jackson 1979), other marine communities (Osman 1977; Barkai & McQuaid 1988), old-field vegetation (McBrien *et al.* 1983), Diptera (Kneidel 1983), Hymenoptera (Cole 1983) and Odonata (Morin 1984).

What general conclusions can be extracted from this mass of work? Biological communities are complicated entities, and even the simple analogues of natural communities to which theoreticians and experimenters must resort exhibit complex properties. But a number of general features have been observed in empirical studies (Table 1.2), and equivalent behaviour has been observed in theoretical studies. The features I wish to concentrate on are informed by the inclusion of evolution in the community assembly model. Alternative stable states in ecological models have a parallel in evolutionarily stable strategies in evolutionary models. Historical effects can be significant in genetic models as well as ecological ones (Spencer & Marks 1988). Resistance to invasion can arise for genetic mutants as well as ecological species.

The developmental approach can be used to model these features of evolutionary systems, but any model which is used must draw upon the theory of the evolution of interacting species, which I shall now discuss.

1. Multiple or alternative stable states (Sutherland 1974; Connell 1978; Buss & Jackson 1979; Cole 1983; McCune & Allen 1985; Gilpin *et al.* 1986; Robinson & Dickerson 1987; Barkai & McQuaid 1988, Robinson & Edgemon 1988; Drake 1990b).

2. Alternative pathways for assembly (Connell 1978; McCune & Allen 1985).

3. Historical effects (Kneidel 1983, McBrien *et al.* 1983).

4. Build-up of invasion resistance (Sutherland 1974; Barkai & McQuaid 1988).

(Rearranged, after Drake 1990a, Table 1, and Pimm 1991, especially Table 11.1.)

Table 1.2. Some features of community assembly observed in empirical studies.

1.4 EVOLUTION OF INTERACTING SPECIES

One problem with ecological assembly models is that they do not include evolutionary change. Although the study of food webs in the field takes place over a much shorter time-scale than the evolutionary one, it seems reasonable to assume that successful invasions of species would occur fairly rarely in most communities, over such a long time-scale that some significant evolutionary effects might occur. Thus evolutionary changes in food webs need to be considered.

It ought to be made clear at this point that evolution of food webs does not imply that the whole food web is evolving as a unit. This would imply group selection, which, although it may occur under certain restrictive conditions (Wilson 1983), is not thought to be a major component of selection in nature (Dawkins 1982; Mayr 1988). Instead we are referring to evolution at the individual level within species in food webs. Stenseth (1985) has suggested that the dynamical stability hypothesis (e.g. Pimm 1982) implies group selection for locally stable food web configurations: I will not deal in detail with this assertion, but merely refer to assembly models which show (individual) selective processes can lead to stable states (Spencer & Marks 1988).

Evolution of species in food webs may be coevolution, by the definition of Futuyma & Slatkin (1983a),

"...a trait of one species [which] has evolved in response to a trait of another species, which trait itself has evolved in response to the trait in the first...",

since the only reason the species are in a food web is by virtue of their interactions. The essential features of this definition are reciprocity and specificity- are they satisfied in the wide range of circumstances which could be called coevolution in food webs? (See Futuyma & Slatkin 1983b; Nitecki 1983).

In the case of predator-prey interactions (Rosenzweig 1973; Rosenzweig &

Schaffer 1978; Schaffer & Rosenzweig 1978) this seems possible. This would account for some interactions in a food web; but others may be more diffuse (after Janzen 1980; Fox 1981) such as insect-plant interactions (Futuyma 1983; Levin *et al.* 1990). Here each insect species on a plant may have a very minor effect on the host- and it is disputed as to whether coevolution actually affects insect-plant interactions to any degree (Strong *et al.* 1984).

In the evolution of a predator-prey interaction it has been suggested that the negative effect may lead to arms race coevolution (Dawkins & Krebs 1979); but see Abrams (1986a, b) and Thompson (1986). Analysis of the effects of predation has provided some evidence for arms race coevolution (Vermeij 1982; Vermeij & Covitch 1978). The term "arms race coevolution" indicates a feedback operating within the coevolutionary interaction. This could encompass positive feedback leading to extreme values of traits in each species, in which case one might expect coevolution to be halted by counter-selection eventually. So arms race coevolution could lead to a stable state. Alternatively each species might cycle between alternative traits, in response to changes in the other species, in which no stable state might be reached.

These two alternatives are thought to be two possible long-term outcomes of coevolution. A third, extinction, can be ignored. It would be useful to distinguish between the two effects. Will it lead to a stable state, what exactly will this be? Different theorists have developed a number of different definitions. Will a community evolve to; a coevolutionary steady state or CSS (Rosenzweig & Schaffer 1978; Schaffer & Rosenzweig 1978), a coevolutionary ecological system or CES (Vasco *et al.* 1987), an ecologically and evolutionarily stable community (Stenseth 1983), or a coevolutionarily stable community or CSC (Matsuda & Namba 1991, and in a different context, Brown & Vincent 1987a)? Distinct approaches to the problem have generated a number of, not necessarily compatible, solutions.

A number of theoretical studies have provided tests for Red Queen coevolution. Models of community (Levins 1975; Lawlor & Maynard Smith

1976; Rummell & Roughgarden 1983, 1985; Stenseth 1983, 1986; Rosenzweig *et al.* 1987; Vasco *et al.* 1987; Ginzburg *et al.* 1988; Akçakaya & Ginzburg 1989; Szathmáry *et al.* 1990; Vida *et al.* 1990) and predator-prey (Rosenzweig 1973; Rosenzweig & Schaffer 1978; Schaffer & Rosenzweig 1978; DeAngelis *et al.* 1984, 1985; Brown & Vincent 1987a, b) evolution have generated varying results.

Rosenzweig (1973) and Rosenzweig and Taylor (1980) present models and fossil evidence for a kind of unstable coevolution akin to Red Queen coevolution. However Schaffer and Rosenzweig (1978; Rosenzweig & Schaffer 1978) interpret Red Queen coevolution as leading to a coevolutionarily stable state (their term), and Rosenzweig and colleagues (1987) suggest that Red Queen coevolution cannot evolve for any realistic parameter values. Perhaps Red Queen coevolution is itself unstable, and will decay to stasis, an-ESS-like state, over time (as implied in Rosenzweig 1973).

Models of the evolution of communities, although providing many useful insights, have not delineated clearly between the two alternatives. Rummel and Roughgarden (1983; 1985) modelled invasions by new species related to preexisting species by a generating function. Thus, these invaders had some of the characteristics of resident species and were akin to invading mutants. They compared competition communities assembled under conventional ecological assumptions with those in which evolution had been allowed to occur. They found that the inclusion of evolution made species more stable, and yet more vulnerable to invasion, so cycling of the species in the community could occur. It appeared that evolution could produce communities structured differently from those in which only ecological assembly processes operated. This conclusion depended however, upon an analysis of evolutionary stability which has been regarded as inappropriate by other workers (Brown & Vincent 1987a). The implications of other definitions of evolutionary stability have been explored with reference to ecological stability by Stenseth (1983, 1986; Reed & Stenseth 1984) and Vasco *et al.* (1987). Their work has not generated any clear-cut conclusions about the existence of Red Queen coevolution or evolutionary stasis.

Ginzburg and co-workers (Ginzburg *et al.* 1988; Akçakaya & Ginzburg 1989, 1991) pioneered a novel approach to modelling community evolution, where new species invading an ecological system were chosen as "ecologically continuous" mutants of their progenitors. That is to say, mutant characters were sampled upon a distribution related to, or centred upon, ancestral values of those characters. This approach seems reasonable in view of the known affects of mutation upon ancestral phenotypes. Their models of competition communities showed that evolution could result in ecologically stable configurations; resistance to invasions did not arise during the simulation implying that continuous evolutionary change (Red Queen coevolution) could occur.

Vida and others (Vida *et al.* 1990; Szathmáry *et al.* 1990) developed a model of community evolution by combining a modified Lotka-Volterra population model with resource dynamics and speciation built in. Their models showed many features of community change over evolutionary time, and appeared to support the Red Queen hypothesis in certain versions of the assumptions used (Szathmáry *et al.* 1990). The amount of computer time used for simulation restricted the conclusions which could be drawn, as might be expected with a model of such a complex system. Considering models of community evolution in general, a substantial amount of theoretical work has considered evolutionary stability conditions; rather less work has consider dynamical change and assembly processes which may or may not lead to evolutionarily stable states. That which has been performed has not produced consistent results.

Empirical studies of extinction in the fossil record can also be used to test for Red Queen coevolution (Hoffman 1991). Hoffman and Kitchell (1984) examined the fossil record for pelagic plankton, and concluded that the observed record fitted more closely the predictions of the Red Queen hypothesis than the opposing Stationary hypothesis (Stenseth & Maynard Smith 1984); the evidence was however ambiguous, due to the inconstancy of the abiotic environment. Kitchell, DeAngelis, and co-workers (Kitchell *et al.* 1981; DeAngelis *et al.* 1984, 1985) compared data on prey selection by naticid gastropods from the fossil record and from experiments with the predictions of a model of predator-prey coevolution. They were primarily concerned with phyletic trends in size of predators and prey, but their models suggest that optima for predator and prey fitness may occur, leading to a stable evolutionary state. However, the models they examined, although based on empirical evidence from the fossil record (Kitchell *et al.* 1981), still fall short of the complexity of real predator-prey interactions. The Red Queen hypothesis is by no means disproved.

Indeed it may be almost impossible to prove with experimental or fossil evidence, since the abiotic environment is never constant (Hoffman 1991). Models provide the only way for controlling for abiotic environmental change, but even so, as described above, do not often produce clear results. The models I shall develop in this thesis will be used for such a purpose.

Kitchell and co-workers (Kitchell *et al.* 1981; DeAngelis *et al.* 1984, 1985) studied a predator-prey interaction in which predator and prey sizes acted as important constraints. The ecological effects of size are important and wide-ranging (Hespenheide 1973; Peters 1983; Calder 1984; Ebenman & Persson 1988), thus it is not surprising that size should affect predator-prey coevolution. In developing models of the evolution of interacting species, it will be necessary to impose constraints in order to prevent the evolution of unrealistic situations; such as a prey species evolving complete independence from a predator while that same predator is entirely dependent upon it. This could be done by incorporating body size as a constraint; this is an approach I shall investigate.

1.5 AIMS OF THE PROJECT

The general aim of the project is to investigate and describe the evolution of interacting populations, when population dynamics of both species are taken into account, and without adopting such restrictive conditions on the dynamical behaviour of populations as local asymptotic stability. But such an analysis must start with a simple case before moving on to more complex ones; and such is the justification for focusing on predator-prey systems in this thesis, as time was not sufficient to explore larger multi-species systems in any detail.

1.5.1 The dynamics of predator-prey coevolution

Much theoretical effort has been concentrated upon the outcome of predator-prey coevolution (Rosenzweig & MacArthur 1963; Rosenzweig 1973; Schaffer & Rosenzweig 1978). In general, the suggested outcomes can be divided into two (Stenseth & Maynard Smith 1984); stasis, where predator and prey reach evolutionarily stable states, or Red Queen coevolution, where continuous coevolution occurs in each species, caused by change in the other. Both these outcomes are statements about the dynamics of evolutionary change; fundamentally the dynamics of gene frequency change, or at a higher level of observation the dynamics of phenotype change. So questions about the outcome of predator-prey coevolution are questions about evolutionary dynamics: and to find general conclusions about the evolutionary dynamics of predator-prey systems is the first aim of the project. Due to the complexity of combined genetical and ecological models, this will frequently be considered at a phenotypic level.

1.5.2 The coexistence of predator and prey under selection

Studies of the population dynamics of predator and prey have frequently exposed the paradoxical situation of the predator effect on prey driving the prey, and then the predator, to extinction. This is paradoxical because we do not observe this in nature. One reason could be that it is difficult to find evidence for species extinction after the fact; but the ease of producing this situation in a model contrasts with the many predator-prey interactions that are known to have a considerable evolutionary history.

Given that it should be a selective advantage for a predator to become more efficient, for a long time arguments about the coexistence of predator-prey over evolutionary time depended upon such poorly defined notions as "prudent predation" (Slobodkin 1961), in the absence of better reasoning to show that a predator would not evolve to eat its prey to extinction.

Theoretical arguments for the coexistence of evolving predator and prey have advanced since then (e.g. Slobodkin 1974; Schaffer & Rosenzweig 1978) but it is still of interest to investigate the coexistence of predator and prey when both are evolving, as no general argument for the coexistence of predator and prey has been developed to cover the wide variety of natural situations. The case when only one species evolves is also of interest; this could correspond to lack of genetic variance for predatory or anti-predatory traits. To investigate this in systems involving both ecological and evolutionary dynamics, is the second aim of the project. This will involve both mathematical and simulation models.

1.5.3 The maintenance of allele polymorphism

Spencer and Marks (1988, 1992; Marks & Spencer 1991) investigated the question of the stability of allele polymorphisms using models with two different types of assembly rule. In the first model, alleles were generated at random (with random fitness effects), and combined to form a random single-locus polymorphism. It was found that the chances of forming a stable polymorphism declined very rapidly with the number of alleles included, and indeed were very small for not very high numbers of alleles, such as six or seven.

The second model produced very different results: here alleles were generated and invaded at random, but then subjected to viability selection, that is their frequency in succeeding populations after iteration depended upon their contribution to the stability of the polymorphism. These randomly generated polymorphisms were thus subject to a process akin to natural selection. Spencer and Marks found that this model, in contrast with their first, produced stable polymorphisms for allele numbers as high as five and six. A similar result was derived by Kingman (1988), using analytical methods. This model is surely a more realistic representation of the natural selection of allele polymorphisms, although it still fails to generate allele polymorphisms of the magnitude of those found naturally (although some of these may arise by processes other than viability selection).

In later work (Spencer & Marks 1992) the fitnesses of mutant alleles were derived as a function of the fitnesses already in the population (compare Ginzburg *et al.* 1988, for interspecific interactions). This resulted in values for allele numbers comparable with the larger polymorphisms found in nature.

These models are interesting because they provide an insight into the way to model evolution in interacting species. It is possible to allow new mutants to invade, sequentially, in a form of "mutant bombardment". If we assume that selection is density-dependent, so that population density is a true reflection of the fitness of the population, then in a haploid model population dynamics and fitness can be represented by the same dynamical system. This avoids unrealistic limitations on the configurations of multi-species communities that can evolve imposed by using local (asymptotic) stability as a criterion of establishment.

The models of Spencer and Marks are also interesting in that they show how allele polymorphisms at single loci may be maintained purely by a process of sequential invasion. They acknowledge the similarity between ecological community assembly models and their genetic assembly model. This leads to the question: will allele polymorphisms be maintained by assembly processes in interacting species? The haploid two-species case is equivalent to the single-species diploid case for the purposes of investigation of this problem (C. Cannings, *pers. comm.*). I aim to investigate it using simulation models of interacting species.

1.5.4 Invasions and the Red Queen

The Red Queen hypothesis makes assumptions about rates of evolution in interacting species. If it is correct, then continual coevolutionary change should be expected. This implies that the rate of evolution in each species remains constant, or at least does not fall to zero. In order to maintain evolutionary change, variation must be produced and new mutants must establish themselves frequently. If resistance to mutant invasion has built up, then they will not be able to establish and evolutionary change will stop.

It therefore follows that if it was possible to look at the success rate of mutant establishment over time, a persistent decline in success would indicate the build-up of invasion resistance, and if the success rate fell to a very low level, would imply an approach to an evolutionary stable state. If the Red Queen hypothesis is correct, one would not expect this to happen, but would expect invasion success to remain relatively constant over time.

The construction of community assembly models incorporating evolutionary change provides a way of examining the success rates of mutant invasions, and thus of testing the Red Queen hypothesis, and detecting any evolutionary or coevolutionary stable states that may be proposed by alternative hypotheses. To investigate this aspect of coevolutionary theory is the fourth aim of this project.

1.5.5 The dynamical consequences of evolution

It is well known that simple ecological models can exhibit complex cyclic and chaotic dynamics (May 1974; May & Oster 1976). The evidence of biological field data is less clear (Hassell *et al.* 1976; Schaffer 1984, 1985; Schaffer & Kot 1985; Berryman & Millstein 1989; Godfray & Blythe 1990), but it seems at least quite likely that chaotic dynamics occur in some natural systems.

For the Lotka-Volterra equations, as used in predator-prey or food web models, more than two species must be present for chaotic dynamics to be possible (the dimension of the system must be greater than two). Chaotic behaviour therefore seems not unlikely for food webs, with a dimensionality somewhat difficult to assess in real systems, but certainly higher than two.

This is for purely ecological systems; what affect will the inclusion of evolution in ecological models have on their dynamical properties? The answer depends upon the relationship of evolutionary to ecological change (Godfray & Blythe 1990). I propose to examine models in which evolutionary and ecological dynamics takes place on similar timescales, so one might expect evolution to affect the demographic parameters of the ecological population models.

Metz, Godfray, and co-workers (Godfray *et al.* 1992; Metz 1992; Metz & Godfray 1992; Metz *et al.* 1992), have examined the evolution of demographic parameters in single-species population models using the technique of Lyapunov exponents. Their results suggest that natural selection may operate to move demographic parameters into zones of stable dynamics, under certain conditions. Under different conditions, or using slightly different models, cyclic or chaotic dynamics may be selected for.

It is not yet possible to use these techniques on multi-species systems, and so simulation must be used. The simulation models of evolution in interacting species to be described in this work incorporate population dynamics; and so observation of the time series of population dynamics generated by the simulation should provide insights into the dynamical consequences of evolution in interacting species. Exploration of this area is the final aim of this project.

1.6 LAYOUT OF THE THESIS

The layout of the thesis is intended to reflect both the order in which the work was done, and an underlying theme of analysis of similar systems at different levels of complexity and organisation. The research work presented in this thesis covers both complex output from simulations, and the slightly simpler conclusions extracted from analysis of mathematical models. Models of the evolution of interacting species are examined both at the level of population genetics, and that of population dynamics, as well as in a combination of the two.

Early experimentation with the simulation models, and published work on other, similar models (described earlier in this chapter) suggested that the results they produced would be complex, and would require considerable amounts of computer time. In an effort to circumvent this problem, a theoretical approach to examining evolution in predator-prey systems related to the simulation models, was developed. Results of the analysis are described in Chapter 2, with relevance to both evolutionary and ecological stability.

A theoretical approach is also presented in Chapter 3, but in this chapter a numerical method is used to examine the invasion of mutants into a predator-prey system similar to that of the previous chapter. This allows the evolutionary dynamics of the system to be evaluated more thoroughly that in Chapter 2. The long-term outcome of predator-prey coevolution, evolutionarily stable states or Red Queen coevolution, is investigated in this chapter.

Chapter 4 describes the simulation models which were constructed to model evolution in interacting species. This chapter provides a basis for the results of the simulations, collected together in Chapter 5.

Three main areas of investigation were considered using the simulation models; invasions of alleles into interacting species, the maintenance of allele polymorphism, and the population dynamical consequences of the evolution of predators and prey. Issues that arise from the use of the simulation models to study these questions are also discussed.

In Chapter 6 the results presented in the previous chapters are discussed. The limitations of the both the approach taken, and the results obtained are contrasted with other, similar, studies. It is argued that this study provides a number of novel insights on which to base further work. The relevance of work on evolution in predator-prey systems to related areas of research is considered. Questions for future investigation are outlined.

Finally, in Chapter 7, the conclusions are presented. The importance of integrating evolutionary and ecological aspects of theory is emphasized.

Chapter 2. EVOLUTIONARY INSTABILITY IN PREDATOR-PREY SYSTEMS

2.1 SUMMARY

The dynamical stability properties of Lotka-Volterra equations have been used frequently to predict the persistence of predator-prey assemblages and trophic webs, yet they do not take into account evolutionary change. The incorporation of genetic variation into a stable food web will make it less stable in many cases. Since populations containing genetic variation do persist in nature, such theoretical results appear paradoxical. In order to attempt to resolve this paradox, we develop a model based on phenotypic change in investment in predatory or anti-predator traits, in coevolving species. The model is akin to previous models of arms-race coevolution using evolutionarily stable strategy theory, but we seek to understand the evolutionary dynamics in phenotype space, as well as to identify any evolutionarily stable states that may occur. The relationship between investment and the Lotka-Volterra interaction terms is defined in a very general form, so as to cover a wide range of cases in nature. From the general case and more specific examples based on hypotheses about the factors affecting predator-prey interactions, we derive conditions for the occurrence of coevolutionarily stable states, where both species are playing evolutionarily stable strategies with respect to their interaction with the other species. Coevolutionarily stable states are found to be unusual outcomes of predator-prey coevolution. However, lack of evolutionary stability is not seen to imply ecological impermanence, as natural selection is found to prevent mutual extinction of predator and prey under certain conditions.

2.2 INTRODUCTION

Lotka-Volterra systems have been widely used for modelling the population dynamics of interacting species (Maynard Smith 1968; May 1981b). In the form of the dynamical stability hypothesis (for example, Pimm 1982), the stability properties of Lotka-Volterra equations have been used, with considerable success (Lawton 1989) to explain the patterns of present-day food webs and biological communities. The dynamical stability hypothesis states that trophic webs are the way they are today, because their constituent populations must be dynamically stable to persist over biologically significant time periods. Dynamical stability is usually taken to mean local asymptotic stability (local stability: May 1973) in this context. Local asymptotic stability is a population measure, and states that the set of interacting populations at equilibrium are resistant to small perturbations away from their interior equilibrium point. That is, given some time, the populations will return to that equilibrium if moved by some small amount away from it.

This interpretation of the dynamical stability hypothesis does not take into account any evolutionary change, despite being applied, at least implicity, to periods of time consistent with evolutionary change, and being used explicitly to model community construction and succession (Post & Pimm 1983; Drake 1990a; but see Taylor 1988). Although much ecological theory has been based on the assumption that evolutionary change takes place on a very different timescale to that of population dynamics, it is clear that this assumption is, at best, unreliable, in the case of the dynamic stability hypothesis which refers to persistence over long periods of time. However, population dynamic change certainly can occur at a different rate to changes in gene frequency, and this is assumed in this paper. This assumption by no means implies that the two processes are disconnected.

Evolutionary biologists have considered the interaction of evolution and population dynamics through models mixing population dynamics and simple genetics (e.g., Roughgarden 1976, 1979, 1983; Levin 1978; May & Anderson 1983a; Jayakar & Zonta 1990). Other theorists have used evolutionarily stable strategy (ESS) theory to predict the results of evolution while including the effects of population size (Lawlor & Maynard Smith 1976; Knowlton & Parker 1979; Parker & Knowlton 1980; Parker 1983, 1985; Reed & Stenseth 1984; Brown & Vincent 1987a). The complicated equations that arise when genetics and population dynamics are combined means that many simplifications have to be adopted. The use of ESS models has avoided some of the problems of population genetic models, but inevitably has concentrated upon the evolutionarily stable points which evolution is expected to reach, at the expense of dynamics away from any stable points. Evolutionary dynamics away from evolutionarily stable states have rarely been investigated (but see; Maynard Smith & Brown 1986; Takada & Kigami 1991; Godfray *et al.* 1992): we present a general theory which examines such dynamics in this paper. We account for the effects of population dynamic change by deriving the fitness function of predator and prey from the Lotka-Volterra equations for population dynamics, taking genetic variation into account.

It seems reasonable to assume that distinct genotypes would correspond to different state variables for genotype density in Lotka-Volterra equations. However, if different genotypes were represented as different populations in a Lotka-Volterra system, then this would immediately affect the stability properties of the system. Harrison (1979) has shown that a simple food chain described in continuous time, with *n* species and *n* minus one trophic links between the species, and self-limitation in the basal species, will be globally asymptotically stable if it has a feasible (all densities positive) interior equilibrium point. That is, the system will return to the interior equilibrium after any perturbation, even a large one, away from it. Such a stability condition is justified due to the structural instability (Lewontin 1969) of the system, when taking evolution into account.

And yet this result is entirely dependent upon the trophic structure being that of a simple food chain, with one less link between species than number of state variables (number of species). If we introduce a different genotype at any trophic level, represented by a genotype density, the number of links will increase to at least the same number as there are state variables. Then the global stability condition will no longer necessarily be satisfied. Even if the interior equilibrium point is still asymptotically stable, this is only a local result, and some large deviation from the equilibrium could send one or more populations to extinction. This means that we have no guarantee of the persistence of the trophic web over evolutionary time. Despite this, some of the predator-prey interactions that we see in nature today have persisted over evolutionary time, and they do contain genetic variation, some of which affects the interaction between predator and prey, and indirectly, other interactions in the food web to which the predator and prey belong.

Perhaps the representation of a genetic variant is at fault. An obvious approach to modelling genetic variation within trophically interacting populations would be to add extra equations to the system of population dynamical equations, one for each genetical variant. Since this leads to a decrease in the stability of the interior equilibrium, as described, we do not follow that approach here, but instead consider genetical variation within a population in the aggregate, and look at the resultant overall trait for the entire trophic species.

One can then predict the action of natural selection upon this variation. Although evolution has a stochastic component, namely the generation of variation, the action of natural selection is clearly not random, depending as it does on the selectedness of individual organisms, a property of the interaction of their phenotypes and the environment. The organisms considered here are in Lotka-Volterra populations, and their phenotypes are investment in predatory and anti-predator traits.

2.3 ANALYSIS

Consider a Lotka-Volterra simple food chain, represented by

$$\frac{dx_i}{dt}=x_i\left(r_i+\sum_{j=1}^{n}\alpha_{ij}x_j\right), \tag{2.1}$$

(where x_i is population density of species *i*, r_i is intrinsic growth rate, and α_{ij} is the interaction coefficient defining species *j*'s effect on species *i*). Note that in this general form α_{ij} are assumed to be positive or negative constants. Let this have one less trophic link between the species than different species. It may be as small as a predator-prey system, or a larger simple food chain. (In this paper, predator-prey systems only are considered). Having such a structure we know (Harrison 1979) that any interior equilibrium that exists will be globally asymptotically stable. Since we wish to consider the effects of natural selection, we further assume that the time required for convergence to the interior equilibrium is small with respect to the timescale we are studying, and thus we can assume that the populations are at their equilibrium densities. Since we are concerned with modelling biological populations, we shall only be concerned with positive equilibrium densities, that is, feasible equilibria.

The genotypes of the populations determine their level of investment in predatory or anti-predator adaptations (we assume environmental effects are constant in this model), as appropriate, and these levels of investment may vary from zero to some maximum, according to the quantity s_i, for each species *i*. The value of s_i determines the phenotype of each species, in terms of its interaction coefficient with each other species. So we can define α_{ij} as $f_{ij}(s_i,s_j)$, for α_{12} and α_{21} in a predator-prey system. Since the phenotype directly affects the population dynamics, we can assume density-dependent fitnesses. So the fitness function of species *i*, W_i becomes identical to the per capita growth rate of each species

$$\begin{aligned} W_1 &= r_1 - \alpha_{11}x_1 - \alpha_{12}x_2, \\ W_2 &= -r_2 + \alpha_{21}x_1, \end{aligned} \tag{2.2}$$

and at ecological equilibrium

$$\begin{aligned} 0 &= r_1 - \alpha_{11}\hat{x}_1 - \alpha_{12}\hat{x}_2, \\ 0 &= -r_2 + \alpha_{21}\hat{x}_1. \end{aligned} \tag{2.3}$$

Mutants conveying different levels of investment will arise over time in both populations. If they convey a fitness advantage they will increase in density. In this two-species case, it can be shown that a selectively favourable mutant will go to fixation if α_{11} is held constant.

This follows from consideration of the zero isoclines for the population dynamics of predator, prey, and invading mutant. If the mutant is in the prey species, the zero isoclines for the prey and prey mutant will be the same for predator density zero, and in the absence of an intersection of the isoclines, there can be no interior equilibrium with both prey and mutant prey present. Hence we expect invading mutants in the prey, which can establish themselves when initially rare, to go to fixation. A similar argument can be used in the case of a mutant of the predator species, since the isoclines for different genotypes of the predator will be parallel, and thus no interior equilibria can occur. As selectively advantageous mutants go to fixation, our task of analysis of the evolutionary genetic dynamics is simplified considerably.

Considering the fitness at an equilibrium density held constant, we can predict the direction of the change in investment over time (although not the rate of change, since we know nothing about the sources of variation). This is done by differentiating the fitness function with respect to investment while holding x_i constant. If $\partial W_i/\partial s_i$ is positive then this shows that mutants of larger

s_i can invade, if it is negative the reverse is true.

Defining f_{ij} is clearly very important. In a predator-prey system this is not easy due to the wide range of phenotypic characters affecting the interaction. Here we attempt to minimise problems of definition by adopting functions of very general form, that could cover a wide range of ecological situations. If we assume that the strength of each interaction has a unique maximum and declines both sides of this maximum, and further that the second derivative of the function does not change sign (there are no points of inflection), then we can define f_{ij} as a concave function. (A concave function is one which (Jeffrey 1989) has the property that a chord joining two points on its surface always lies below the graph of the function between these two points).

The assumption of concavity would be satisfied by many functions found in biological situations. Whether the interaction function will have a unique maximum, as required by our assumption of log concavity, is more difficult to establish. However the existence of local maxima would make the function very difficult to generalise analytically, and it is certainly possible to envisage cases where there could be a unique maximum (for example, where investment is correlated with size, and both predator and prey with extreme sizes suffer reduced fitness).

In addition we assume that the function is log concave, that is the log of the function is a concave function. This seems reasonable in the light of the large number of biological relationships that are related by a power function (Harvey & Pagel 1991; chapter 6). Logging the equation of a power function produces a linear equation, and clearly dealing with linear relationships is more convenient. Using such techniques, body size has been shown to vary linearly with a wide range of ecological, physiological and physical variables (Peters 1983; Calder 1984). It is certainly possible that size, and variables correlated with size are related to intensity of predator-prey interactions in both predator and prey (Vézina 1985; Warren & Lawton 1987).

In order to allow f_{ij} as general a form as possible, we can let

$$f_{ij}(s_i, s_j) = f_{ij}(\rho), \tag{2.4}$$

where ρ is some function of s_i and s_j subject to the constraints that $\partial\rho/\partial s_i$ and $\partial\rho/\partial s_j$ are never zero. We apply these constraints in order to be able to determine the direction of the dynamics of fitness without loss of generality in specifying f_{ij}. We define the maximum for each f_{ij} as θ_{ij} where $\alpha_{ij} = f_{ij}$ for $i, j = 1, 2$. So if $\alpha_{12} = f_{12}$ then f_{12} has a maximum at θ_{12}, which represents a particular value of ρ. This will allow a wide range of assumptions to be made about the way that investment in the two species interacts to produce the effect of the interaction on each of the species population dynamics. To show why these conditions are justified we must examine the consequences, in general, of differentiating the fitness functions.

2.4 EVOLUTIONARY DYNAMICS IN GENERAL

From equation (2.4) substituted into equations (2.3), the fitness functions for two species, at ecological equilibrium, are;

$$\begin{aligned} W_1 &= r_1 - \alpha_{11}\hat{x}_1 f_{12}(\rho)\hat{x}_2 = 0 \\ W_2 &= -r_2 + f_{21}(\rho)\hat{x}_1 = 0, \end{aligned} \tag{2.5}$$

where f_{12} and f_{21} are subject to the constraints above. Differentiating with respect to investment while holding the system at $\hat{x}_1$, $\hat{x}_2$ produces

$$\frac{\partial W_1}{\partial s_1} = -\hat{x}_2 \frac{\partial f_{12}}{\partial \rho} \frac{\partial \rho}{\partial s_1},$$
$$\frac{\partial W_2}{\partial s_2} = \hat{x}_1 \frac{\partial f_{21}}{\partial \rho} \frac{\partial \rho}{\partial s_2}. \tag{2.6}$$

In order to examine the evolutionary dynamics of investment, we need to build up a global picture of the directions in which selection will be expected to drive s_i. Consider the two-dimensional space defined by s_1 and s_2; this represents the space of possible phenotypes that we are considering. If we could find where each derivative in equations (2.6) was zero then we could obtain a qualitative understanding of the evolutionary dynamics on the phenotype space. But we already have placed the constraint that $\partial\rho/\partial s_i$ is not equal to zero for i=1,2, and since $\hat{x}_1$ and $\hat{x}_2$ must be greater than zero (we are only dealing with feasible equilibria), then if $\partial f_{12}/\partial\rho$ or $\partial f_{21}/\partial\rho$ are equal to zero, then the derivatives of fitness must also be zero. This will occur at a maximum or minimum of f_{ij}, so there will be a unique solution at a maximum for the absolute value of $f_{ij}(\rho)$.

Ideally we would like to find evolutionarily stable strategies (Maynard Smith & Price 1973; Maynard Smith 1982) for each of the investment variables. Evolutionarily stable strategies for the combined evolution of two interacting species have been defined (and described) in a number of different ways (Schaffer & Rosenzweig 1978; Stenseth 1983, 1986; Brown & Vincent 1987a, b, for example). Our definition for an evolutionarily stable strategy (ESS) for two interacting species follows that of Brown and Vincent (1987a, b) in considering both density-dependence and frequency-dependence. We use similar techniques to locate ESSs, but we also wish to examine the evolutionary dynamics away from any ESS that may occur.

When we consider the existence or otherwise of evolutionarily stable states, it is clear that the fitness function for each species (W_i) must be at an equilibrium. So $\partial W_i/\partial s_i$ will be equal to zero, subject to the constraint that $\partial^2 W_i/\partial s_i^2$ is less than zero. Here instead of locating any evolutionarily stable states that may occur directly, we derive the trajectories of the evolutionarily dynamics, from which ESSs may be predicted. The method of investigating evolutionary dynamics used here is virtually identical to the method of finding evolutionarily stable strategies by differentiating fitness functions (Parker & Maynard Smith 1990). For a coevolutionarily stable state then all $\partial W_i/\partial s_i$ must be zero simultaneously. We might say that the lines in the phenotype space on which $\partial W_i/\partial s_i = 0$ must intersect for an ESS to exist. If these lines do not intersect, then a ESS cannot occur.

Generally the dynamics of s_1 and s_2 will be determined by the signs of $\partial\rho/\partial s_1$ and $\partial\rho/\partial s_2$. There are four possible cases. The conditions on $\partial\rho/\partial s_i$ tell us that there will be no stationary points, so $\partial\rho/\partial s_1$ and $\partial\rho/\partial s_2$ can each be either negative or positive. What evolutionary dynamics do occur will depend upon the form of the lines where $\partial W_i/\partial s_i = 0$. These cannot be determined in general. However, if we let the lines intersect at one point in the phenotype space, then the dynamics can be analysed graphically. Where this is allowed (implying the possibility, although not certainty, of a ESS), then in some cases the equilibrium can be asymptotically stable, but these do depend on specific forms of the lines $\partial W_i/\partial s_i$. If no intersections are allowed, and there may be reasons to support this viewpoint, then of course no ESSs can occur, since the conditions for an ESS are not satisfied.

In general, ESSs may be unlikely. But the lack of evolutionary stability need not imply ecological instability. This follows from consideration of the dynamics of investment at the edge of the zone of feasible equilibria. We consider the evolution of investment as ecological (population dynamical) equilibria, $\hat{x}_1$ and $\hat{x}_2$, are held constant. By rearrangement of the fitness functions $\hat{x}_1$ and $\hat{x}_2$ may be expressed in terms of f_{ij}, that is to say

$$\hat{x}_1=\frac{r_2}{f_{21}}, \tag{2.7}$$

and

$$\hat{x}_2=\frac{\left[r_1-\frac{(\alpha_{11}r_2)}{f_{21}}\right]}{f_{12}}. \tag{2.8}$$

We have defined f_{ij} as log concave, so f_{ij} can never be zero, and as a result $\hat{x}_1$ will always be greater than zero. However $\hat{x}_2$ will be zero when $r_1 = (\alpha_{11}r_2)/f_{21}$, and this will be the limit of the zone of feasible equilibria within which we consider the evolutionary dynamics. Since f_{ij} are defined as log concave this will occur for two values of ρ.

If we consider the evolutionary dynamics at this boundary, $\partial W_1/\partial s_1$ will be zero since $\hat{x}_2$ is zero, so only the evolution of the predator fitness function is of interest. We have already established that the rate of change of fitness with respect to investment in the prey will be zero at the stationary point of the respective f_{ij}. Since f_{ij} are log concave, we know that such values will occur between the boundaries of the zone of feasible equilibria for all possible f_{ij} and ρ.

Let us denote the values of ρ at which $\hat{x}_2 = 0$ as γ_1 and γ_2, and make $\gamma_2 > \gamma_1$. From equations (2.6) above, at $\rho = \gamma_2$, $\partial W_1/\partial s_1$ is negative always, and at $\rho = \gamma_1$, $\partial W_1/\partial s_1$ is positive always. Since the zone of feasible equilibria lies at intermediate values of ρ, it is clear that natural selection upon the investment traits will always act to maintain populations within the zone of feasible equilibria. This is not a form of group selection, since it arises purely from pair-wise interactions between individuals in the predator and prey species.

Thus the lack of evolutionary stability is no hindrance to ecological stability.

In the next two sections some special cases of the ρ function will be considered, where the dynamics of fitness can be elucidated explicitly. In these cases the existence or otherwise of ESSs will be shown, and the effect of natural selection in promoting the coexistence of species will be demonstrated graphically.

2.5 EVOLUTIONARY DYNAMICS WITH $\rho = s_2/s_1$

Consider the significant role that body size plays in determining the ecological characteristics of species and their interactions (Peters 1983; Calder 1984). The size of individuals is clearly important in structuring predator-prey interactions. In general predators attack prey smaller than they are (Hespenheide 1973; Vézina 1985), and parasites attack prey larger than they are. If size is an important determinant of predator-prey interactions, then the interaction terms of the Lotka-Volterra equation may be considered as functions of the ratio of sizes of the predator and prey. In this case we assume that s_1 and s_2 are proportional to the sizes of individual prey and predators respectively. Then $\rho = (s_2/s_1)$. Following the techniques described in preceding sections, the dynamics of fitness with respect to investment are described by

$$\begin{aligned} \frac{\partial W_1}{\partial s_1} &= \frac{\partial f_{12}}{\partial \rho}\left(\frac{s_2}{s_1^2}\right)\hat{x}_2, \\ \frac{\partial W_2}{\partial s_2} &= \frac{\partial f_{21}}{\partial \rho}\left(\frac{\hat{x}_1}{s_1}\right). \end{aligned} \tag{2.9}$$

In an earlier section the minimum of f_{12} was defined as θ_{12} and the maximum of f_{21} as θ_{21}. Equating $\partial W_i/\partial s_i$ to zero, we find that $\rho = \theta_{12}$ for species 1, and $\rho = \theta_{21}$ for species 2. If we put $\theta_{12} = \theta_{21}$, so that what is best for the predator is worst for the prey, then the phenotype space is as shown in Figure 2.1. $\partial W_i/\partial s_i$

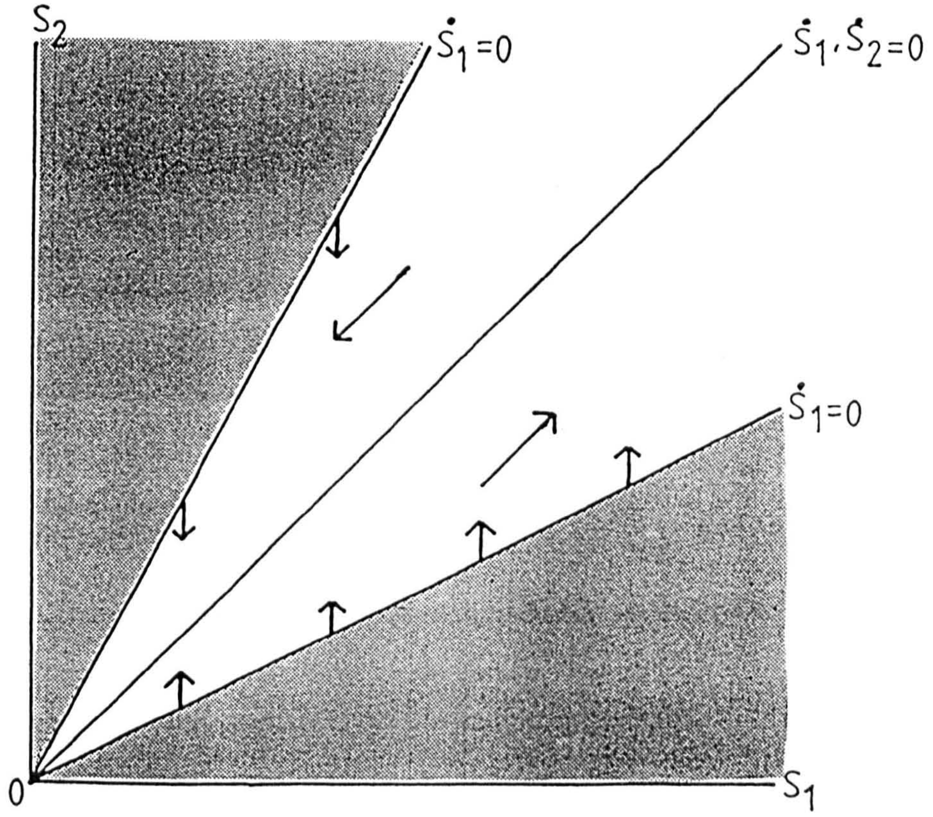


Figure 2.1. Dynamical system for investment in predator (s_2) and anti-predator (s_1) traits when $\rho = (s_2/s_1)$ and $\theta_{12} = \theta_{21} = \theta$. Hatched areas indicate zones of non-feasible interior equilibria. Arrows indicate direction of the evolutionary dynamics.

$= 0$ along straight lines from the origin; none of them intersect except at the origin, but in this special case θ_{12} and θ_{21} coincide and thus there is a line of equilibria along $\rho = \theta_{12} = \theta_{21}$. But these equilibria may not be stable, since selection causes s_1 and s_2 to tend to zero when $\rho > \theta_{12}$, and to infinity when $\rho < \theta_{21}$.

The line satisfies one of the conditions for a ESS; namely that the first derivatives of fitness with respect to investment are zero. But the prey species fitness is at a minimum, since α_{12} is at a maximum for its absolute value. So the prey species is vulnerable to invasion by mutants with higher fitness, and the stability condition of a ESS is not satisfied.

As described above, the boundary of the zone of feasible interior equilibria is given by the values of ρ when $\hat{x}_2$ equals zero. The boundary of the feasible region of population dynamics is shown in the diagram, and it is only the interior of this region that we need to consider.

We can denote ρ when $\hat{x}_2$ is zero as γ_1 and γ_2, with $\gamma_2 > \gamma_1$. We find $\partial W_2/\partial s_2$ is negative at γ_2 and positive at γ_1. Thus natural selection on traits in populations close to the boundary on the phenotype plane should drive phenotype values into, rather than out of, the zone of feasible equilibria. This is despite any other dynamics in the interior of the zone of feasible equilibria which may produce trajectories directed towards the edge of that zone.

We might not expect such a perfect symmetry between the interaction effect on the predator, and the interaction effect on the prey, although they will, clearly, be related. Once we allow θ_{12} to differ from θ_{21}, then the two lines where $\partial W_i/\partial s_i = 0$ will not coincide. There are four possible results in this case, depending on the value of ρ when $\partial W_2/\partial s_2$ is zero. The lines where $\partial W_1/\partial s_1 = 0$ must always occur in the order shown, due to f_{12} being log concave, but the line where $\partial W_2/\partial s_2 = 0$ can occur in any one of four possible positions with respect to them. One such result is shown in Figure 2.2. There will be no ESSs. The dynamics considered far from the boundary of the zone of feasible equilibria suggest trajectories which lead out of that region, implying extinction of the predator species. However we have shown above that all trajectories lead away from the boundary of the zone when populations have evolved sufficiently close, so predator extinction should not occur.

2.6 EVOLUTIONARY DYNAMICS WITH $\rho = s_2 - s_1$

If the investment in predation traits in the predator and anti-predator traits in the prey interact additively, then we could put $\rho = s_2 - s_1$. A possible example of this would be where predators pursue their prey, and predator and prey attempt to run faster in order to catch, or escape, respectively. In this situation we might imagine that increased investment in prey-catching traits in the predator would lead to a proportional increase in speed of running, and corresponding adaptations would have the same result in the prey. Although the Lotka-Volterra interaction term, α_{ij}, depends upon properties of individuals, over a large population we can assume that an adaptation which goes to fixation in a large population will affect the overall per-capita interaction. We assume that, although capture or escape of prey in an individual predator-prey encounter is still to a large extent dependent on chance factors such as terrain, condition of the animals, and weather, these factors have a constant overall effect.

So in this case, s_i is assumed to be proportional to average speed of running in pursuit of prey, or escaping from predators. Then the dynamics of fitness

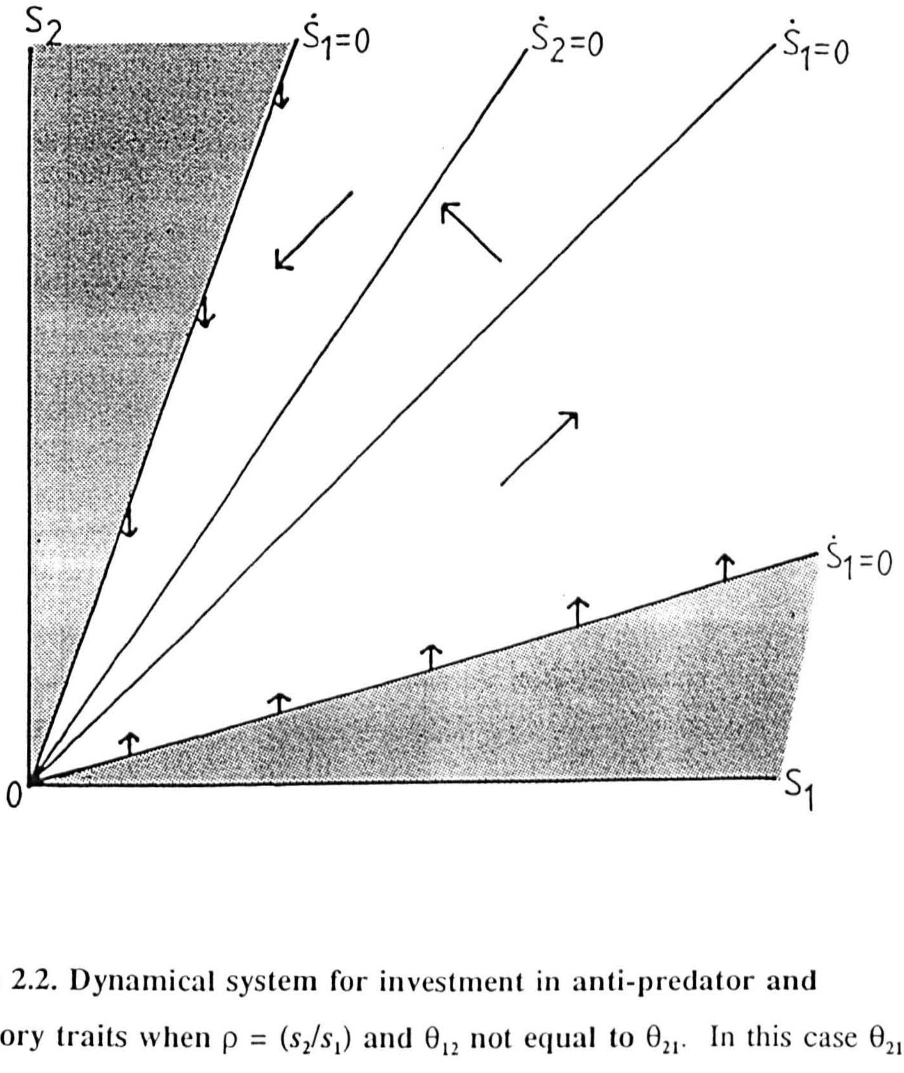


Figure 2.2. Dynamical system for investment in anti-predator and predatory traits when $\rho = (s_2/s_1)$ and θ_{12} not equal to θ_{21}. In this case $\theta_{21} > \theta_{12}$. Arrows in the interior of the zone of feasible equilibria indicate the direction of the evolution of traits on the investment plane. The action of natural selection in promoting coexistence of predator and prey is shown by the arrows along the margin of the zone of feasible equilibria. The hatched zone denotes the non-existence of feasible equilibria.

with respect to investment are given by

$$\begin{aligned}\frac{\partial W_1}{\partial s_1}&=\hat{x}_2\frac{\partial f_{12}}{\partial \rho},\\ \frac{\partial W_2}{\partial s_2}&=\hat{x}_1\frac{\partial f_{21}}{\partial \rho}.\end{aligned} \tag{2.10}$$

If $\theta_{12} = \theta_{21}$ in this case (Figure 2.3), then $\partial W_1/\partial s_1$ and $\partial W_2/\partial s_2$ will be zero when $s_1 = s_2$. This is a line of equilibria, but it will not be a line of ESSs, since the prey fitness is at a minimum and as a result the prey equilibrium for fitness is unstable. Below the line, s_1 and s_2 increase, while above the opposite occurs. As in the previous example, if we write down $\hat{x}_2$ explicitly in terms of f_{12} and f_{21}, then we find there are two values of ρ where $\partial W_1/\partial s_1$ is zero due to $\hat{x}_2$ being equal to zero. These represent the boundaries of the zone of interior equilibria, and natural selection will act to keep evolutionary trajectories within this zone. Once again, if symmetry in predator and prey interactions is removed, then the two lines where $\partial W_i/\partial s_i = 0$ do not coincide and no ESSs are possible. The coexistence of predator and prey will still be maintained by selection in this case.

2.7 DISCUSSION

We have shown that coevolutionarily stable states are rare in predator-prey systems. In this system with density-dependent fitnesses, one might have expected that lack of evolutionary stability would imply ecological instability, since only certain regions of ecological parameter space will permit a population dynamical interior equilibrium, and there is no reason for natural selection to cause a population to remain at an interior equilibrium even if it exists. However, we have found that at the boundaries of the zone of feasible

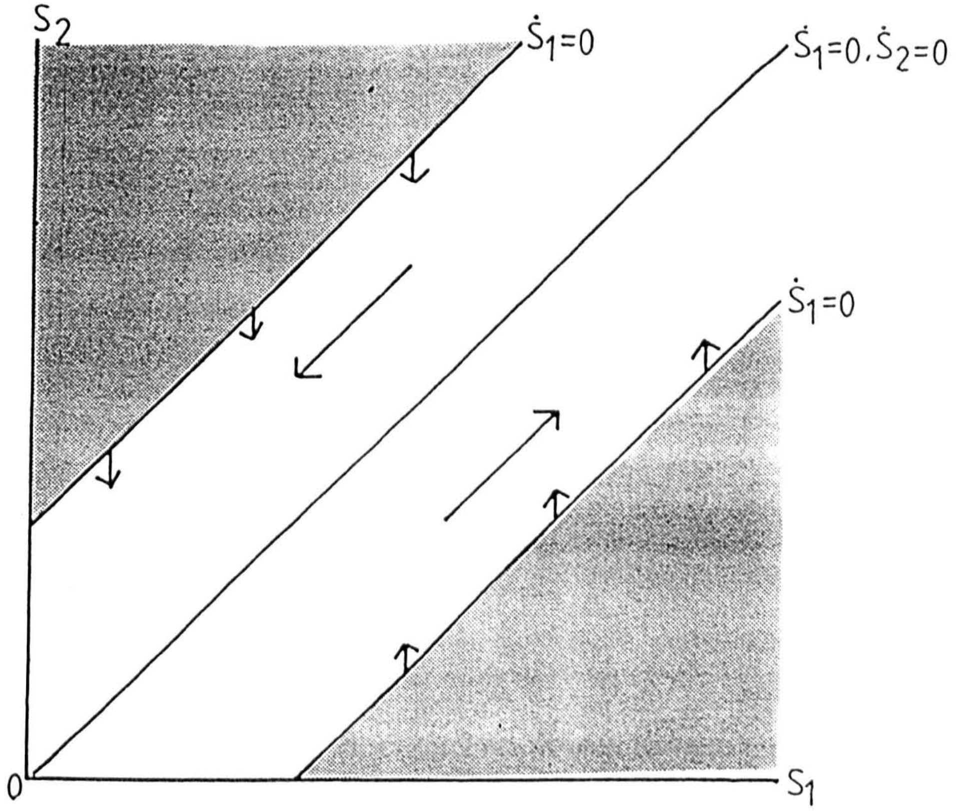


Figure 2.3. Dynamical system for investment in predatory and anti-predator traits when $\rho = s_2 - s_1$. $\theta_{12} = \theta_{21}$, and hatched areas are zones where only boundary equilibria for investment occur. The dynamics are indicated by arrows on the investment plane.

equilibria in trait space, the direction of evolution of investment in predator and prey is such as to move the trait variables values away from that boundary. It appears that natural selection acts to promote the coexistence of predator and prey, even in the absence of evolutionary stability.

These results are intriguing, firstly since it is so often assumed that persistence over ecological time will require ecological stability (for example, Lawton 1989), and where natural selection is introduced, ecological stability will depend upon evolutionary stability. The second result is of interest since we have no *a priori* reason to expect this, apart from the evidence of observation and the fossil record in documenting the coexistence of particular predator and prey pairs over periods of time consistent with evolutionary change.

Many different definitions (and terms) for evolutionarily stable states (Maynard Smith 1982) in interacting species and/or biological communities have been used (coevolutionary steady state, Schaffer & Rosenzweig 1978; coevolutionarily stable community, Roughgarden 1979; ecologically and evolutionarily stable community, Stenseth 1983; coevolutionary ecological system, Vasco *et al.* 1987; coevolutionarily stable community, Matsuda & Namba 1991; see also Lawlor & Maynard Smith 1976; Reed & Stenseth 1984; Stenseth & Maynard Smith 1984). We have attempted to consider explicitly selective features of the predator-prey interaction, while retaining the conventional Lotka-Volterra dynamics for predator and prey. We suggest that the rarity of ESSs in our model may be due to our attempt to link directly the consideration of the interaction of ecological and evolutionary change to the Lotka-Volterra population models, and to consider explicitly the conflict of interests between predator and prey (Dawkins & Krebs 1979).

The lack of evolutionarily stable states may depend partly upon our choice of global and local asymptotic stability. Global asymptotic stability is an extreme case, the strongest stability condition one could obtain, so it is perhaps unsurprising that conditions for its occurrence are violated so easily, in systems more general than the ones considered here. We may expect that global asymptotic stability will occur only rarely. The same cannot be said for local asymptotic stability however, which refers only to a very small region of the phase space. The lack of locally asymptotically stable critical points in the predator-prey investment space under natural selection may be a better indicator of instability resulting from evolution. But the relationship between local and global stability is unclear, indeed undefined and unknown, so lack of local asymptotic stability does not preclude stability in some global sense.

In the analysis above differential equations framed in continuous time have been used, since they are more tractable in this form than the corresponding difference equations. But population dynamics, dealing with discrete individuals, suggests modelling by a discrete process. We have used the Lotka-Volterra equations for population dynamics due to their known tractability and proven record of application to biological problems (see for example, Hofbauer & Sigmund 1988). The Lotka-Volterra equations in discrete time are less "well behaved" than the continuous time forms, and less is known about their properties. It is clear that in an ideal world, where any required mathematical system could be solved explicitly, some sort of more complicated difference equation would be used to model population dynamics of interacting populations, including all the factors that are so conveniently ignored in much of mathematical biology. In the real world such equations which could be written down are completely intractable, and thus defeat the object of our analysis. Despite their well-known simplification, Lotka-Volterra equations for population dynamics have been used to generate testable hypotheses about real populations in nature, thus it is reasonable that their properties under natural selection should be analysed as preliminary steps to understanding the effects of selection on the dynamics of natural populations.

It may be that models of predator-prey coevolution are in fact over-simplified. The non-existence of many potential predator-prey interactions can be seen to arise from other constraints on adaptation (such as potential predator and prey occupying different habitats). It could be that predator-prey coevolution does not occur very often, and thus has little effect on population dynamics and trophic structure (Vermeij 1982). A very detailed study of the coevolution of ungulates and their vertebrate predators (Bakker 1983) showed that coevolutionary change was in fact very irregular, with long periods of stasis and some periods when the predators were becoming less, rather than more, adapted to pursuing their prey. Nevertheless experimental evidence does exist for the coevolution of predators and prey (Taylor 1984: chapter 11).

An alternative explanation consistent with the models used here is that ecological instability is not a consequence of evolutionary instability. A wide range of models have been put forward to explain why predator-prey coevolution should lead to stability rather than mutual extinction (Pimentel 1961; Rosenzweig 1973; Slobodkin 1974; Gilpin 1975b; Schaffer & Rosenzweig 1978; Roughgarden 1983). Others have suggested that continual change in the form of an 'arms race' (Dawkins & Krebs 1979) is more likely, although the arms race analogy is thought by some to be too simplistic (Abrams 1986a, b, 1990).

It may be that tightly coupled predator-prey interactions are in fact much less important in nature than their utility in theoretical models would lead us to believe. Detailed studies of food web interactions have shown that some predators which utilize particular prey species as a large proportion of their diet may have little if any effect on the prey's population dynamics (Hall *et al.* 1990a, b). On the other hand this conclusion is not general for all predator-prey interactions; it is easy to find examples where the reverse is true (Taylor 1984). Paine (1980) has suggested that most interactions in food webs may be very weak, with only a few strong ones. Even if this is so, the existence of an optimal level of investment for the predator at which the interaction is more intense (in terms of effects on population dynamics) than at any other level, even if very weak, will still satisfy the assumptions of our models based on log concave functions. It is certainly true that many predators take more than one species of prey, but this does not prevent them having significant effects on the population dynamics of each prey species. Much of population ecological theory is built upon two-species models, despite the existence of many n-species interactions in nature. These models have generated a large number of testable hypotheses and insights about nature which vindicates their use, despite their simplicity.

There is also the possibility that population dynamics may be less important in structuring interspecific interactions than other features of the interacting species, such as their body size. The static, cascade, model of Cohen and co-workers (Cohen *et al.* 1990a) can explain a number of common features of trophic webs by reference to a trophic hierarchy, such that species in the hierarchy are only fed upon by those above them in the hierarchy, and are only predators of those below them in the hierarchy. Warren and Lawton (1987) have suggested that differences in body size may provide the trophic hierarchy. In addition Cohen and Newman (1988) propose that communities at the frontier of stability will show characteristics similar to those found in nature. There is little observational support for this model apart from its explanation of regularities in food webs, but if it were found to be of prime importance in the regulation of predator-prey interactions in food webs, then we might not require an explanation of why evolution of Lotka-Volterra parameters leads to instability. Despite the advances that have been made in recent years in documenting regularities in food web features (Lawton & Warren 1988), with empirical data from food webs in its current state (Cohen *et al.* 1990a chapter IV), a role for population dynamics in structuring interactions in food webs, probably in some pluralistic explanation (Cohen *et al.* 1990b attempt this), must be considered.

We have shown that instability as referred to in the title does not refer to both evolutionary and ecological stability. Evolutionary stability is seen to be precluded in many cases by the conflicting interests of predator and prey, perhaps in some form of continual "arms-race" or Red Queen (Van Valen

1973) coevolution. Due to the greater complexity of multiple species systems with greater than two species, we have no reason to suspect that evolutionarily stability will be any more likely in more realistic models of trophic interactions.

Fortunately our second conclusion implies the decoupling of ecological stability from evolutionary stability. Our use of Harrison's (1979) result on the stability of simple food chains, means that we can infer stability merely from the existence of an interior equilibrium, and we have shown that such an equilibrium will be selected for under natural selection. This result is consistent with observations of genetic variation and genetic change in natural populations. Evolutionary effects can no longer be isolated from population dynamics, and the models described here are a contribution towards the development of a theory of evolutionary ecology which promises to generate more realistic predictions about the dynamics of natural populations under selection. In this paper, we have only considered populations at ecological equilibrium; future models will require the consideration of cyclic and chaotic dynamics. Techniques recently developed may enable this (Ellner *et al.* 1991; Godfray *et al.* 1992).

Chapter 3. COEVOLUTIONARY DYNAMICS OF PREDATOR-PREY INTERACTIONS

> "Well, in *our* country," said Alice, still panting a little, "you'd generally get to somewhere else-- if you ran very fast for a long time, as we've been doing."
> "A slow sort of country!" said the Queen. "Now, *here*, you see, it takes all the running *you* can do, to keep in the same place. If you want to get somewhere else, you must run at least twice as fast as that."
>
> Lewis Carroll, *Alice through the looking-glass*

3.1 SUMMARY

I examine predator-prey coevolution under density-dependent selection through a model derived from the Lotka-Volterra equations for predator and prey, where I introduce a haploid genetic system. The traits under selection are the body sizes of predator and prey, and I present a numerical method for examining the dynamics of coevolution across the phenotype space generated by the combination of predator and prey traits. I identify several qualitatively different types of coevolutionary dynamics that occur, including evolutionarily stable states (ESSs) and Red Queen coevolution. The results of this model show that the loser at the ecological level (the prey) is often the primary determinant of the coevolutionary process. They also show that the view of evolution as climbing the peaks of an adaptive landscape is misleading as we model an adaptive hill-climbing process on a flat adaptive landscape. Coevolutionary maximisation of population density is also not supported by this model.

3.2 INTRODUCTION

The integration of population dynamics and population genetics is a fundamental goal of evolutionary theory. Evolution, considered purely as change in gene frequencies can be considered solely by the use of population genetics theory, but this ignores the rich variety of phenomena that can arise when change in gene frequency is dependent in some way upon population density (e.g. Roughgarden 1979).

A number of studies have addressed this problem by using simple population genetical models, combined with simple population ecological or epidemiological models of population dynamics (Levin 1978; Roughgarden 1979; May & Anderson 1983a; Jayakar 1984, for example). However such models become intractable when extensions to more complex genetics or population dynamics are considered. Alternatively, the complexities that arise in manipulating population genetical equations have been avoided by using phenotype-based evolutionarily stable strategy models (ESSs; Maynard Smith & Price 1973; Maynard Smith 1982) taking into account population size (Knowlton & Parker 1979; Parker & Knowlton 1980; Parker 1983, 1985; Brown & Vincent 1987a, b). The use of ESS techniques, although very effective in many contexts, does not give any information about the dynamics of evolutionary change away from evolutionary equilibrium. Especially in the context of interspecific interactions, where one might expect complex coevolutionary change, it would be desirable to have this information.

In a previous paper (Marrow & Cannings 1992; Chapter 2, this thesis), I developed a model which incorporated a simple haploid genetic system into a Lotka-Volterra predator-prey system. I assumed that natural selection would act upon predatory and anti-predator traits in each species in an 'arms race' (Dawkins & Krebs 1979) interaction. By specifying the relationship between the genotype of each species and the Lotka-Volterra interaction terms in a general way, it was possible to describe the coevolutionary dynamics of evolution in the predator-prey phenotype space. I used a technique of differentiating fitness functions with respect to predator or prey phenotypes. This method, while working well with general functions, could not always be used to generate explicit solutions with more specific forms of the relationship between Lotka-Volterra interaction term and phenotype. Ideally, to better understand the coevolutionary dynamics of interspecific relationships, it would be appropriate to use a technique which was applicable to a wide range of more specific functions.

In this study, I introduce a technique, following on from previous work (Chapter 2; Marrow & Cannings 1992) and the work of Brown and Vincent (1987a, b), which, through a simple numerical method, can be used to characterise the coevolutionary dynamics of a predator- prey interaction. I examine the results of this method for a range of functions relating genotype to Lotka-Volterra interaction. I identify several kinds of qualitatively different evolutionary dynamics that are found in the system. Approaches to a more general understanding of the coevolutionary dynamics of the system are outlined.

3.3 METHOD

The evolutionary model that I use includes population dynamics of Lotka-Volterra form,

$$\frac{dx_i}{dt} = x_i(r_i + \sum_{j=1}^{2} \alpha_{ij} x_j), \qquad (3.1)$$

(where x_i is the population density of species i, r_i is the intrinsic growth rate and α_{ij} is the interaction coefficient defining species j's effect on species i). I consider only predator prey systems so i and j can only take the values 1 or 2.

When genetic variation is present the per capita rate of increase will give a measure of the fitness of a genotype. In recognition of this, I will write the per capita rate of increase as W_i and the equations for population dynamics as

$$\frac{dx_i}{dt}=x_iW_i \tag{3.2}$$

so the fitness functions of predator and prey, where W_i is the mean individual fitness of species i, become

$$\begin{aligned} W_1&=r_1+\alpha_{11}x_1+\alpha_{12}x_2,\\ W_2&=r_2+\alpha_{21}x_1, \end{aligned} \tag{3.3}$$

where α_{11} and α_{12} are negative variables, α_{21} is a positive variable, and r_1 is a positive and r_2 a negative constant.

Utilising a result of Harrison (1979), we know that any feasible interior equilibrium for population dynamics in the predator-prey system must be globally asymptotically stable. Assuming that such a feasible equilibrium occurs, we can then consider the evolution of the system at an ecological equilibrium, as all trajectories starting with both species present in the population dynamical phase space will converge to it. At the equilibrium W_i = 0.

In order to examine the consequences of evolution in predator and prey I introduce a phenotypic variable s_i, which represents body size. The evolution of body sizes has been investigated previously by Maynard Smith and Brown (1986), and Mirmirani and Oster (1978), in different contexts. Body size is likely to have a significant effect on predator-prey interactions (Hespenheide 1973; Vézina 1985; Warren & Lawton 1987), so we can make the interaction terms in the Lotka-Volterra equations functions of the body sizes s_1, s_2, of the interacting individuals, i.e.

$$\alpha_{ij} = F_{ij}(s_i, s_j), \tag{3.4}$$

What form F_{ij} will take is very important. To make F_{ij} reasonably general, I assume that the predator effect on prey (α_{12}) and prey effect on predator (α_{21}) are defined by bell-shaped functions of s_1 and s_2. So we have

$$F_{12} = -p_1 \exp\left(-\left[\delta_1^2 - 2p_2\delta_1\delta_2 + \delta_2^2\right]\right), \tag{3.5}$$

where

$$\delta_1 = (s_1 - p_3)/p_4, \quad \delta_2 = (s_2 - p_5)/p_6,$$

and

$$F_{21} = p_7 \exp\left(-\left[\delta_3^2 - 2p_8\delta_3\delta_4 + \delta_4^2\right]\right), \tag{3.6}$$

where

$$\delta_4 = (s_2 - p_9)/p_{10}, \quad \delta_3 = (s_1 - p_{11})/p_{12}.$$

p_1 to p_{12} are constants. p_3, p_5, p_9, and p_{11} affect the positions of the peaks of the bell-shaped distributions, while p_4, p_6, p_{10} and p_{12} modify the degree of spread of the functions. p_2 and p_8 define a cross-product term similar to the correlation between predator and prey effects. p_1 and p_7 modify the height of the α_{21}, or the trough of the α_{12} function respectively: these parameters control the height of the peaks of the bell-shaped functions. Contrast them with p_3, p_5, p_9, and p_{11}, which control the location of the peaks of these functions in the phenotype space. Note that although the functions defining α_{12} and α_{21} the two reciprocal interaction terms for the predator-prey interaction, are parameterised in a similar fashion, this does not restrict them to be exact mirror images.

The coefficient of density-dependence or self-limitation in the prey, α_{11}, is defined in a simpler fashion, intending to reflect its dependence on body size in the prey only. I define it as

$$F_{11} = -(p_{13} - p_{14}s_1 + p_{15}s_1^2). \tag{3.7}$$

p_{13}, p_{14} and p_{15} may take any values such that $F_{11} < 0$.

I wish to describe the evolution of the body size of predator and prey. To do this I shall introduce the concept of the phenotype space. This is a space defined by the body size value of the prey (s_1) and the body size value of the predator (s_2). Evolution will result in changes in these values, and so evolutionary change can be thought of as movement in the phenotype space. If no evolutionary change occurs, for example at an ESS (evolutionarily stable strategy), the results of evolution will be represented by a point. I look at evolution in this way in attempt to describe the evolutionary dynamics away from evolutionarily stable points, rather than just locate those ESSs that may or may not occur.

Note that the phenotype space is *not* a phase space, as it is not defined by the state variables of a continuous dynamical system. I have already introduced a phase space for the dynamical system representing the population dynamics of predator and prey. Movement in the phenotype space occurs in small, but discrete steps, through mutation and fixation of mutants of different body sizes. Although I shall refer to paths or trajectories on the phenotype space, these are not continuous paths as in a dynamical system, but are made of many small discrete changes in the combined phenotypes of predator and prey.

In order to determine the direction of the evolutionary dynamics, we consider the consequences of the invasions of mutants of small effects on the body sizes of predator and prey. Before mutation, suppose that the body size of the prey is s_1 and of the predator s_2. Mutants will have different body sizes, $s_1 + \varepsilon_2$, $s_2 + \varepsilon_2$, where ε_i is small, from the original populations, and these will result in altered interaction terms,

$$\begin{aligned} \alpha'_{11} &= F_{11}(s_1+\varepsilon_1), \\ \alpha'_{12} &= F_{12}(s_1+\varepsilon_1,s_2), \\ \alpha'_{21} &= F_{21}(s_1,s_2+\varepsilon_2). \end{aligned} \tag{3.8}$$

The mutant individuals are assumed to arise in a population at equilibrium for the current body sizes s_1, s_2, $(\hat{x}_1, \hat{x}_2)$, and so the mutation event can be considered to take place at these equilibrium densities. So the equations for fitness of the mutants, W_1', W_2', can be written as

$$\begin{aligned} W_1' &= r_1 + F_{11}(s_1+\varepsilon_1)\hat{x}_1 + F_{12}(s_1+\varepsilon_1,s_2)\hat{x}_2, \\ W_2' &= r_2 + F_{21}(s_1,s_2+\varepsilon_2)\hat{x}_1, \end{aligned} \tag{3.9}$$

and these will be unlikely to be equal to zero, for most values of s_i. In the early stages following mutation I am assuming that a mutant is much less likely to interact with another mutant than with one of the original types. By definition, the fitnesses of the original types are $W_1 = 0$, $W_2 = 0$ at $\hat{x}_1$, $\hat{x}_2$. I assume that the effect of each mutant on body size, ε_i, is sufficiently small that the effect on fitness is linear. If W_i' is greater than zero, then this implies that a larger mutant will be able to invade, while if W_i' is less than zero, then the opposite will be true, and a smaller mutant will be able to invade. The direction of selection at any point will be the direction in which selection is expected to alter body size with respect to predator and prey simultaneously. This is equivalent to evaluating the partial derivative of W_i with respect to s_i at a point in the phenotype space. If the evaluation of fitness functions is repeated for a grid of points over all of the phenotype space, then a picture of the dynamics globally can be built up, even though information is only available about local consequences of selection.

In order to predict the direction of evolution, we must be sure that any invading mutant will go to fixation, rather than forming a polymorphism with the ancestral population. In order to determine whether this is so, we must examine the four-dimensional system created by mutants invading in predator and prey.

A sufficient condition for mutants to go to fixation is given by the following (R. Law, *pers. comm.*).

(1) ·No equilibria occur at which more than one type of prey or more than one type of predator have non-zero densities.

(2) The only strictly saturated equilibrium (Hofbauer 1988) is the one in which only the two mutant types are present. That is, the per capita rates of increase of the missing types (in this case the original types of predator and prey) are negative. This corresponds to the equilibrium being non-invadable.

To visualise the coevolutionary dynamics in terms of motion on the phenotype space, we developed programs which calculated the fitnesses under mutant invasion for a grid of points over the space, and then plotted out the resulting direction of selection at each point, which could be predicted from the fitness values. The programs were written independently in C (by Richard Law) on a Sun SparcStation, and in Pascal (by Paul Marrow) on a VAX 8650/8550 Cluster. We took the similar results from the two programs as one verification of the techniques we used, and which I present here.

Numerical evaluation of the population dynamics was also used to check on the results of the program. We (R.L. and P.M.) used numerical integration routines from the NAG library (NAG Ltd., 1990) to evaluate the dynamics of the mutant, invading at a low density, when both the original populations of predator and prey were set to their equilibrium densities. The interaction terms for the original populations were calculated using a particular pair of sizes, s_i, chosen to occur within one of the five possible regions of dynamics possible on the phenotype space. We then introduced mutants with slightly different s_i at low densities, and observed if they increased or decreased in accordance with the predictions of the technique described above. That this did in fact occur supported the use of the numerical method.

3.4 EVOLUTIONARY DYNAMICS IN THE PHENOTYPE SPACE

Consider first a predator-prey system in which the prey self-limitation, α_{11}, is set to a constant. So p_{13} is a positive constant and p_{14} and p_{15} are zero. In this system we define the predator effect on prey and prey effect on predator to be related to predator and prey body size by two bell-shaped functions, inverted in the case of the predator effect on prey. For simplicity we assume that what is best for the predator is worst for the prey, and vice versa. This means that the maximum value of α_{21}, the prey effect on predator, corresponds to the minimum value of α_{12}, the predator effect on prey. In this case we also make the degree of spread of the two functions defining the predator-prey interactions the same. We keep the parameters affecting the cross product term between predator and prey interactions positive. Figure 3.1 shows a specific case of this.

We can divide up the phenotype space into regions where the predator and prey body sizes will evolve in different directions by identifying the lines where $\partial W_i/\partial s_i = 0$. On these lines selection on one of the species' body size will be zero, hence I shall term them "lines of zero selection". I use this term in order to distinguish them from zero isoclines in a phase space.

In the outer region the equilibrium value of the predator density would be negative. So we say that the predator equilibrium is not feasible and the predator cannot coexist with the prey in this region of the phenotype space. In the central region, the predator and prey coexist. Since we wish to consider the consequences of predator-prey coevolution, it is this central portion that we must concentrate upon. Inside this region evolution moves the body sizes

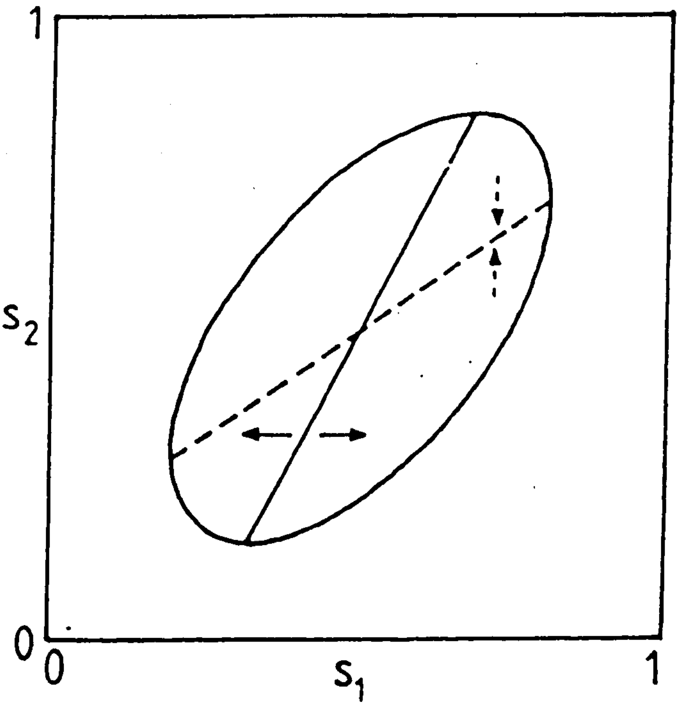


Figure 3.1. A phenotype space for body sizes s_1 and s_2 of prey and predator respectively, when prey self-limitation is constant. Inside the elliptical region the predator can coexist with the prey; outside it cannot. Lines on the phenotype space represent lines of zero evolution in predator or prey. Arrows represent the expected direction of evolution of phenotypes under selection. In this case only one unstable evolutionary equilibrium occurs. Parameters are as follows; $r_1 = 0.5$, $r_2 = -0.05$, $p_1 = 1.0$, $p_2 = 0.6$, $p_3 = 0.5$, $p_4 = 0.22$, $p_5 = 0.5$, $p_6 = 0.25$, $p_7 = 1.0$, $p_8 = 0.6$, $p_9 = 0.5$, $p_{10} = 0.22$, $p_{11} = 0.5$, $p_{12} = 0.25$, $p_{13} = 3.0$, $p_{14} = 0.0$, $p_{15} = 0.0$, $\varepsilon_1 = 0.001$, $\varepsilon_2 = 0.001$.

towards two extremes, at which the predator is on the edge of extinction. Outside the region, mutants in the prey are selectively neutral, and no evolution occurs. This system is similar to the one discussed in the previous chapter (Marrow & Cannings 1992), in which the self-limitation term was held constant, while α_{12} and α_{21} were allowed to evolve. However, in that case, selection acted to move the coevolving traits away from the zone of predator extinction, while here evolution moves body size values to the edge of that zone. The difference between the two systems is a consequence of the more complicated functions used to define α_{21} and α_{12} in the latter model. This implies that the maintenance of coexisting predator and prey populations through selection on body sizes is not very robust to change of model parameters; but the example discussed above represents only one class of qualitative dynamics observed in this system, and it will become clear that evolutionarily stable points can arise at other points in the region of coexistence.

The biological consequences of this example are perhaps a little unexpected; it suggests that coevolution of predator and prey should lead nearly to predator extinction in all cases, and if such extinction occurs then selection should halt. How robust is this result? Could it not be the case that the intensity of the predator-prey interaction decreases much more slowly moving away from the maximum (or minimum for prey) for each interaction term? This would mean that the parameters controlling the degree of spread of the bell-shaped functions would be much larger, and result in the zone of predator-prey coexistence being larger. This is conceivable, but what is also likely is that there are combinations of predator and prey traits where the predator and prey are so different that they are almost or entirely unable to interact. This would result in very low values for α_{ij}, the interaction terms. This is what is represented in the region around the edges of the phenotype space in Figure 3.1.

Whether or not the predator and prey coexist over all the phenotype space, our conclusions about the evolutionary dynamics inside the zone of predator-prey coexistence are the same. There are two points to which evolutionary pathways from within the zone of coexistence tend to, on the edges of the zone of coexistence. However as phenotypic values approach these points, we expect evolutionary change to slow, as successive mutants have less effect on the per capita rate of increase of each species. In the limit, infinitesimally close to either point, evolutionary change should proceed infinitesimally slowly. So these are not evolutionary attractors. The only equilibrium point inside the zone is an unstable evolutionary saddle point. That is to say, evolutionary paths in one species approach it, while in the other species they move away from it (by analogy with the saddle point of dynamical systems). No evolutionarily stable points occur. This type of evolutionary dynamics is qualitatively very robust, but are there cases when evolutionarily stable attractors can occur, leading to the possibility of evolutionarily stable states?

The symmetrical diagram on the phenotype space given in Figure 3.1 is in part a consequence of the constant prey self-limitation. Making α_{11} defined by a quadratic function with a peak at a value of s_1 outside the zone of coexistence (so it is monotonic over the zone of coexistence), enforces an asymmetry between the predator and prey. In Figure 3.2 the results of this are shown. The parameters defining the interaction between predator and prey are identical. Yet the evolutionary dynamics on the region where predator and prey coexist is very different.

Within this region the line where selection on prey size is zero is no longer straight, but has looped in on itself to form a region within the larger zone defining the coexistence of the two species. Selection on predator size is not affected by the modified self-limitation term, and so the direction of predator coevolution within the ellipse is still given by a straight line. The intersection of the line and the ellipse means that another evolutionary equilibrium point arises in the system. This is not a saddle point but an attractor. The successive replacement of predator and prey mutants with combinations of body

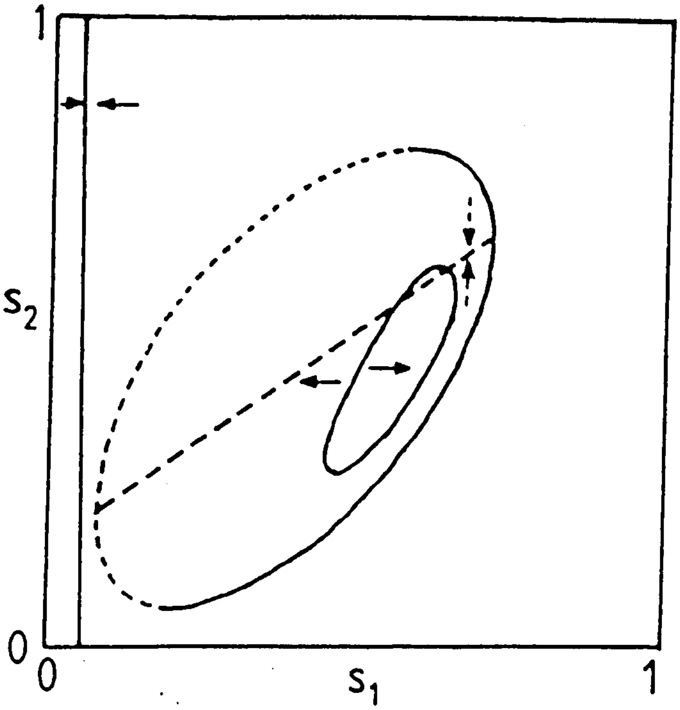


Figure 3.2. A phenotype space for the body sizes of predator and prey (s_1 and s_2 respectively), with prey self-limitation linear monotonic in the region of predator-prey coexistence. The lines on the phenotype space divide up regions where different combinations of large or small mutants in predator and prey are expected to invade. The arrows denote the expected direction of evolution of predator and prey size within each region. The predator has a negative equilibrium density outside the larger elliptical region and is thus assumed to have gone extinct in this region. In this example α_{11} the prey self-limitation is monotonic across the zone of predator-prey coexistence, and one evolutionary attractor occurs. The parameter set for this example is; r_1 = 0.5, r_2 = -0.05, p_1 = 1.0, p_2 = 0.6, p_3 = 0.5, p_4 = 0.22, p_5 = 0.5, p_6 = 0.25, p_7 = 1.0, p_8 = 0.6, p_9 = 0.5, p_{10} = 0.22, p_{11} = 0.5, p_{12} = 0.25, p_{13} = 1.0, p_{14} = -1.0, p_{15} = 10.0, ε_1 = 0.001, ε_2 = 0.001.

sizes near to this equilibrium will tend to approach it. Once at the attractor, if either predator or prey body size is perturbed from it, selection will return the body size to it. This attractor thus appears to satisfy the two conditions for an ESS (Hofbauer & Sigmund 1988:121).

In the phenotype space overall, there appear to be two possible outcomes of coevolution. Within part of the elliptical region of coexistence of predator and prey, body sizes are attracted towards an evolutionarily stable point. Elsewhere selection attracts predator body size to a point on the margin of the zone of coexistence where the predator becomes extinct; selection then drives the prey body size over the boundary of the region, so that the predator becomes extinct.

The existence of an ESS lends support to the empirical observation that predator and prey manage to coexist and coevolve for long periods of time. However this does depend on the self-limitation in the prey which results in somewhat artificial consequences when the predator is absent: the prey is selected to shrink down to very small size. A more realistic assumption would be that the prey body size is selected to some intermediate value, and this motivates the third example, shown in Figure 3.3. α_{11} here is dependent upon s_1, the prey body size, through a quadratic function with a peak at an intermediate value of s_1. In the absence of the predator, selection moves prey size to this maximum.

This has unexpected consequences for the evolutionary dynamics when predator and prey are both present. The more complicated self-limitation function means that the line separating the different directions of selection in the prey loops back on itself and intersects the line of zero evolution in the predator three times. One evolutionary equilibrium is the saddle point previously observed, and the other two are both evolutionary attractors. Within the zone of predator-prey coexistence most evolutionary trajectories lead to an evolutionarily stable state. In portions of the zone of coexistence

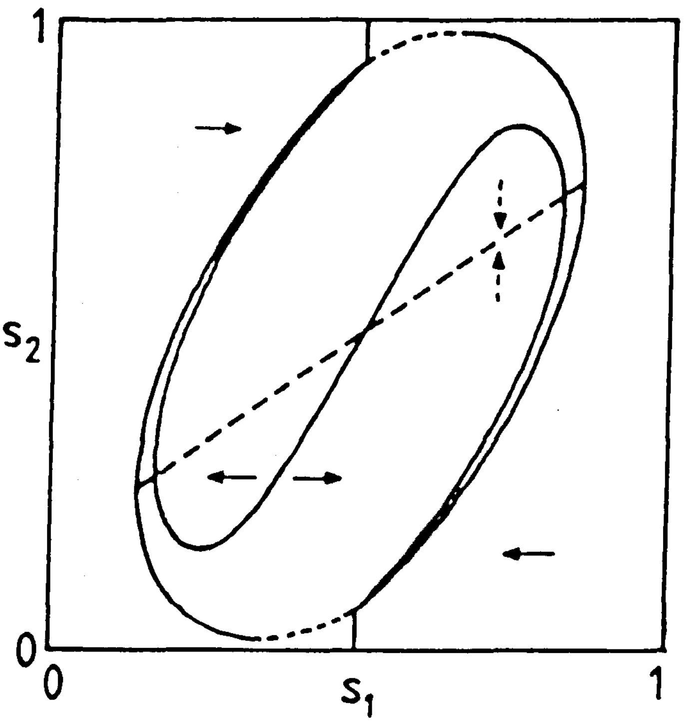


Figure 3.3. A phenotype space for predator and prey body size (s_1 and s_2 respectively), showing the occurrence of multiple ESSs. The lines on the phenotype space divide it up into regions where different coevolutionary dynamics are expected: the arrows within each region denote these dynamics. Three evolutionary equilibria are found within the zone of predator-prey coexistence; the central one is a saddle and the other two are evolutionary attractors. In this case the prey self-limitation term (α_{11}) is a quadratic function with a peak at $s_1 = 0.5$. The parameters of this example are; $r_1 = 0.5$, $r_2 = -0.05$, $p_1 = 1.0$, $p_2 = 0.6$, $p_3 = 0.5$, $p_4 = 0.22$, $p_5 = 0.5$, $p_6 = 0.25$, $p_7 = 1.0$, $p_8 = 0.6$, $p_9 = 0.5$, $p_{10} = 0.22$, $p_{11} = 0.5$, $p_{12} = 0.25$, $p_{13} = 3.0$, $p_{14} = -10.0$, $p_{15} = 10.0$, $\varepsilon_1 = 0.001$, $\varepsilon_2 = 0.001$.

near the maximum or minimum for s_2 prey mutants can invade that will take the combination of predator and prey sizes over the boundary of the zone. In the absence of the predator, the prey is selected to an intermediate body size.

The results presented so far support the prediction of evolutionary stasis in coevolving interacting populations (Stenseth & Maynard Smith 1984; Rosenzweig *et al.* 1987). However Red Queen coevolution (after Van Valen 1973), that is continual coevolutionary change, does not seem to occur. We obtain either evolutionarily stable states where predator and prey coexist, or the prey goes to an evolutionarily stable body size in the absence of the predator. Although this latter case could be called an ESS, it is of little interest since coevolution does not occur in the absence of the predator. The three types of coevolutionary dynamics presented so far are specimens of three broad classes of qualitatively different results that the ensemble of model systems exhibits, and are relatively robust to perturbation of parameters. Is there any opportunity in this model for Red Queen coevolution to arise?

For Red Queen coevolution to occur we require that there are no evolutionary attractors within the elliptical space of coexistence of predator and prey, and that there be no escape from the region of coexistence. If we allow the weaker case where continual evolutionary change occurs only for a limited time, then we can omit the latter condition. The evolutionary attractors shown in Figures 3.2 and 3.3 arise from the intersection of the curved line of no selection in the prey with the straight line of no selection in the predator. If the line of zero selection in the prey only intersected the zero selection line for the predator at one point, then it is possible that cyclic dynamics might occur.

If we assume that the magnitude of the benefit to the predator is restricted, so that the value of the maximum of the α_{21} function is reduced, but its shape is not otherwise changed, then we obtain the situation shown in Figure 3.4. The line on which selection on prey size is zero has been rotated, so that it now only intersects with the line of no selection in the predator at one point, an evolutionary saddle point. The coevolutionary dynamics within the ellipse of

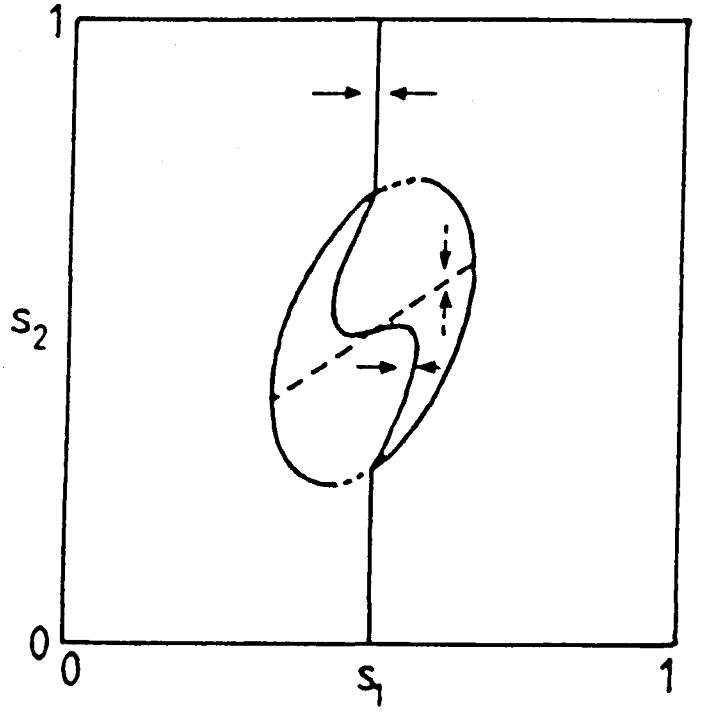


Figure 3.4. A phenotype space for the coevolution of predator (s_2) and prey (s_1) body size, showing the occurrence of Red Queen coevolution. The phenotype space is divided up into regions where different mutants of the predator and prey are expected to invade. The arrows denote the direction of evolution within each region. In this case only one evolutionary equilibrium occurs within the zone of predator-prey coexistence, and continuous coevolutionary change (Red Queen coevolution) occurs around it. The parameter set for this example is; $r_1 = 0.5$, $r_2 = -0.05$, $p_1 = 1.0$, $p_2 = 0.6$, $p_3 = 0.5$, $p_4 = 0.22$, $p_5 = 0.5$, $p_6 = 0.25$, $p_7 = 0.11$, $p_8 = 0.6$, $p_9 = 0.5$, $p_{10} = 0.22$, $p_{11} = 0.5$, $p_{12} = 0.25$, $p_{13} = 3.0$, $p_{14} = -10.0$, $p_{15} = 10.0$, $\varepsilon_1 = 0.001$, $\varepsilon_2 = 0.001$.

coexistence cycle around the saddle point, with most trajectories remaining within the region of coexistence and thus satisfying the conditions for Red Queen coevolution.

A few combinations of sizes can result in trajectories which leave the ellipse near the maximum or minimum for predator size, and thus cause predator extinction and the prey to move to an evolutionarily stable intermediate size. However the observation that Red Queen coevolution can occur in part of the phenotype space is stronger support for the idea than some other theoretical approaches have given (Stenseth & Maynard Smith 1984; Rosenzweig *et al.* 1987).

3.5 DISCUSSION

The antagonistic interaction between predator and prey has often been characterised in terms of an evolutionary "arms race" (Dawkins & Krebs 1979). This implies that an evolutionary (positive) feedback operates, such that increase in one trait in the predator affecting predation ability is balanced by a corresponding increase in a trait affecting anti-predator defence in the prey. Despite conflicting opinions (Abrams 1986a, b; Thompson 1986) this analogy seems to have a good intuitive basis, although only limited experimental support (Vermeij & Covitch 1978; Vermeij 1982, 1983; Bakker 1983; Stanley *et al.* 1983; West *et al.* 1991).

The model I have presented here could be regarded as an arms race model- although I do not suggest that a direct positive feedback may be operating all the time, merely that there is some feedback (positive or negative), such that change in size of one species will have coevolutionary consequences resulting in a change in size in the other. If it is considered as an arms race model, there can be no clear prediction about what result we should expect.

One might expect arms race coevolution to result in continual evolutionary change in each species, as each evolved a more effective adaptation which was then countered by the other species; this might correspond to Red Queen coevolution (Stenseth & Maynard Smith 1984; after Van Valen 1973). But such an outcome might be considered unrealistic as no organisms are likely to possess unlimited genetic variation for characters affecting predator-prey interactions, and in any case, a cost to adaptation might occur, resulting in reduced adaptiveness with respect to some other characters. So the outcome might be evolutionary stasis, or an evolutionarily stable state, as coevolution was halted by counter-selection.

The dichotomy between continuous evolutionary change and evolutionary stasis has been the motivation behind a number of theoretical studies (Stenseth & Maynard Smith 1984; Rosenzweig *et al.* 1987) of coevolution in interacting species, often competition communities, which have failed to resolve the question of which type of evolutionary outcome should result. The results presented here seem to suggest that both outcomes are possible.

Evolutionarily stable states occur robustly when predator and prey coevolve, and they attract most combinations of predator and prey size that are compatible with coexistence. A small number of combinations of predator and prey sizes may lead to predator extinction and evolution of the prey alone, but these do not affect the conclusions greatly: that all combinations of predator and prey are not compatible is clear from experimental and field observations.

Red Queen coevolution occurs under rather more restricted conditions: we have to limit the magnitude of the benefit the predator obtains from predation, not in itself too ecologically unreasonable, when inefficient conversion of energy and metabolism is taken into account. In addition we cannot make the maximum of α_{21} too small, since this would result in the predator being unable to live on the prey.

The lack of robustness of Red Queen coevolution with regard to model parameters in comparison to evolutionarily stable states is not surprising: for Red Queen coevolution the former must not occur, and yet there must be a special sort of dynamics in the zone of coexistence which prevents evolutionary trajectories leading to predator extinction.

The status of Red Queen coevolution has been in doubt since the discovery that it might only occur for unbounded phenotypic traits able to evolve to ever more extreme values (Rosenzweig *et al.* 1987). But the traits here are bounded in the sense that they only allow coexistence of the predator and prey within a limited region of the phenotype space. That we should find a Red Queen dynamic in so simple a model (arguably one of the simplest possible coevolutionary systems) suggests that such behaviour could occur readily in the more complex systems of the real world. It would seem that it is not necessary to invoke changes in the abiotic environment to provide a continuing driving force for evolution; interactions between the organisms are in themselves sufficient. This is not to deny the role of abiotic causes of evolution -- just to point out that they may not be essential. More complex multi-species models of coevolution may be required to further distinguish the two outcomes, particularly as experimental or data-based approaches to the problem may be unable to prove or disprove the existence of Red Queen coevolution as it is not possible to obtain accurate data on the intensity of selection (Hoffman 1991).

An additional curious feature of coevolution of predator and prey is that the loser at the ecological level (i.e. the prey) is often the primary determinant of evolution of the system. It might be said that the most advantageous position in phenotype space from the point of view of the predator would be at the maximum of the bell-shaped function defining α_{21} since it is here that the individual predator gains most from its prey. But this is also the worst position for the individual prey, and there is no way that evolution can tend to this point because any prey mutant with a different body size will invade and replace it. As the system evolves, the body sizes move away from the maximum of α_{21}, to a region where the interaction between predator and prey is at most weak. Such a property has been observed in the evolution of life histories under predation; evolution in the prey brings about a lower reproductive value at life stages of high mortality (Slobodkin 1974; Michod 1979; Edley & Law 1988), thereby reducing the effect of the predator on prey dynamics. We might term this property the 'loser wins' principle. There is no mechanism in the predator population that can counter this; evolution continues until mutants in both species are unable to invade.

Particularly in the context of host-parasite interactions, it has been suggested previously that evolution might lead to a weakening of positive/negative links where one species and the other gains at the ecological level:

"...Nature prefers that neither host nor parasite should be too hard on one another" (Burnet & White 1972:82).

Their argument appealed specifically to group selection:

"For Nature, survival of the species is all that counts..."

It is therefore of some interest to find that there is a counterpart to this that stems from selection at the individual level.

The 'loser-wins' principle is only one of a number of phenomena which suggest there may be an asymmetry in the evolution of predators and prey (Endler 1991). The life-dinner principle (Dawkins & Krebs 1979) -- a predator failing in a predation attempt looses only a meal, while a prey organism failing to escape its predator looses its life -- suggests the existence of unequal selection pressures. Prey may have shorter generation times than predators leading to more rapid evolutionary responses than in predators (*ibid.*). Prey may be able to evolve specialised defences more easily than predators can evolve to specialise on one type of prey; this may be a consequence of it being easier to select for one trait than for many, as shown by studies of the evolution of pesticide resistance, for example (Endler 1986), or of aposematic effects where rare prey types have an advantage. Thus it is not surprising that the model presented here shows an evolutionary advantage to the prey that cannot be counteracted by the predator.

Such asymmetry and consequent lack of specialisation on the part of the predator, has led some workers to suggest that the evolution of interacting predator and prey is not coevolution, but should be referred to as 'diffuse coevolution' (Janzen 1980), an 'arms-race' (Dawkins & Krebs 1979), or 'escalation' (Vermeij 1987). The model discussed here is a coevolutionary one, and I refer to the evolution of interacting predator and prey as coevolution, since I only consider one species of each type. The widespread occurrence of polyphagy means that this model, like many others of predator-prey interactions is difficult to apply to more complex natural situations directly. But the kinds of evolutionary phenomena it produces can be used as indicators of the outcomes we should expect in evolving natural systems. As always in modelling there has to be a trade-off between mathematical tractability and biological realism, and this two-species model provides a basis for understanding natural systems which are actually more complicated (but see Levin *et al.* 1990, for a more complex model of coevolution).

Whether or not predator-prey coevolution leads to a optimal solution from the point of view of either predator or prey, it would be interesting to know whether, as the predator and prey populations evolve across the phenotype space, they can be envisaged as improving in some biologically interpretable sense. The intuitive measure of fitness would be the per capita rate of increase, the term in brackets in the Lotka-Volterra equations (Equation 3.1). This arises because the condition for the invasion of a mutant at some point in the phenotype space is that its W_i be greater than zero at the current equilibrium. Indeed if one were to stand at this point in the phenotype space and look around at the two surfaces (for predator and prey) generated by the W_is one would appear to be at a height of zero in two gradient-like landscapes. The mutants which succeed in invading are those that take us a step up these surfaces. Unfortunately this hill-climbing is of no avail because, once the successful mutants have reached fixation, the ecological dynamics have taken us back to equilibrium densities at which the mutant W_i's are now zero; we are in effect back at a height of zero. This illustrates the point made by Fisher (1958:46) that the changes brought about by natural selection must be offset against the deterioration of the environment (see discussion by Frank & Slatkin

1992). What does happen as we 'strenuously' climb these horizontal surfaces is that the gradients underfoot gradually change, and we may reach a point at which further steps appear to be downhill on both surfaces. We are then at an evolutionary attractor. By analogy with Red Queen coevolution, where:
"It takes all the running you can do merely to stay in the same place." (Carroll 1974:149), on the adaptive landscape it takes all the climbing one can do just to attain the same height!

An alternative measure of fitness would be the equilibrium population density. As pointed out by Roughgarden (1979:483), there is one sense in which equilibrium density is maximised. Suppose for instance that we fix the predator body size at some constant value and also hold its population density constant. The prey body size that maximises the equilibrium density of the prey population under these conditions then has the greatest fitness; in effect the prey is evolving in a constant environment. This is however a very restricted sense. Even if there is no evolution in the predator, its equilibrium density will change as the prey evolves and the prey population density is then not necessarily at a maximum at the evolutionary attractor. If in addition predator body size can evolve, the equilibrium density of the prey can be pushed still further from a maximum.

It may be rather misleading to envisage such coevolution as climbing up a landscape of equilibrium population density. Figure 3.5 gives the equilibrium population densities associated with s_1, s_2 pairs across the phenotype space. It is clear that there are substantial regions near the middle of the region of coexistence in which the successful predator mutants come to equilibrium at a density lower than those they replace. This is because of the severity of their effects on the equilibrium population density of the prey. Moreover it is evident that, in the region of the evolutionary attractors, the prey density is not at a local maximum for constant predator body size. A declining equilibrium population density is evidently quite compatible with the evolution in this

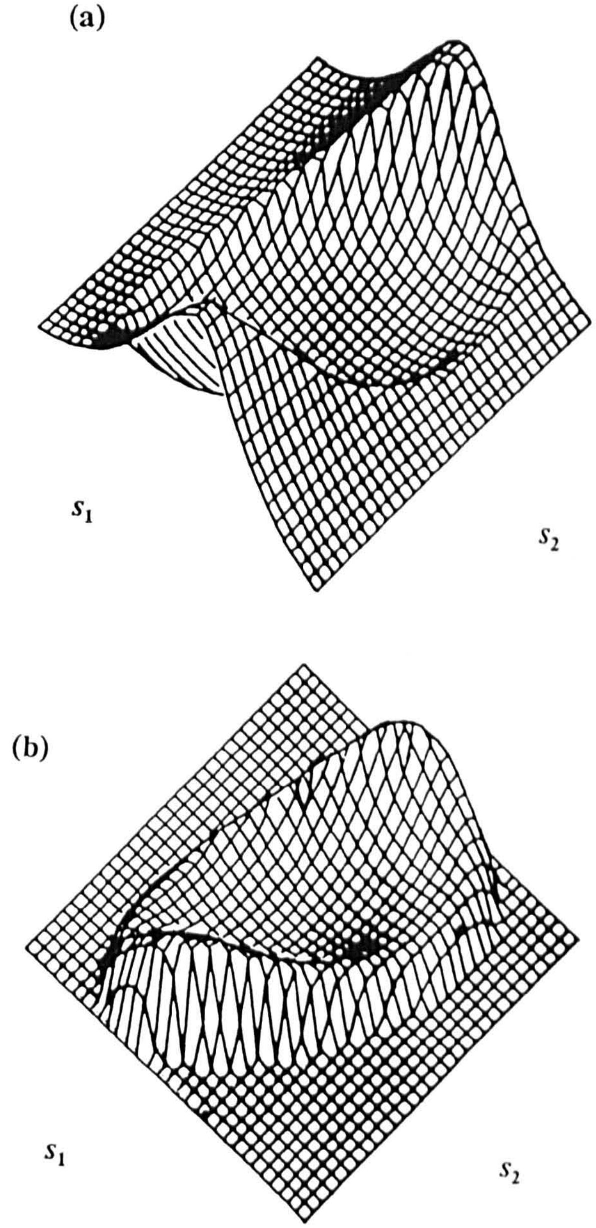


Figure 3.5. The effect of coevolution of predator and prey body size on equilibrium density of predator and prey populations. (a) prey; (b) predator. The vertical axis represents equilibrium population density in each case. The parameters used are the same as in Figure 3.3.

system.

The results presented in this paper have been the consequences of changes in the α_{11} function, and of the degree of benefit to the predator in relation to prey size. A more global analysis of the model dynamics with respect to changes in all interaction terms was not performed for two reasons. Firstly, we performed extensive perturbation tests where we altered one parameter and observed the effect of its change on the dynamics in the phenotype space. It was observed that in many cases the results obtained were extremely robust to changes in parameters of the α_{12} and α_{21} interactions. Secondly, we explained the dynamics in terms of the two body size parameters s_1 and s_2, rather than the three interaction terms α_{11}, α_{12}, and α_{21}, since a two-dimensional phenotype space is heuristically more useful than a three- or higher-dimensional space, which becomes more difficult to visualise. In this work it was intended to present certain biologically interesting examples of the results; work is now in progress upon a more comprehensive explanation of the system.

One method that could be used to further understanding of the system would be to consider it in the context of an evolutionary random walk (C. Cannings, *pers. comm.*). Since we have a condition for mutants going to fixation, if this is satisfied then evolution can be thought of a series of steps either in the s_1 or the s_2 direction. Evolutionary change can then be modelled as a stochastic process on the phenotype space. This would enable values to be assigned to the probability of proceeding along any particular pathway: and so the relative changes of ESSs or Red Queen coevolution in a system where they both occurred could be assessed. Limitations of time have prevented the use of this method in the current study, but it remains a potential approach for future work using similar models to those presented here.

The accuracy of the observation of evolutionarily stable states and continuous coevolutionary change (Red Queen coevolution) depends upon us being able to determine the directions of evolutionary change. This in turn depends upon mutants which invade going to fixation. As already described, we have a sufficient condition for this to occur. To test for mutants going to fixation we apply this condition over a large grid of points all over the phenotype space. Outside the zone of coexistence of predator and prey the result is of no consequence; we know that for the mutants we have chosen, interior equilibria cannot occur with the ancestral prey types. Over most of the elliptical space in which predator and prey both occur, only one equilibrium is found, and this is the one in which the mutants replace the ancestral populations, as we expect. So in most of this region, the mutants do go to fixation. However, current work suggests that over part of the phenotype space alternative states may occur where mutants coexist with the original types.

If these results occur in regions surrounding the evolutionarily stable points, we cannot tell whether all trajectories within the region will approach such points, or they do approach, whether the system will remain at those points. So they are not, strictly speaking evolutionarily stable states. However if the size of the known region is small in comparison to the phenotype space which we are investigating, then we will still have a very good idea of the overall dynamics, and it seems likely that predator and prey with size combinations close to the evolutionary attractors, would remain close to those attractors for a long period.

It may be possible to define the bounds of the regions near the evolutionary attractors where coevolutionary trajectories must remain even under conditions of polymorphism (C. Cannings, *pers. comm.*). If these bounds become smaller as one mutant replaces another then the conditions for the occurrence of an ESS may be satisfied in full. If they do not, we may still have an evolutionary attracting point with significant effects on the coevolutionary dynamics. These problems are currently under investigation.

The model depends upon the widely used Lotka-Volterra formulation for the population dynamics of interacting species (Equations 3.1). These equations have been severely criticised for having parameters which are very difficult to measure in natural systems and for being unrealistic (but see Peschel & Mende

1986), however they do have the advantages of being mathematically tractable and being related to a large body of theoretical work (Hofbauer & Sigmund 1988). The models used here did not include such features of some other predator-prey models such as functional response (e.g. Abrams 1990) but this simplicity enables the models to remain very general, such that broad evolutionary conclusions that can be drawn from them.

The observation of interesting coevolutionary phenomena in these models, some of the simplest that could be formulated to address this problem, suggests that a wealth of novel coevolutionary results could be awaiting discovery in the more complicated systems in nature. Further work will be required to evaluate this; for example, in this work populations with dynamics other than stable equilibria were not considered. However, for Lotka-Volterra systems which possess an interior equilibrium and remain at non-zero densities, it is known (Hofbauer & Sigmund 1988:62; Hofbauer *et al.* 1987) that the long-term average per capita growth rate of an invading mutant can be given by the per capita growth rate of that mutant evaluated at the equilibrium point. Thus we may be able to use systems similar to the ones described here to investigate interacting populations with chaotic or cyclic dynamics.

Chapter 4. A SIMULATION MODEL OF EVOLUTION IN PREDATOR-PREY SYSTEMS

> Nothing amuses more harmlessly than computation, and nothing is often more applicable to real business or speculative enquiries. A thousand stories which the ignorant tell, and believe, die away at once, when the computist takes them in his gripe.
>
> Dr Samuel Johnson

4.1 SUMMARY

A simulation model of the evolution of predators and prey is described. The model is based upon the Lotka-Volterra equations for population dynamics, modified to include genetic variation with respect to the interspecific interaction coefficients. Two versions of the model are considered; in the first selection acts directly upon the interaction coefficients, which are allowed to evolve independently of each other. In the second, the interspecific interactions are made dependent upon other traits, representing investment in predatory or anti-predator traits. These traits could be equivalent to predator and prey body size. The incorporation of the traits imposes constraints on the coevolution of reciprocal interaction effects.

To make the model an evolutionary one, mutants varying in interaction intensities or body sizes are allowed to invade predator and prey populations, and under the assumption of density-dependent selection the population dynamics of predator and prey represent the results of selection. Population dynamics can be evaluated in either discrete or continuous time in this model.

The organisation of the program which was used to solve the model is described, and the initial conditions and output of the simulation is described. Finally the method of implementation of the program to generate the results presented in the next chapter is given.

4.2 INTRODUCTION

In this chapter will be described a simulation model of the evolution of predator and prey. The model is intended to examine the evolution of ecologically interacting species, while including population dynamics. It is often assumed that evolutionary change occurs on a much longer time scale than ecological change, and thus that ecological dynamics always tends to equilibrium before evolutionary events (e.g. Post & Pimm 1983; but also models presented in this thesis; see Chapters 2 and 3). In this chapter I relax this assumption and model ecological dynamics explicitly in between mutation events. The model is related to those presented in the previous chapters (Chapter 2, Marrow & Cannings 1992; Chapter 3, Marrow *et al.* 1992), and is inspired by the simulation models of Spencer and Marks (1988, 1992; Marks & Spencer 1991) on the maintenance of allele polymorphism.

In this chapter I will describe the nature of the model represented by the simulation, and how the program to implement the model is constructed. Technical details of the program, where possible, have been left to an appendix (Appendix A). The source code is given in Appendix B. The results that the program produces, and their implications, have been left until the next chapter (Chapter 5).

Here I shall describe first the mathematical model which underlies the simulation, and which the program is intended to solve numerically. Then I shall go on to describe the way in which the mathematical model is incorporated into a computer program, and how that program works. The user-defined initial conditions of the simulation will then be detailed. Finally the way in which the program was implemented in the specific computing environment used to generate the results of the next chapter will be mentioned.

4.3 MODEL FORMULATION

This section describes the mathematical models which underlie the simulation, and the assumptions which underlie them.

4.3.1 Population dynamics

The models I present here assume a haploid genetic system, and are based upon genotype densities rather than gene frequencies. The models are derived from the Lotka-Volterra community model,

$$\frac{dx_i}{dt}=x_i(r_i+\sum_{j=1}^{n}\alpha_{ij}x_j) \tag{4.1}$$

(where n denotes any number of species), but I wish to consider in the main the case when i and j can take the values one or two: this is a predator-prey system. I shall adopt the convention that a subscript of $i, j = 1$ denotes a prey characteristic, while $i, j = 2$ denotes a predator. The simulation model of which this system is the basis is designed in such a way that any number of species could be included, but constraints on time and computing resources meant that predator-prey systems were the only ones studied in detail.

For an evolutionary model I consider each population density x_i to be made up of a number of different genotypes m of densities x_{im}. The genotypes vary in their interactions with other genotypes in the same and other species. The intrinsic growth rate term, r_i, is also split up in the same way, and becomes a vector of genotypic growth rates, r_{im} for each genotype m. However, to distinguish between different genotypes and different species, I assume that the intrinsic growth rates of one species do not vary, and that all new mutants invading that species take the ancestral value. The distinction between mutants within species and new species might be said to depend upon how closely related the new types are to those already present. An alternative assumption might be to allow new mutants to have intrinsic growth rates r_{im} near to, but different from, ancestral populations; but this was not explored in the simulations considered here.

The most significant features of the population dynamic model are the interspecific interaction coefficients, α_{ij}. Departing from normal practice in the use of this type of model, I shall allow the α_{ij} to vary within each species. So each interspecific interaction coefficient will be represented by a number of intergenotypic interaction coefficients, α_{ijmn}, where the subscript denotes the effect of the *n*th mutant, or genotype, of species *j* on the *m*th genotype of species *i*. In the following sections where I refer to α_{ij} for notational convenience, the statement can be taken to apply to intergenotypic interaction coefficients also. The varying interaction terms can be thought of as introducing genetic variation into the population dynamical model. This is a haploid genetic system, and as a result I shall use the terms *genotype*, *mutant*, and *allele* almost synonymously, an action which is only appropriate in this type of genetic system.

4.3.2 The relationship between ecology and genetics

For the purposes of using the population model to study evolution, further assumptions have to be made about the relationship between different interspecific interactions. This arises out of the use of two parameters to describe different aspects of the same interspecific interaction in the Lotka-Volterra equations. Where species 2 is a predator, and species 1 its prey, then α_{12} and α_{21} describe the same interaction but are often assumed to be completely independent of each other. Conventionally, these parameters are fixed, and their independence does not matter. By introducing natural selection we have allowed them to vary. For this reason our assumptions about the relationship between them have to be made explicit.

Two sets of assumptions are considered in the simulation models. The first (hereafter described as Model 1) includes only the assumption that the different α_{ij} evolve independently of each other. The traits under evolution in this system are the interaction coefficients directly.

The second set (Model 2) introduces intermediate variables, s_i, such that $|\alpha_{ij}| = F_{ij}(s_i,s_j)$ where F_{ij} is some function. s_i represent investment in predatory or anti-predator traits. This could be accounted for by the size of predator and of prey (Hespenheide 1973; Thompson 1975; Peters 1983; Calder 1984; Vézina 1985; Warren & Lawton 1987), and I shall sometimes refer to s_i as "body size", following the usage of Chapters 2 and 3 (and Marrow & Cannings 1992; Marrow *et al.* 1992). In this system selection acts indirectly upon the interaction terms, through the s_i. The s_i define the relationship between parameters representing reciprocal effects in the same interaction.

In order to define the nature of this relationship, I make two assumptions. Firstly, that what is best for the predator is worst for the prey, and vice versa. I let $\alpha_{12} = -\alpha_{21}$. Such perfect symmetry may be unlikely in nature, but serves as a useful first approximation to the real nature of the antagonistic interaction.

Secondly, in order to define the shape of the F_{ij}, I assume that for the predator, optimal investment in predation traits will occur at intermediate levels of s_2, and that predators that invest more or less will obtain less benefit. Thus the relationship between s_2 and α_{21} could be of Gaussian (normal) form. But we also have to consider the effect of s_1 on α_{21}. Prey investment will affect suitability of the prey for the predator; I suggest that this may also be represented by considering an intermediate level of s_1 as most suitable for the predator. So we can assume also that s_1 is also related to α_{21} in a Gaussian relationship, and the overall form of the α_{21} function with respect to the two investment variables is that of a bivariate normal function. So

$$F_{21}=\frac{k_1e^{-(k_2(s_1-0.5)^2)}k_3e^{-(k_4(s_2-0.5)^2)}}{c_1}-c_2 \tag{4.2}$$

where k_1, k_2, k_3, and k_4 are constants. In the runs described in the next chapter they are set to 1.0. c_1 and c_2 are constants of transformation, used to transform interaction intensities to a scale of 0 to 1. They are defined in the runs described in the next chapter as follows:

$$c_1=1-e^{-0.5}, \tag{4.3a}$$

$$c_2=\frac{e^{-0.5}}{(1-e^{-0.5})}. \tag{4.3b}$$

By our previous assumption, of the symmetry of the reciprocal interactions, the α_{12} function is represented by an inverted bivariate normal function, with a trough instead of a peak, and $F_{12} = F_{21}$ since we are dealing with absolute values of interactions.

The relationship of α_{11} to s_1 and s_2 is a special case, since we are not strictly speaking, dealing with an interspecific interaction. This is incorporated into the general body of assumptions of Model 2 by considering what s_1 could represent. If s_1 represents body size, as suggested previously, then α_{11}, the dependence of a prey or basal species on its own density, will become more intense with increasing size. So α_{11} will increase in absolute value with investment. We write F_{11} as a simple linear function of s_1,

$$F_{11}=k_5s_1, \tag{4.4}$$

in reflection of this, since it depends only on interactions within the prey species.

4.3.3 Density-dependent fitness

I have already defined implicity a density-dependent genetic system by describing the population dynamical system in terms of genotype densities. So we can consider the per capita growth rates of the two species as given in the Lotka-Volterra equations as equivalent to fitness functions for those species. So, if W_{im} is the fitness function for the *m*th genotype in the *i*th species, and there are a maximum of ten genotypes in each species, we have

$$\begin{aligned} W_{1m} &= r_{1m} + \sum_{n=1}^{10} \alpha_{11mn} x_{1n} + \sum_{n=1}^{10} \alpha_{12mn} x_{2n}, \\ W_{2m} &= r_{2m} + \sum_{n=1}^{10} \alpha_{21mn} x_{1n}. \end{aligned} \tag{4.5}$$

4.4 PROGRAM DESIGN

This section outlines the way in which the mathematical models presented above were incorporated into computer programs. Some of the computing techniques which were used, and which are most important to the understanding of the simulation model are given, but this section is not intended to document fully the programs.

4.4.1 Overall structure

Two simulation programs were written, one for Model 1 and one for Model 2. They shared a large number of routines, differing mainly in the way new mutants were generated and in the output which was presented. Both programs had the same overall layout, which is represented in Table 4.1. Both programs incorporated routines for evaluating dynamics in discrete or continuous time. They were designed in such a way that the type of dynamics could be chosen

```
1. Input used-defined parameters.
2. Generate parameters defined by the program.
3. Start time counting.
4. Choose {discrete time} OR {continuous time}

    {discrete time}
    5. Calculate new genotype densities
    6. Generate, and allow to invade, new mutants.
    7. Record data for output
    8. Add to time count
    (Repeat 5-8 until end of simulation)

    {continuous time}
    5. Solve numerical integration for genotype densities over a range.
    Initial conditions are previous final densities.
    6. Generate and invade new mutants.
    7. Record data for output.
    8. Add to time count.
    (Repeat 5-8 until end of simulation)

{at end of simulation}
9. Output graphical results, and/or files with numerical results.
```

Table 4.1. Overall structure of the simulation programs. The numbered lines (1-9) represent states in the execution of the program. Many minor functions of the program have been omitted in this very simplified outline. The list represents features which are common to both Model 1 and Model 2.

by the user, and did not otherwise affect the program's function.

4.4.2 Random number generation

Models of evolution depend upon a source of random variation: in these models this was provided by a group of NAG pseudo-random number generating routines, G05DDF (normal distribution), G05DBF (negative exponential distribution), and G05CAF (uniform distribution). These are all based on the multiplicative congruential method (Numerical Algorithms Group 1990). The number of calls to these routines in the simulations did not exceed the square root of the period of the pseudo-random series, approximately $2^{28.5}$, or about $380 * 10^6$, and so I concluded that the statistical properties of the random numbers generated did not generate bias in the results.

4.4.3 Initialization

The programs were designed so that the parameters required to define the evolutionary model could be input by the user from a terminal at the start of the simulation. Due to the large amount of computer time required to run the simulation, especially in continuous time (see Appendix A), the program was most frequently run non-interactively, as a batch process. In this case the parameters which were otherwise input by the user could be input from a text file.

Parameters input by the user enable a choice to be made between having the initial parameters of the Lotka-Volterra system defined by the user, or randomly generated by the program. This allows both the effects of specific parameter combinations to be explored, and parameter space to be explored at random.

4.4.4 Evaluating population dynamics

4.4.4.1 Discrete time

The discrete time exponential analogues of equations (4.1) above (see Hofbauer *et al.* 1987),

$$x'_{im}=x_{im}e^{\left(r_{im}+\sum_{j=1}^{2}\sum_{n=1}^{10}\alpha_{ijmn}x_{jn}\right)},\qquad(4.6)$$

where variation among genotypes is taken into account, were solved directly once per iteration for the discrete time model. No special routines were required.

4.4.4.2 Continuous time

The population dynamics equations,

$$\frac{dx_{im}}{dt}=x_{im}\left(r_{im}+\sum_{j=1}^{2}\sum_{n=1}^{10}\alpha_{ijmn}x_{jn}\right),\qquad(4.7)$$

were evaluated in continuous time via numerical integration. This was performed using the D02EAF routine of the NAG library (Numerical Algorithms Group 1990). This is a routine for evaluating systems of 'stiff' ordinary differential equations over a range, given initial conditions. The Lotka-Volterra equations are stiff in that they have very persistent transients, which render many techniques for numerical integration inappropriate. A variable-order, variable-step method based on the Backward Differentiation Formulae (Gear 1971) is used. Error checking was defined by the *tol* parameter, set here to 10^{-8}, implying an accuracy of about seven decimal places, that is to say, greater than the threshold at which extinction occurred (10^{-6}).

Because the invasion of mutants could potentially introduce discontinuities in the population dynamics (as an invading population goes suddenly from 0 to 10^{-6}), numerical integration was performed step-wise over a range between the mutant invasions. Each stage of mutant invasions and population dynamics will be referred to as an *iteration*, although this does not imply discrete dynamics. So the numerical integration was performed once per iteration. The range over which integration was performed effectively defined the amount of ecological dynamics taking place in between evolutionary events. As the number of iterations was decreased to save computer time, the amount of dynamics was increased. After a mutant had invaded the initial conditions were reset to the final conditions of the previous iteration and the integration was repeated.

4.4.5 The mutation process

4.4.5.1 Invasions of new mutants

The core of any simulation which represents evolution must be the way in which mutants are generated. The program allows a fixed maximum number of genotypes to be present in each species at any particular time. If this maximum number is present, a new mutant will not be generated; but this did not occur very frequently in the simulations considered here.

Mutant generation is density-dependent, so the probability of a mutation occurring is proportional to the total density of the species at that time. The mutation rate is set by a parameter, which represents the probability of mutation when the species' population density is 1.0. A random value is generated to test whether the mutation actually occurs or not.

If it does, then the genotype density of an empty element in the array for that species' density is set to 10^{-6}, and the growth rate of the mutant is set to the ancestral value (since we do not allow growth rates to vary in these models). The generation of interactions then follows.

4.4.5.2 Interaction evolution

The processes used to generate mutant characteristics in Model 1 and Model 2 are similar, except that in Model 2, the investment values s_i are generated first; and the interaction terms derived from these. The generation of mutant characteristics is intended to reflect the ecological closeness of mutants to their ancestral stock. In Model 1, each interaction is generated on a normal distribution with mean the weighted mean of absolute values for interactions already present. The interaction coefficients for genotypes already present in the system are weighted by the probability of occurrence of each particular intergenotypic interaction, in the following way:

$$I_{ij}=\frac{\sum_{m=1}^{10}\sum_{n=1}^{10}\alpha_{ijmn}x_{im}x_{jn}}{\sum_{m=1}^{10}\sum_{n=1}^{10}x_{im}x_{jn}}, \tag{4.8}$$

where I_{ij} is the weighted mean of interaction intensities for the interaction where species j has an effect on species i. The standard deviation is expressed as a fraction of the mean. We find that this restricted sampling of mutant characters is more appropriate than sampling from a uniform distribution, which produces very abrupt, unrealistic changes in parameter values, often leading to unstable parameter values and to extinction. The generation of investment values in Model 2 proceeds by a similar method.

The generation of interactions in this way is a conservative method, in the sense that new genotypes tend to have characters close to the ancestral ones. This may retard the progress of evolutionary change to some extend. One alternative approach to the generation of mutant characters (C. Cannings, *pers. comm.*) could be to choose some particular intergenotypic interaction and centre the distribution for character generation upon that. Since this would not make use of a mean of characters, this would have the advantage that evolutionary change might be more rapid. However it is difficult to find biological justifications for choosing any particular value; and the approach I use does have the advantage that it reflects the rarity of large mutational changes.

Once the interactions have been generated in Model 1, they are checked to ensure that they are greater than zero, if this is not the case then the process is repeated. Then each interaction is multiplied by a constraint parameter, which merely represents the sign of the interaction, as required by our model. We are representing a predator-prey interaction where species 1 is the predator and species 2 the prey, so α_{11} and α_{12}, constrained negative, are multiplied by -1, while α_{21} is positive and thus multiplied by 1, and α_{22} is zero and is multiplied by 0. Finally the α_{11} values are checked to ensure that their absolute values lie above the minimum self-limitation. This minimum is set to prevent the prey population exploding out of control as it escapes from restriction by crowding, and thus causing the program to crash. Such a restriction does not appear very unrealistic, since species are usually restricted in some way in the densities which they can survive.

In Model 2 the investment values for predator and prey are generated in a similar way to the basic values for the interaction terms for Model 1. The interaction terms are then derived from these according to the relationships described above. The same restrictions apply on the interactions in Model 2 (absolute value greater than zero, α_{11} greater than minimum self-limitation value) as do in Model 1.

4.4.5.3 Preventing identical genotypes

Since new mutants are generated at random, on a restricted normal distribution, it is possible in our model to generate a mutant with some characters very close to those of pre-existing alleles. In such a simplified set of phenotypes that I simulate, this is clearly unrealistic, and so I have incorporated routines to check whether a mutant identical to a previous genotype has been genérated, and if it has, to remove it. If this is done, then another mutant is generated to replace it.

Since interaction terms or investment values as generated are Pascal double precision numbers (equivalent to real numbers with sixteen decimal places), it is perhaps unlikely that they will ever be exactly identical. Instead, we regard a genotype as possessing an interaction identical to another genotype if those two genotypes are in the same species, interacting with the same mutant of the same or a different species, and the two interactions are identical to three or more decimal places. Thus we allow scope for mutants of very nearly similar effects. In Model 2, since the investment values are generated first, we merely compare the investment values of two genotypes, and subject them to a similar condition.

These additions to the basic model, although having no specific biological equivalent, do prevent a number of identical genotypes accumulating at a peak of fitness, and thus prevent the observation of a polymorphism under conditions when it should not occur.

4.4.6 Generating output

Output from the simulation was generated in two forms. Graphical output was generated on a pen plotter using the Simpleplot graphics package (BUSS Ltd. 1985). The results that were output are shown in Table 4.2. Where pen plotter output was not appropriate, or it was desired to pass results to statistical

---

For both Model 1 and Model 2.

1. Population dynamics (total density of all genotypes present) of prey and predator through time.
2. Number of different genotypes in prey and predator over time.
3. Weighted mean of absolute value of α_{11} over time.
4. As (3.) for α_{12}.
5. As (3.) for α_{21}.

For Model 2 only.

6. Arithmetic mean of body size (s_i) for predator and prey over time.

Table 4.2. Graphical output from the simulation program. The weighted mean used to calculate the interaction intensity is the same that used to generate new mutants; see Equation (4.8). This output was produced by the Simpleplot graphics package on a pen plotter. In many cases the output did not reproduce well and has therefore not been included in this thesis; the examples of output from the simulation shown in the next chapter (Chapter 5), are mainly generated from the numerical data output by the programs. However, the same data set is used in both cases.

packages for analysis, the results could also be output as a text file of numerical data. The file could then be used as input to a graphical or statistical package.

4.5 INITIAL CONDITIONS

This section details the parameters which control the model explored in the simulation, and how they can be varied. The simulation was designed so that a large number of initial conditions could be varied according to the requirements of the numerical experimentation anticipated.

At the start of the simulation the user can input a number of different parameter values controlling the initial state of the system. Table 4.3 shows the main parameters of the simulation; others have been omitted, of technical interest only.

4.5.1 Densities of predator and prey

The initial density of predator and prey can be controlled, so that the simulation starts in a particular region of phase space. At the start of the simulation there is only one genotype present in each of predator and prey, and it is the density of this, that "initial density" refers to. In most of the simulation results recorded in this thesis the initial density was kept at 1.0 for each species, as there was insufficient time to explore the effects of varying it. In many runs, the initial density did not seem to matter since the populations converged to an equilibrium which was then altered by equilibrium (see section 5.5).

Description	Value
Number of species	2
Maximum genotypes per species	10
Prey initial density	1.0
Predator initial density	1.0
Density of invader	10^{-6}
Threshold of extinction	10^{-6}
Minimum self-limitation	10^{-3}
Mutation rate	0.5
Standard deviation of mutant sampling distribution	1
Type of initialisation	random
Mean of negative exponential distribution	0.25
Numerical system	continuous
Range of numerical integration	100
Tolerance for numerical integration	10^{-8}
Constraint on α_{11}	-1.0
Constraint on α_{12}	-1.0
Constraint on α_{21}	1.0
Constraint on α_{22}	0

Table 4.3. Main simulation parameters, and typical values. Not all the parameters shown here are user-definable; some are defined within the program, but all are alterable without difficulty.

4.5.2 Invasion and extinction thresholds

The density at which new mutant genotypes invaded could also be altered. It was reasonable to keep this at a low value to reflect the rarity of mutation events. The density at which extinction occurred could also be altered by the user, and was kept low in order to allow population dynamics to take place over a wide range of densities. Making the extinction threshold the same as the invasion density (Table 4.3) enabled the criterion for invasion of a new allele to be equivalent to the conventional criterion of population genetics (Roughgarden 1979:108) for the increase of a new allele when rare.

4.5.3 Minimum prey self-limitation

It was also necessary to place a lower bound upon the self-limitation term in the prey (α_{11}), since test runs of the simulation had shown that the prey self-limitation could be selected to zero, causing the prey population to explode out of control and the simulation program to crash. Such behaviour has been observed in models of the evolution of community structure before (Taylor 1988), but populations growing unregulated by density do seem ecologically unreasonable.

4.5.4 Mutation rate

The rate at which evolution takes place in the simulation model can be controlled by varying the mutation rate parameter. Each iteration during the simulation, a random number is generated to test whether a mutant is generated or not. The random number generated depends on the density, so mutation is density-dependent. The mutation rate parameter controls how likely mutation is to occur: it corresponds to the probability of mutation when total density of the species is 1.0. There is a upper limit of one mutation per iteration in the model. During the simulations the mutation rate was usually kept high in order that a large amount of evolutionary behaviour could be observed for the minimum amount of computer time. This was especially significant in the continuous time case.

4.5.5 Degree of divergence of mutants from ancestors

Mutants were generated in the simulation model to be similar to their ancestral populations (compare Akçakaya & Ginzburg 1989), and the degree of similarity was controlled by a parameter which regulated the standard deviation of the normal distribution from which new mutant characters were sampled. This was kept large in the simulations presented here to produce rapid evolutionary change.

4.5.6 Initial growth rates and interaction terms

The initial parameters of the Lotka-Volterra system representing the initial genotype of predator and prey could be defined either by the user or by the program. If they were defined by the program the values (of r_{11}, r_{21}, α_{1111}, α_{1211}, and α_{2111}) were generated on a negative exponential distribution, the mean of which can be defined by the user. Otherwise the user could input each parameter, as an absolute value, individually.

4.5.7 Invasion counting and time type

The user is also able to control the number of iterations over which the number of invasions are counted (results from this aspect of the simulation are presented in section 5.3), and the type of numerical evaluation of the population dynamics that is carried out. The use of continuous or discrete time was intended to make as little difference to the operation of the simulation as possible, so the format of output is identical and the equations used are equivalent in a number of ways (Hofbauer *et al.* 1987). However the use of the continuous time alternative does require considerably more computer time (see Appendix A).

4.5.8 Numerical integration parameters

The range over which numerical integration is carried out over each iteration can be controlled; this effectively sets the amount of ecological dynamics that takes place in between evolutionary change. This parameter can also be thought of as affecting the rate of evolution, if such a rate is measured by comparison to ecological change. The degree of accuracy of the numerical integration can also be controlled, and was set throughout the simulations presented to here to a value of 10^{-8}, corresponding approximately to seven decimal place accuracy (lower than the extinction/invasion threshold).

4.5.9 Sign constraints on Lotka-Volterra interactions

Finally, constraints have to be placed upon the signs of the Lotka-Volterra interaction terms, to ensure that a predator-prey interaction is modelled. These can be input by the user. By changing the values of these constraints, a different type of interaction such as a competitive interaction could be modelled. In view of the theoretical work in previous chapters, the simulation results presented in the next chapter will deal only with predator-prey systems.

4.6 IMPLEMENTATION

The programs to implement Model 1 and Model 2 were written in Pascal, and ran on the VAX 8650/8550 cluster of the University of York Computing Service. External numerical integration routines (in Fortran) from the NAG library were used to evaluate population dynamics in continuous time. External routines (also in Fortran) from the Simpleplot graphics library were used to generate graphical output. Additional details of the programs, and their implementation, are given in Appendix A. The source code of the programs is given in Appendix B.

Chapter 5. ECOLOGICAL AND GENETIC FEATURES OF EVOLUTION IN PREDATOR-PREY POPULATIONS: RESULTS FROM A SIMULATION MODEL

5.1 SUMMARY

A simulation model is used to analyse the genetic and ecological consequences of predator-prey coevolution. The model is based upon the Lotka-Volterra equations for population dynamics, modified to include haploid genetic variation in interspecific interaction terms, or in body size, which is likely to have an effect upon interspecific interactions. In the latter model the body sizes of predator and prey can be thought of as acting as evolutionary constraints.

Three features of predator-prey coevolution are examined; the build-up or otherwise of resistance to the invasion of new mutants, the ability of the system to maintain distinct alleles at a polymorphism, and the consequences of coevolution for the dynamical behaviour of the predator-prey populations. Results from the simulation are used to test hypotheses about these features of the predator-prey interaction.

Problems that arise from the use of the simulation model in this way are discussed, and ways in which the simulation method could be improved are suggested. The implications of the use of simulation models for the study of complicated biological scenarios are discussed.

5.2 INTRODUCTION

Simulation models have proved a useful tool in the study of the development of community structure (Post & Pimm 1983; Drake 1990b; Vida *et al.* 1990). Such change may involve both genetics and ecology (Rummell & Roughgarden 1983; Szathmáry *et al.* 1990). In order to understand this, it may be necessary to look at processes which make up part of that change.

In this chapter I wish to investigate some genetical and ecological processes occurring in predator and prey evolving through their ecological interaction. I shall use the simulation model described in the previous chapter, based upon the Lotka-Volterra food web model (e.g. Law & Blackford 1992) for predator and prey only. The two equations representing the two species become systems of equations as genetic variants are introduced into the system.

The evolution of interacting species can be examined theoretically in a number of ways. First, one may ask what sort of evolutionary outcome will evolution of the predator-prey system result in? This is a question amenable to a purely genetical approach, but attention in the area of predator-prey coevolution has often focused upon lag-load models (Maynard Smith 1976b; Stenseth & Maynard Smith 1984) which incorporate extremely simplified assumptions about genetics, and in which ecological dynamics are absent. I use a model which records genotype densities rather than gene frequencies, and thus combines aspects of genetics and ecology. To distinguish between alternative outcomes of coevolutionary change I shall examine the rate of new genotypes successfully invading predator and prey over time, to determine whether invasion resistance arises, which could indicate the occurrence of an evolutionarily stable state. If it does not do so we have some evidence for continuous coevolutionary change, the so called Red Queen coevolution (Maynard Smith 1976a).

Secondly, there is the level of population genetics, where attention focuses on the change in gene frequencies or number of alleles arising from the interspecific interaction. I wish to concentrate upon the latter problem: how many alleles can be maintained at a polymorphism in predator or prey? In a single species with a haploid genetic system under density-dependent selection one would expect only one allele to persist; but can the interspecific interaction change this and maintain polymorphism? I will present results from the simulation model which address this problem.

Finally, one could investigate the consequences of the evolution of predator and prey directly at the level of ecological population dynamics, and incorporate only the most basic assumptions about genetics. The population dynamical consequences of evolutionary change have become of particular interest recently, in the debate over the type of ecological dynamics in natural systems. A large body of theoretical work based upon the assumption that ecological populations spend most of their time, at, or near, equilibrium densities, has been brought into question by the observation of chaos in simple population models (May 1976; Gilpin 1979; Hastings & Powell 1992). This implies that chaotic and other non-equilibrium population dynamics may be easily attainable in natural populations, although the evidence for such occurrence is mixed (Berryman & Millstein 1989; Godfray & Blythe 1990). With regard to evolutionary change, it would be of interest to know whether natural selection could move populations towards, or away from chaos. In the third part of the results from the simulation model presented in this chapter I shall present time series for population dynamics for the two species, and try to account for the dynamical behaviour that is observed.

Results acquired by numerical simulation differ somewhat from results of analytical theory in that the complexity of the underlying simulation program means that we cannot understand the system being investigated as fully when mathematical techniques are applied directly. This is especially the case when the simulation model is intended to be complex in order to mimic the complexity of a natural system. In the final section of the chapter I shall discuss these problems, in the light of the results given in the chapter.

5.3 MUTANT INVASIONS INTO INTERACTING SPECIES: A TEST FOR RED QUEEN COEVOLUTION

5.3.1 Background

The concept of the evolutionarily stable strategy (ESS; Maynard Smith & Price 1973) has proved particularly useful in the study of the evolution of individual species (Maynard Smith 1982; Cannings 1990). When the evolution of a number of species in a community is considered, no clear theoretical treatment was available until Maynard Smith (1976a) developed the concept of the lag load. Using this concept Stenseth and Maynard Smith (1984) were able to make a general analysis of coevolution in multi-species ecosystems; dividing the consequences of coevolution into two categories. The first, evolutionary stasis, was the equivalent of an evolutionarily stable strategy for all individuals in all the species simultaneously. The second category represented continual evolutionary change. This was termed Red Queen coevolution (Maynard Smith 1976b) after Van Valen's (1973) palaeontological hypothesis.

Stenseth and Maynard Smith proposed a theory which made only the most general, minimal assumptions. To test it would require examining more detailed and most realistic systems. Since in general the time scale over which community evolution operates is beyond the scope of most research, testing theories of community evolution has tended to follow one of two pathways (Hoffman 1991). The first is analysis of data from the fossil record, in order to determine whether one of the predicted alternatives was in fact followed in specific groups of organisms. This approach has not produced unequivocal support for one of the alternatives (Bakker 1983; Hoffman & Kitchell 1984;

West *et al.* 1991). This is part due to the impossibility of controlling for abiotic environmental variation, which will confound the biotic variation upon which Red Queen coevolution depends.

The only way to control for environment variation is to use mathematical modelling. This is naturally far more assumption dependent than tests using palaeontological data, but it is the only way to approach some questions which depend on data inaccessible in nature. One such approach is to observe the evolution of species in a community, and detect the build-up of invasion resistance, and the consequent decline in the rate of evolution, as an indicator of the approach of evolutionary stasis. Such invasion resistance has been observed to arise in models of community evolution (Case 1990, 1991). If the rate of evolution remained relatively constant over time them one might hypothesize the occurrence of Red Queen coevolution. Red Queen coevolution has been detected in models of predator-prey coevolution (Stenseth & Maynard Smith 1984; Marrow *et al.* 1992; but see Rosenzweig *et al.* 1987). Observing such phenomena in nature would require examining the gene pools of several species over a long period of time, a colossal undertaking. Using a model one can do this easily, and this is what I propose to do in this section.

The models I shall present are based on the familiar Lotka-Volterra food web equations. Here only two species will be considered, so I will be in fact modelling a predator-prey interaction.

5.3.2 Method

All simulations were started with a single genotype in each of the predator and prey species, set to an initial density of 1.0. The growth rates and interaction terms of the initial genotypes were generated on a negative exponential distribution of mean 0.25. The growth rates and interaction terms so generated were constrained to be greater than zero and less than 1.0. In addition the absolute value of prey self-limitation was constrained to be greater than 0.2, to prevent population explosion in the prey, which could overload the simulation. Constraints were applied to the interaction terms to ensure a predator-prey interaction was modelled.

Three distinct types of mutational regime were used. In the first, mutations were allowed to invade both predator and prey. In the second, mutations took place in the prey species alone; in the third, they occurred in the predator alone.

After the initial populations were established, the simulation went through a series of iterations in the way described in Chapter 4. In discrete time, each run consisted of twenty thousand iterations, while in continuous time each run consisted of five thousand iterations. The difference in the length of simulation in discrete and continuous time was solely due to the much greater amount of computer time required to solve numerically the continuous time system (see Appendix A). The maximum amount of time for each run was restricted by the limit of one hour on the amount of CPU (central processing unit) time a batch job could use on the computer system used.

In the species in which mutations occurred, the mutation rate was set to 0.2 per iteration. This rate was chosen so as to produce relatively rapid evolutionary change during the time-span of the simulation, and yet make mutations still relatively rare. Every time a mutant invaded a species it was counted, as an *attempt*. If the mutant persisted into the next iteration, this was counted as a *success*. This meant that the requirement for an invading mutant to persist was that it should increase in density in the first iteration. This was equivalent to the condition in population genetics for the establishment of a rare allele (Roughgarden 1979:108).

After 100 iterations the total number of *attempts* and *successes* was recorded and the count reset to zero. The *success rate* for a particular period of 100 iterations was recorded as number of *successes* over number of *attempts*. At the end of the simulation the state of the total predator and prey populations was recorded, in terms of the extinction or persistence of each population. The mean density over each time period of 100 iterations was also recorded. This enabled the coexistence of predator and prey, or the extinction of one or both species to be detected.

The numerical experiments were performed both in discrete and continuous time. The number of replicate runs performed under each mutational regime differed in continuous and discrete time since the results of certain runs were lost as they exceeded the maximum time limit for batch processes.

5.3.3 Results

5.3.3.1 Continuous time

One-way analysis of variance and Model I linear regression were performed on the predator and prey success rate data sets over time, for each mutational regime (Table 5.1).

The success rate of prey showed significant variation with time in two cases, in the prey when both predator and prey were evolving, and in the prey when evolution was taking place in the prey alone. The linear regression produced a significant negative relationship in each case (Figure 5.1a, b). The data was very scattered however, producing very low values of r^2 (Table 5.1).

In view of this considerable scatter, it might be questioned whether the relationships predicted by the regression had any validity. Plots of the change in success rate in individual runs of the simulation (Figure 5.2) suggest that they do: resistance to invasion appears to build up in the prey over time.

The data sets which had produced significant results were reanalysed after transformation by the arcsine transformation (Sokal & Rohlf 1981:427); this did

Time Type	Continuous			
Mutation Regime →	Predator and Prey		Prey Only	Predator Only
Statistic ↓	Prey	Predator		
n	229	266	336	287
Number of Replicates	40	40	41	44
One-way Analysis of Variance				
F	14.30	0.710	7.80	1.16
p	0.000	0.712	0.000	0.320
significance	***	*n.s.*	***	*n.s.*
Linear Regression				
b	-0.0403	-0.0087	-0.0317	-0.00424
a	0.442	0.441	0.380	0.392
r^2	0.211	0.006	0.122	0.000

Table 5.1. Success rate of invasions into predator and prey: continuous time. *n* refers to the number of observations of success rates over time which were measurable, as the number of successes were non-zero. (When the number of successes was zero, a missing value was entered, due to division by zero).

In the linear regression, *b* is the slope, *a* is the intercept. The adjusted r^2 is used, as output by the Minitab statistical package (Minitab, Inc. 1989). *n.s.* denotes "not significant", $p > 0.05$, *** refers to a highly significant result, $p < 0.001$.

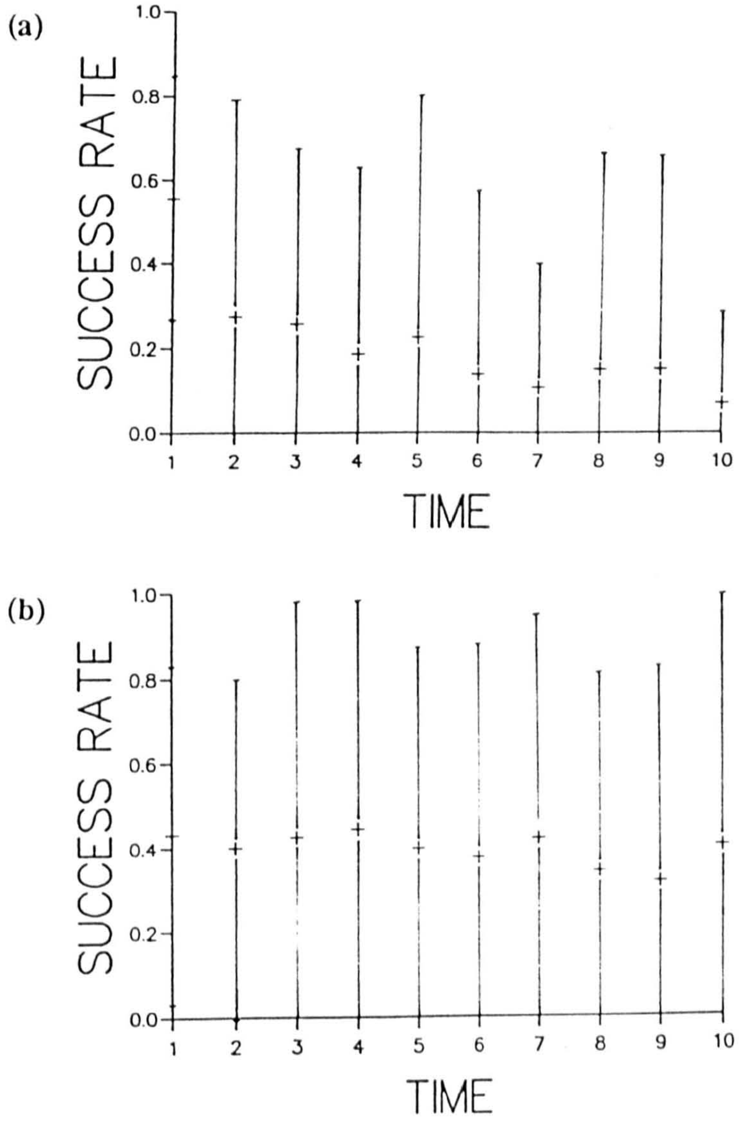


Figure 5.1. Success rate of invasions into predators and prey under different evolutionary scenarios in continuous time. (a) predator and prey evolving; (b) prey only evolves. The *success rate* for each time interval for each run was calculated as the ratio *successes/attempts*. The arithmetic mean success rate for each time interval is marked on the graph: error bars are the 95% confidence intervals.

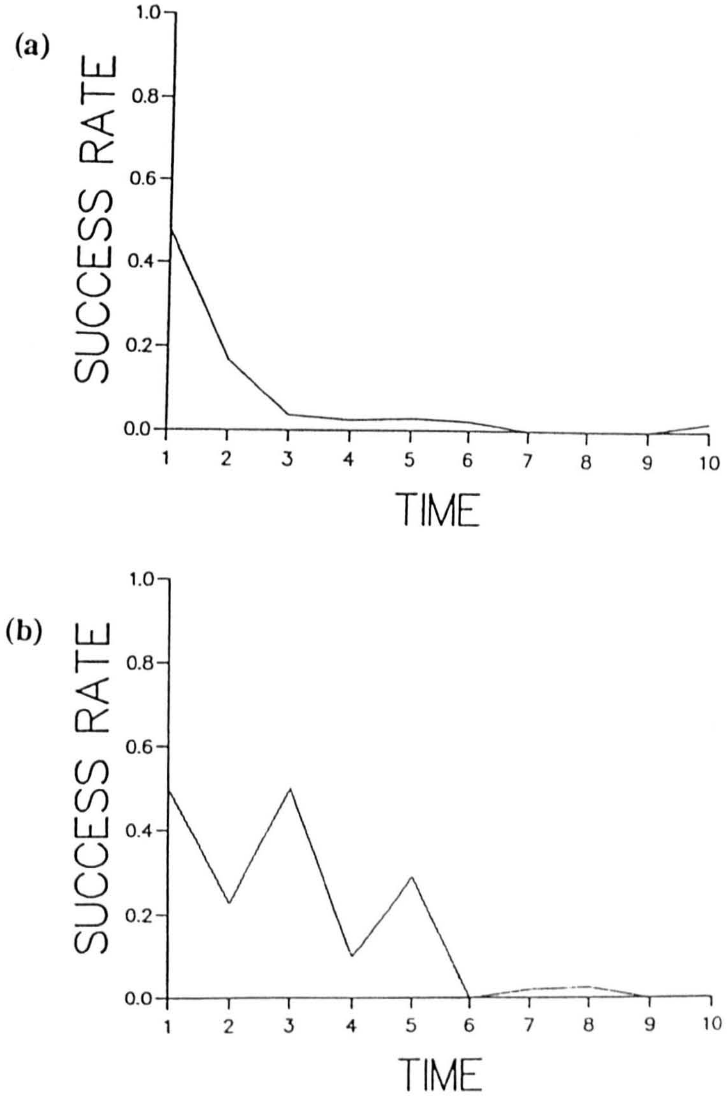


Figure 5.2. Success rate of invasions into prey when predator and prey coevolve in continuous time. Results of individual runs. (a), (b), (c) example runs. Initial parameters were generated at random as described in the text.

(c)

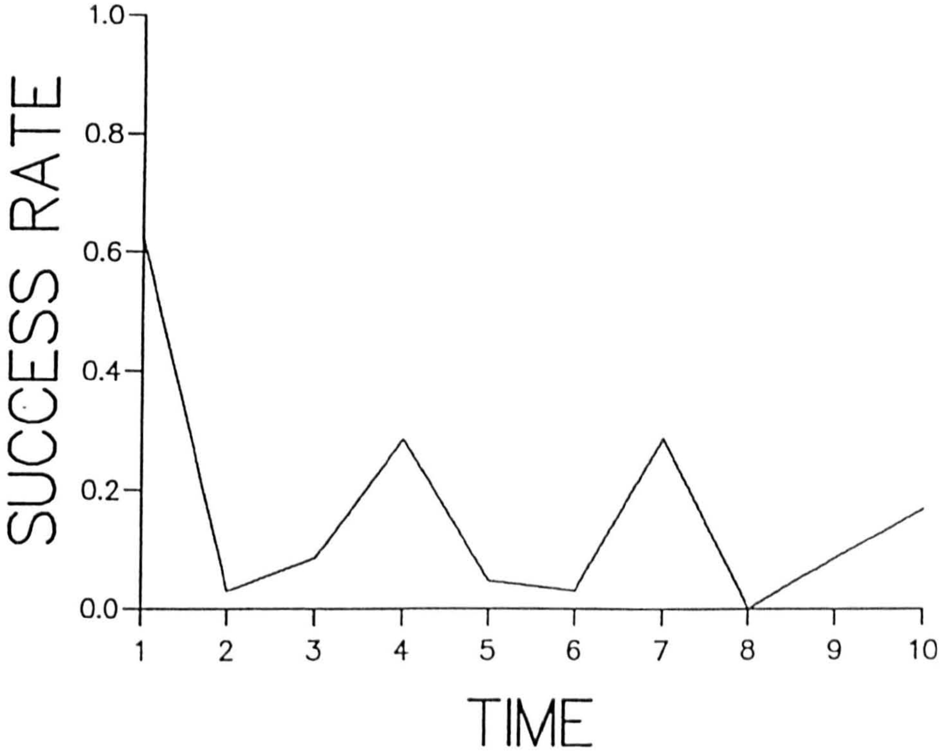


Figure 5.2 (continued).

not alter the conclusions (Table 5.2). No significant relationship was found with respect to invasions into the predator, under any mutation regime. Although linear regression if calculated did give negative slopes, these were not significant, and the values of r^2 produced were very low.

The observation of a decreasing success rate of invasions over time could be due to a lack of elements in the genotype array for new mutants to invade into. If this was the case then one might expect the number of attempted invasions into each species to decline with respect to density, since the mutant generation algorithm does not operate unless there is space for the mutant characters to be stored. The possibility of the genotype array filling up was tested by regression of attempts per unit density versus time (Table 5.3). Where mutant invasion took place into the prey, a significant positive slope was observed, suggesting that elements were not filling up over time. The opposite was observed where invasions took place into the predator.

The recording of average density over time enabled the extinction of one or other species to be observed. The results are given in Table 5.4. The results suggest that predator-prey coevolution does not often prevent predator-prey coexistence. Prey extinction was never observed, and predator extinction was infrequent. There was no significant difference between different mutation regimes in respect to the outcome of the coevolution ($\chi^2 = 0.122$, two degrees of freedom, $p > 0.900$).

5.3.3.2 Discrete time

One way analysis of variance and Model I linear regression was also performed on the discrete time success rate data set (Table 5.5). In this case only one significant result was found, in the case of the success rate of invasions into the prey under evolution in the prey alone (Table 5.5; Figure 5.3). The data set was transformed with the arcsine transformation, which did

Time Type	Continuous			
Mutation Regime →	Predator and Prey		Prey Only	Predator Only
Statistic ↓	Prey	Predator		
n	299	266	336	287
Number of Replicates	40	40	41	44
One-way Analysis of Variance				
F	12.06	0.680	6.58	1.02
p	0.000	0.727	0.000	0.424
significance	***	*n.s.*	***	*n.s.*
Linear Regression				
b	-0.0584	-0.0089	-0.0459	-0.0006
a	0.738	0.723	0.642	0.417
r^2	0.210	0.002	0.114	0.000

Table 5.2. Success rate of invasions into predator and prey: continuous time, transformed data set. Symbols and conventions used in this table are as in Table 5.1. The data set has been transformed with the arcsine transformation before analysis was performed.

Time Type	Continuous			
Mutation Regime →	Predator and Prey		Prey Only	Predator Only
Statistic ↓	Prey	Predator		
n	400	336	410	360
Number of Replicates	40	40	41	44
One-way Analysis of Variance				
F	14.65	8.68	16.23	14.88
p	0.000	0.003	0.000	0.000
significance	***	**	***	***
Linear Regression				
b	1.33	-0.999	1.50	-2.05
a	12.9	25.0	13.8	33.0
r^2	0.033	0.022	0.036	0.037

Table 5.3. Attempted invasions into predator and prey per unit density; continuous time. The number of attempted invasions was divided by the average density over the time interval for measurement, calculated as a running average of the total density of all genotypes in that species per iteration. *** indicates a highly significant result, $p < 0.001$; ** indicates a significant result, $0.001 \le p < 0.01$.

Time Type	Continuous			
Outcome → Mutation Regime ↓	Coexist	Predator extinction	Both species extinct	Total
Predator and Prey	33	7	0	40
Prey only	33	8	0	41
Predator only	35	9	0	44
Total	101	24	0	125

Table 5.4. Coexistence or extinction in predator and prey: effects of different mutation regimes, continuous time. This table summarises the time series of average density which were recorded for all simulations performed to investigate invasion success. Units are number of runs in which that outcome was recorded. A species was deemed to have gone extinct when its average density dropped to zero; this corresponded to a minimum real density at a particular iteration of 10^{-6}, the extinction threshold.

Time Type	Discrete			
Mutation Regime →	Predator and Prey		Prey Only	Predator Only
Statistic ↓	Prey	Predator		
n	444	347	338	231
Number of Replicates	54	54	45	44
One-way Analysis of Variance				
F	0.67	0.67	2.27	0.58
p	0.740	0.732	0.018	0.809
significance	*n.s.*	*n.s.*	*	*n.s.*
Linear Regression				
b	-0.0058	-0.0001	-0.0174	0.0035
a	0.343	0.0266	0.428	0.280
r^2	0.005	0.000	0.041	0.000

Table 5.5. Success rate of invasions into predator and prey: discrete time. Symbols used are as in Table 5.1.

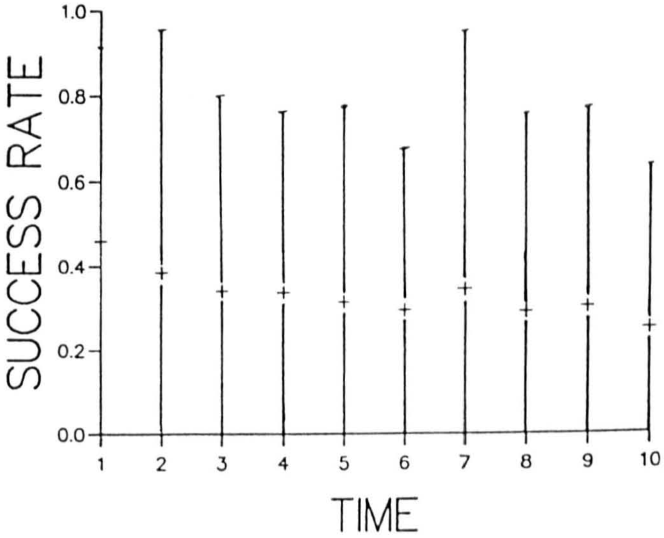


Figure 5.3. Success rate of invasions into prey when prey only is evolving in discrete time. The *success rate* for each time interval for each run was calculated as the ratio *successes/attempts*. The arithmetic mean success rate for each time interval is marked on the graph: error bars are the 95% confidence intervals.

not appear to identify a more significant relationship (Table 5.6). In contrast to the continuous time results, no significant results were obtained when both predator and prey were evolving. Once again no significant results were obtained for invasion resistance in the predator (Table 5.5).

The possibility of elements of the genotype array filling up was tested in the same way as the continuous time data set (Table 5.7). No data was available for when the predator and prey both evolved; however when the prey only evolved a positive slope was observed, and when the predator only evolved a negative slope was found. These results were similar to those of the continuous time data set (Table 5.3); however neither slope was significant.

The coexistence or extinction of predator and prey was also recorded (Table 5.8). Predator extinction, or extinction of both species, was observed much more frequently than in continuous time (the difference is significant, χ^2 for heterogeneity, 18.910, two degrees of freedom, $p < 0.001$). As in continuous time, there was no significant difference between the proportion of outcomes under different mutation regimes ($\chi^2 = 4.698$, four degrees of freedom, $p > 0.10$).

5.3.4 Discussion

5.3.4.1 Red Queen or stasis?

In order to distinguish between Red Queen coevolution and evolutionary stasis, we first need to consider the evidence for ESSs. If it could be shown that the predator-prey system evolved to an ESS in most cases, this would negate the possibility of Red Queen coevolution.

Unfortunately, the evidence for ESSs is not clear cut: only three out of eight possible cases show trends in invasion resistance implying ESSs, the results are not consistent between discrete and continuous time, and in no case does an

Time Type	Discrete	
Mutation Regime → Statistic ↓	Prey Only	Predator Only
n	338	231
Number of Replicates	45	44
One-way Analysis of Variance		
F	1.74	0.71
p	0.078	0.701
significance	*n.s.*	*n.s.*
Linear Regression		
b	-0.0227	0.0042
a	0.685	0.292
r^2	0.031	0.000

Table 5.6. Success rate of invasions into predator and prey: discrete time, transformed data. The same data set was used to generate the results of this table as was used in Table 5.5, except that the values have been transformed with the arcsine transformation before analysis was performed. Data was not available for the case when both predator and prey evolved. Symbols in the table follow the conventions of Table 5.1.

Time Type	Discrete	
Mutation Regime →	Prey Only	Predator Only
Statistic ↓		
n	436	264
Number of Replicates	45	44
One-way Analysis of Variance		
F	0.04	1.80
p	0.849	0.180
significance	*n.s.*	*n.s.*
Linear Regression		
b	0.076	-1.02
a	18.0	45.8
r^2	0.000	0.003

Table 5.7. Attempted invasions into predator and prey per unit density over time; discrete time. The number of attempted invasions was divided by the average density over the time interval for measurement, calculated as a running average of the total density of all genotypes in that species per iteration. Data was not available for the case when both predator and prey evolved. Symbols in the table follow the conventions of Table 5.1.

Time Type	Discrete			
Outcome → Mutation Regime ↓	Coexist	Predator extinction	Both species extinct	Total
Predator and Prey	34	13	7	54
Prey only	32	11	2	45
Predator only	24	12	8	44
Total	90	36	17	143

Table 5.8. Coexistence or extinction in predator and prey: effects of different mutation regimes, discrete time. This table summarises the time series of average density which were recorded for all simulations performed to investigate invasion success. Units are number of runs in which that outcome was recorded. A species was deemed to have gone extinct when its average density dropped to zero; this corresponded to a minimum real density at a particular iteration of 10^{-6}, the extinction threshold.

ESS occur consistently in one system. That is, we do not see the number of successful invasions declining to zero in all replicates of that system.

The much simplified predator-prey coevolution systems of Chapter 3 (and Marrow *et al.* 1992) suggested that mutants spiralled in the phenotype space towards ESSs. This implies slow convergence to equilibrium, and it could be that the simulations investigated here were not run for long enough to observe this. However, the length of each simulation run was severely restricted both because of the large amount of computer time needed to run the simulation, and also because of the need to build up a large number of replicate runs. If such spiralling in to evolutionary equilibrium did occur, it would be possible to detect this by observing the consequent oscillations in body sizes of predator and prey. No clear evidence of such oscillations was detected (see section 5.5), but time did not permit the examination of the dynamics of size evolution in any detail in these simulations.

It is not possible to exclude the possibility that the results observed, in terms of invasion resistance, may arise as a result of the simple genetic system and the constant abiotic environment. We may see invasion resistance building up because no more alleles can be generated which have a positive rate of increase on invasion, as a consequence of the assumptions of the model. But observation of individual trajectories (Figure 5.2) suggests that build-up of invasion resistance does occur in particular cases even if there is no clear overall trend towards it. So invasion resistance may be dependent on the underlying population dynamics of the different genotypes in the predator-prey system.

What evidence is there for Red Queen coevolution? The lack of any trend in success rate of invasions may not be sufficient evidence; this is observed in five out of the eight cases I considered, but lack of overall trend in each case conceals a considerable amount of variation in and between individual runs of each system. Ideally for Red Queen evolution we would require that the success rate of invasions remains nearly constant, but this does not seem to be the case. It is possible that predator-prey systems may not be able to show Red Queen dynamics (Rosenzweig *et al.* 1987), but models comparable to the ones used here (Marrow *et al.* 1992; Chapter 3, this thesis) can exhibit Red Queen dynamics rather easily. The lack of conclusive evidence for Red Queen behaviour may be due to the underlying genotype dynamics being too variable. There is also the possibility of transient dynamics obscuring the long-term behaviour of the population dynamical system, but the methods used in this section did not enable these features of the model to be investigated.

5.3.4.2 Asymmetries in predator-prey coevolution

It is interesting that we observe different results in predator and prey. Significant trends in the build-up of invasion resistance were only found in prey species, in both discrete and continuous time, and evidence for the accumulation of mutants preventing further mutation was only found in predator species. This suggests that an asymmetry exists in this coevolutionary system.

It may be that the predator and prey converge towards evolutionary equilibria at different rates; this conclusion is supported by the results of the (albeit simpler) model considered in Chapter 3 (Marrow *et al.* 1992). While the distance from an evolutionary equilibrium in phenotype space remains large, mutants of each species will be, at a particular time, different distances, from it, and new mutants will be sampled from distributions of different variance, so we should expect the rate of evolution in each species to be different.

This deduction is in agreement with a wide range of evidence on the evolution of predator and prey (Endler 1991), and is consistent with the life-dinner principle (Dawkins & Krebs 1979) which suggests different intensities of selection in predator and prey.

5.3.4.3 Differences between discrete and continuous time

It is well-known that the discrete time version of the Lotka-Volterra equations for interacting species (e.g., Hofbauer *et al.* 1987) exhibits less "well-behaved" dynamical behaviour than the continuous time form. Both forms were used in the implementation of the simulation model used here, in order to see whether the form of the Lotka-Volterra model used would affect the results. Two differences were detected; firstly, there were less significant trends in invasion resistance in discrete time than in continuous time, and secondly, the predator and prey coexisted less frequently in discrete time.

The first difference could result from a difference in the nature of the build-up of invasion resistance in the discrete time system, but the very great variation between individual runs in both discrete and continuous time makes this unlikely. The two time types do differ in number of iterations per run, due to the difference in amount of computer time required. However, one would expect this to work in the opposite fashion to that observed, with the continuous time model being run over less iterations, resulting in less build-up of invasion resistance. This implies that the difference in results cannot be accounted for by failure to run the simulation for long enough.

The second difference observed in the discrete time version, that coexistence of predator and prey occurs less frequently, could be accounted for by the genotype dynamics in that system leading more frequently to extinction of alleles and whole species. At low dimensions, when few mutants are present, one might expect this to be important since a well-known result on two-dimensional differential equations shows that chaotic dynamics cannot occur (Simmons 1974:341). The same is not true of the discrete time equivalent. At higher dimensions, when many mutants are present, one would expect that chaotic or other unstable dynamics could arise both in discrete or continuous time. It may be that higher dimensional systems do not occur very frequently--

as some of the results on the maintenance of polymorphism in this system seem to imply (section 5.4). The understanding of the difference between the two time systems does seem to depend upon the nature of the underlying population dynamics, as does the detection of Red Queen coevolution as opposed to stasis (section 5.3.4.1 above).

5.3.4.4 The coexistence of predator and prey under different evolutionary scenarios

Evolution depends on the availability of sufficient genetic variation, and this will not always be present in the species or system under investigation. For this reason, it is of interest to find out what the consequences of coevolution are where one species does not bear genetic variation in characters adaptive for the interspecific interaction. In the simulation model used here this was done by preventing the mutation process in one or other species. One might expect, that a predator allowed to evolve in combination with an evolutionarily fixed prey, would always or frequently cause the extinction of that prey species. Alternatively, one might expect a prey evolving with a fixed predator always to be able to escape from predation and thus attain a very high population density. So it appears that there should be consequences for the coevolution of predator and prey, when the mutation regime, or evolutionary scenario, under which they evolve, is changed (e.g. Rosenzweig & MacArthur 1963).

However the results of the simulation presented here do not support this view. In both discrete and continuous time, there is no significant difference between the different mutation regimes in terms of their effects on the coexistence of the two species. One reason for this could be inadequate sample size. If the sample size was increased we might get statistical confirmation of these observations, but such an increase would require more computer time, for a simulation which is already very time-intensive (see Appendix A).

A second reason for the lack of distinction between the different mutation regimes could be that the underlying genotype dynamics of the system are so complex as to determine the persistence of the system independently of the type of evolutionary scenario. This is not possible to test with the current results which were derived with the intention of finding a measure of system behaviour independent of population dynamics.

An additional reason is suggested by consideration of the related, but simpler, system analysed in Chapter 3 (and Marrow *et al.* 1992). In many cases in that system, if one species is fixed evolutionarily, the other is expected to evolve to an evolutionarily stable state in any case. It may be that this occurred in many of the cases considered here where extinction of one or both of the species was expected. There are, however, a number of types of evolutionary dynamics observed in the Chapter 3 system which could result in extinction of the predator; although not of the prey.

Finally it might be the case that the effect of the different mutation regime was very much less important than expected. In the constrained system, Model 2, which was used in the simulation, the coevolution of α_{12} and α_{21}, the two reciprocal interaction terms, is limited by making them both dependent on s_i, the body size of each species. This prevents biologically unrealistic values of the interaction terms, but it may also prevent the evolution of parameters in a species evolving while the other is fixed, to a level corresponding to a non-feasible equilibrium. In order to know whether this was the case, it would be necessary to have much more information about the evolution of parameters over time during the simulation. This information was not gathered in the current set of investigations, but is a suitable topic for further work (but see section 5.5 for the evolution of parameters when both species evolve).

5.3.4.5 Statistical tests of simulation results

In using regression analysis to test the results of a computer simulation, we are violating one of the basic assumptions of that statistical test, that observations are independent. Because the state of a computer simulation at any time depends on its previous states, the data used in the regression are correlated. Hence, in using this test I am not seeking to establish a formal linear relationship, but to give an approximate indication of trends in the system. It is, in any case, possible that since I am using pooled data from a number of simulation runs in each regression analysis, the serial correlation between points in this pooled data set should be very low, even if high within individual series. For these reasons I argue that the use of the technique is appropriate, even if unconventional.

5.3.4.6 Problems, and conclusions

The analysis of the results from the simulation experiments has exposed a number of problems with the method used. Among these are; the haploid genetic system, the assumption of constant fitnesses, the lack of information about the underlying population dynamics, the lack of knowledge about the related dynamics of interactions and sizes, and the limited number of replicate runs.

Modifications that could overcome these problems include the following. Firstly, the incorporation of diploid genetics would greatly increase the utility of the model, making it directly comparable to many population genetical models, such as those of Spencer and Marks (1988, 1992; Marks & Spencer 1991). It would also prevent artifacts that might arise from the use of haploid genetics. But the modification does have the disadvantage that it would make the simulation model even more complex, and would result in even larger amounts of computer time being required to run it. Many other models in evolutionary theory have been derived without the use of diploid genetics, partly for this reason.

Secondly, the incorporation of a varying external environment, specifically one in which fitnesses were continually rescaled as the environment deteriorated, would add realism to the model and prevent the accumulation of alleles at, or near, the maximum fitness. As in the case of diploid genetics, this would involve a loss of computational efficiency, which precluded its incorporation in the current model.

Thirdly, the use of more simulation runs could enable clearer results to be obtained. The only limitations on this being implemented are temporal, specifically the amount of time required to compute each run, which is considerable, up to fifteen minutes computer time in the case of the continuous time version, and the amount of time required to process the results. In this set of numerical experiments, considerably more runs were performed than are actually recorded in the results. Those that were omitted were excluded because they exceeded the time limits for simulations run as batch jobs, and thus did not output their results. The amount of time taken for each run was very dependent on the population dynamics, and more complex dynamics could result in much longer times taken to compute the results, as more calls to numerical integration routines were required.

Fourthly, the gathering of more information about the evolution of sizes, and consequently the evolution of interactions, would enable the coevolutionary process to be understood more fully. This is a problem of the amount of information produced by each run however; as two coevolving species implies two time series of size evolution, and three time series of interaction for each run.

Since the evolution of these parameters has a direct effect upon the population dynamics, it would be reasonable to include them also in the output, and this would remedy the final problem, that of possible dependence of the system upon the population dynamics, and lack of information about them. In the current analysis the population dynamics was excluded as it was intended to draw conclusions that were independent of the population dynamical behaviour of the system. However if the success rate of invaders is affected by the type of dynamics of the genotypes already in the system, then there is no reason not to include such dynamics. In the final section of this chapter I shall examine the population dynamics of the predator-prey system as evolution occurs. The understanding of the general consequences of this will be a useful preliminary to examining the population dynamics and invasions into those species together.

In conclusion, there is no clear evidence for the system being considered evolving either to an ESS or continually changing in Red Queen coevolution. In some runs the approach to an ESS did appear to occur, but this was not consistent within one type of mutation regime and time type, quite apart from across different cases. The mutation regime, or evolutionary scenario imposed on the system also did not seem to have any clear effect. Only the time type (continuous or discrete) seemed to have a consistent effect on the persistence of predator and prey populations, a feature which could probably be observed in simpler models not incorporating evolution. The failure to obtain clear-cut results on the main hypothesis being tested did however point to some improvements of the simulation method which could be use in future investigations of this type.

5.4 THE MAINTENANCE OF ALLELE POLYMORPHISM

5.4.1 Background

The problem of the maintenance of genetic variation in natural populations has been present ever since electrophoretic and other studies showed the great allelic diversity to be found in nature (e.g. Keith 1983; Lewontin 1974). Numerical and analytical work suggests that randomly constructed polymorphisms are almost vanishingly unlikely to be stable (Bodmer & Cavilli-Sforza 1971; Eshel 1971; Guess 1974; Gillespie 1977; Lewontin *et al.* 1978; Karlin 1981; Karlin & Feldman 1981). How are the large polymorphisms found naturally maintained under selection?

Karlin (1981) showed that the probability of obtaining a stable polymorphism was increased by incorporating fitness structure in the models, and Karlin and Feldman (1981) demonstrated that such models could maintain a relatively large number of alleles at equilibrium under certain conditions. Heterosis has been suggested as a possible causal factor, but the work of Gillespie (1977) and Lewontin *et al.* (1978) suggests that this is not sufficient. It has also been argued that heterosis evolves as a result of selection rather than preceding it (Ginzburg 1979), so that models where viabilities as well as allele frequencies evolve should be considered (Turelli & Ginzburg 1983).

The work of Spencer and Marks (Spencer & Marks 1988, 1992; Marks & Spencer 1991) suggests a solution to the problem. They generated alleles with random fitnesses, and allowed them to invade a population sequentially, but in some cases did not wait for the system to reach equilibrium between invasions of mutants. They found (Spencer & Marks 1988) that such "mutant bombardment" could maintain a reasonable degree of polymorphism over evolutionary time. Later modifications of their original model were able to maintain polymorphisms of similar size to those in natural populations, including about thirty alleles (Spencer & Marks 1992).

The maintenance of allele polymorphism as a problem of theoretical population genetics is akin to the ecological problem of the assembly of stable communities (Spencer & Marks 1988). Yet, interactions between species in a community are rarely taken into account in population genetical models, which are often based on single species. The maintenance of genetic variation under selection has attracted a considerable amount of interest in the ecological literature, in connection with the coadaptation of hosts and parasites (Anderson & May 1982; Hamilton 1982). It thus seems reasonable to consider what effect the ecological interactions between populations might have on the maintenance of polymorphism.

Here I shall use the simulation model presented in the preceding chapter to investigate whether many alleles can be maintained at a single locus, even in the absence of diploid genetics, by predator-prey interactions.

5.4.2 Method

The simulation models described in Chapter 4 were used throughout the investigation. Thirty-two runs were performed of each of the unconstrained model (Model 1) and the constrained model (Model 2). Continuous time models were solved using numerical methods in all cases. The initial conditions of the runs were standardised as far as possible, in order to make them replicates. All runs were started at fixed initial densities, for one type only in each species, of 1.0. The initial parameters for each species; that is, r_{11}, α_{1111}, and α_{1211} for the prey, and r_{21} and α_{2111} for the predator, were generated by random sampling on a negative exponential distribution. The mean of the distribution was set to 0.25, in order to reflect the distribution of interaction intensities observed in real food webs, where many weak and few strong interactions have been found (Hall & Raffaelli 1991; Paine 1992).

Evolution was simulated by allowing populations with different interactions to invade at low densities, as described in Chapter 4 (section 4.4.5). Parameters for the invading types were produced by simulating mutation at a constant rate of 0.5. The pseudo-random number generating routine used in creating new mutants was initialised differently for each run so as to create a different sequence of random numbers. This corresponded to a different evolutionary history in respect of the origin of new mutations. The simulation was run for one hundred iterations of mutation and population dynamics. The population dynamics of the predator and prey genotype densities were solved over a range of 100 and with an accuracy of approximately seven decimal places (precise assignment of accuracy is not easily possible when numerical integration algorithms of the type used here are considered; for more information see Chapter 4 and Numerical Algorithms Group, 1990).

The total population density of all genotypes in each species was recorded at each iteration, along with the number of mutant types present at that time. The output was in the form described in Chapter 4. The persistence of a large number of genotypes over a period of time was taken as indicative of the maintenance of polymorphism under selection. The population densities of the types present were also recorded in order to distinguish when species had gone extinct.

5.4.3 Results

The results of the simulation runs are summarized in Table 5.9. Statistical analysis was performed using the Minitab statistical package (Minitab, Inc. 1989). The types of behaviour observed in Model 1 and Model 2 were significantly different (χ^2 for heterogeneity, 26.2, 5 degrees of freedom, $p < 0.001$).

Simulations run under the assumptions of Model 1 most commonly exhibited

Number of alleles	Model 1	Model 2
Many	0	9
One/Many	4	11
Many/One	0	3
One	10	3
Total Coexisting	14	26
Predator Extinct	14	6
Both Species Extinct	4	0
TOTAL	32	32

Table 5.9. Results of simulations on the maintenance of allele polymorphism. The state given is the one which the system reached, and maintained over a large number of iterations, towards the end of the run. *Many* indicates that more than one genotype was maintained in each species. *One/Many* indicates that only one genotype was maintained in the prey, with several maintained in the predator. *Many/One* indicates the reverse. *One* implies that only one genotype was found in each species. *Coexisting* species were those that did not go extinct throughout the simulation run. All values given in the table are numbers of simulation runs. All simulations were performed in continuous time.

only one genotype in each species. In a number of cases a number of different genotypes were maintained in the predator in combination with just one genotype in the prey.

It is difficult to determine whether the results of evolution in Model 1 are representative of behaviour of the system, since species went extinct so frequently in this class of simulations. The number of runs in which both species coexisted throughout the simulation (Table 5.9) is significantly different between the models (G-test for independence with Williams' correction, 9.68, 1 degree of freedom, $p < 0.01$). I suggest that this arises from the lack of evolutionary constraints on Model 1 (see Chapter 4 and section 5.5 below).

The results of evolution in Model 2 are more interesting with regard to hypotheses about the maintenance of allele polymorphism. Several alleles were maintained in both species simultaneously in a number of runs; but the presence of only one type in the prey, and several in the predator was also common, and a number of other behaviours were observed.

5.4.4 Discussion

5.4.4.1 The maintenance of allele polymorphism by predator-prey interactions?

In the case of the system without constraints on the evolution of interactions,Model 1, there is little support for the maintenance of allele polymorphism by predator-prey interactions. In no cases were a number of different genotypes maintained in both species at the same, implying the persistence of allele polymorphisms under selection. In a few examples a polymorphism persisted in the predator only, but there are two difficulties in using these cases as support for the maintenance of polymorphism.

If only one prey type occurs in the Model 1 system, then irrespective of how many predator types are found, they all have to adapt to consume only one prey. Thus the trait in any predator individual of a particular genotype relating to interaction with the prey are entirely defined by one parameter, α_{21mn} where the *m*th genotype of the predator is interacting with the *n*th genotype of the prey, the only one currently present. This can result in the accumulation of predator types all with identical, optimal values for their interaction with the prey type. Since we hold the predator intrinsic growth rate term r_2 constant, and there is assumed to be no self-limitation in the predator, this will be the only trait under selection. Thus we may observe the build up of apparently distinct genotypes which are in fact identical with respect to natural selection.

A second problem which obscures any conclusions we can draw from the Model 1 system is the possibility that the presence of several alleles in one or other of the species over time is not a result of the long-term dynamics of the genotypes, but rather a consequence of transient dynamics resulting from the continual invasion and extinction of many alleles. The hypothesis of the maintenance of allele polymorphism implies that the same alleles are present at a locus over long periods of time.

The system of Model 2, with evolutionary constraints on the evolution of interactions introduced via the intermediate variables s_i, or body size, offers slightly better support for the hypothesis of the maintenance of allele polymorphism. The presence of different alleles over a period of time in both species is what we should expect, but there are also a wide range of other behaviours exhibited by this system (Table 5.9). The proportions of the different behaviours observed when predator and prey coexist are not significantly different from random expectation (χ^2 for heterogeneity, 7.33, 3 degrees of freedom, $p > 0.05$).

Nevertheless, the problems raised in connection with Model 1 may also be relevant to Model 2. If we look at the time series of number of alleles present in each species over time (Figure 5.4), we find both in species where only one

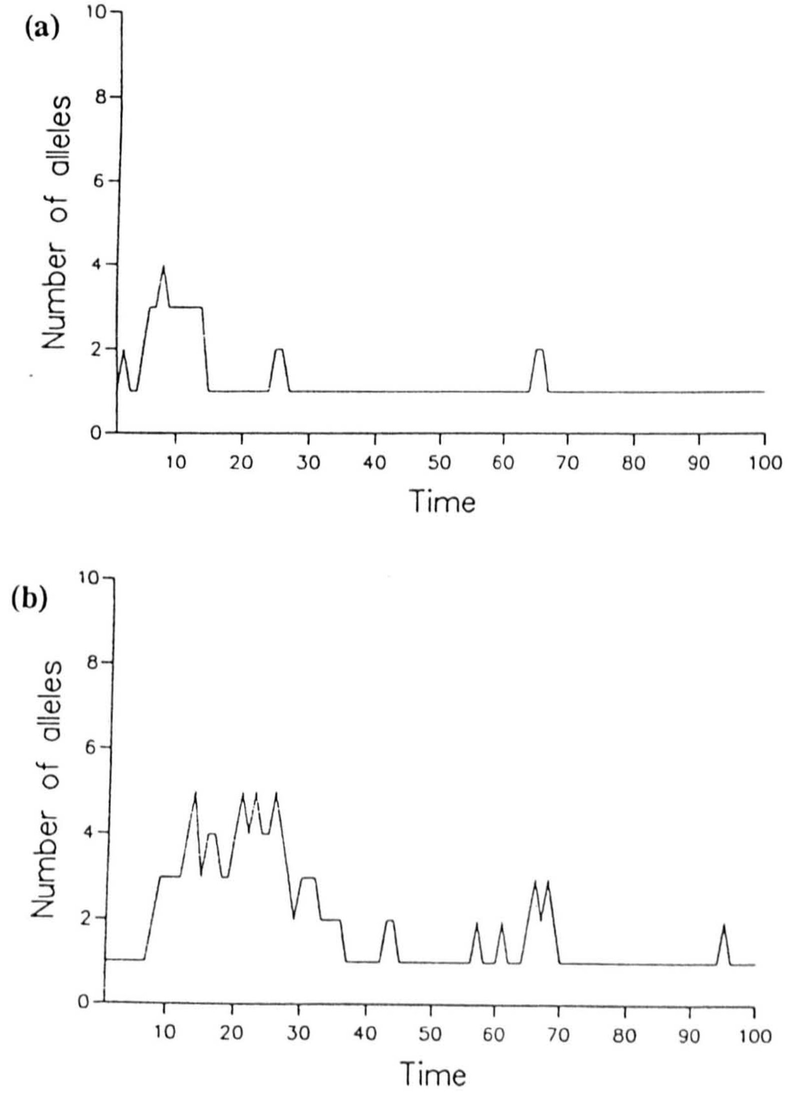
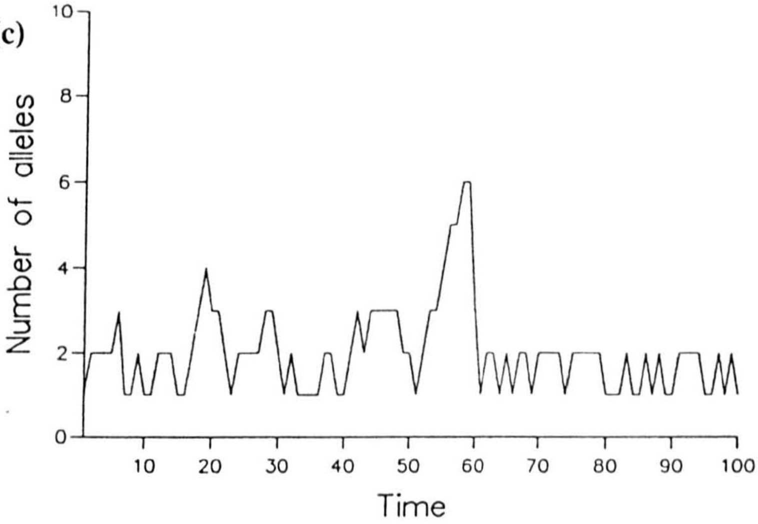


Figure 5.4. Numbers of alleles present in predator and prey over time. (a) Model 1, prey; (b) Model 1, predator; (c) Model 2, prey; (d) Model 2, predator. The number of alleles present was the number of genotypes at a density greater than or equal to the extinction threshold (10^{-6}). The maximum number of genotypes in each species was ten. The two runs shown are typical of the simulations.

(c)



(d)

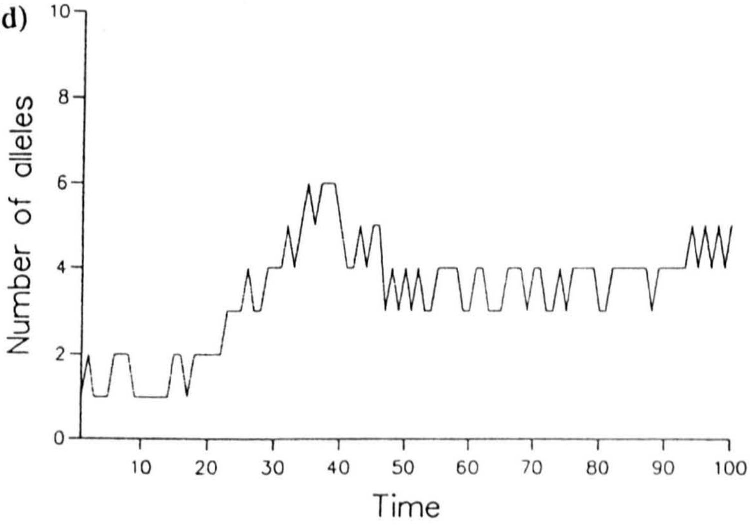


Figure 5.4 (continued)

allele persists (Figure 5.4 (a)), and ones in which an apparent polymorphism occurs (Figure 5.4 (b), (c) or (d)), the number of alleles present fluctuate quite considerably over time, implying transient behaviour. It is also possible that identical predator types may accumulate, in a similar manner to Model 1. However there do appear to be some ways in which the simulation method could be improved.

5.4.4.2 Distinguishing transient dynamics

Displaying the genotype dynamics of each genotype within a species would allow transient turnover and long-term maintenance of alleles to be distinguished. This would lead to a considerable increase in the amount of information output by the simulation, but would assist in further understanding of the results.

When the genotype dynamics are modelled explicitly, it might be possible to show that the system had approached an attractor, although there would be some difficulty with this approach due to the high dimensionality of the system. (The predator-prey system modelled here has a maximum dimensionality of twenty).

It might also be effective to reduce the mutation rate in order that the system was not returned to transient dynamics by too frequent invasions of new alleles. But here arises the trade-off between rapid, but unrealistic evolution, and evolution on a more realistic timescale with the resulting problem that the simulation has to be run for a very long time before any biologically interesting consequences happen. The simulation model used here was already very time-intensive (see Appendix A), even after the number of iterations had been reduced by increasing the amount of ecological dynamics between each one.

5.4.4.3 Preventing the build-up of similar genotypes

Having removed the problem of transient dynamics, there still remains the one of the build-up of identical or near-identical alleles at a peak of fitness. This problem arises from two features of the simulation model; the constant environment, and the fact that only one variable represents the interaction of one genotype with another particular genotype.

The constant environment external to the predator and prey themselves means that fitnesses always have the same values for the same combinations of genotypes. Hence there can be values of traits which will always give the maximum fitness in the system. So it is possible for alleles to accumulate with nearly identical characters near the peak of fitness. I have tried to prevent the accumulation of precisely identical alleles by restricting the number of combinations of values of interactions that can occur, that is, the genotypes are sampled from a limited pool of characters. It might be of more interest to make the traits under selection (the Lotka-Volterra interaction terms) vary continuously, as many characters do vary in this way in nature.

5.4.4.4 Altering the mutation process

We have assumed that mutants are generated at random on a range of character states. This is intended to reflect the fact that mutations do not arise *de novo*, but are ecologically close to their progenitors (Akçakaya & Ginzburg 1989). Turelli (1984) has distinguished between "house of cards" and "continuum of alleles" models of genetic systems under mutation-selection balance. The former derive alleles at random, while the latter derive new alleles by some process from ancestral ones. We argue that in considering the interaction of ecology and genetics, the latter approach is more appropriate.

As a result we have to deal with a large number of possible combinations of characters leading to fitnesses. An alternative approach to the study of evolution in connection with interacting species has been taken by Kauffman and colleagues (Kauffman & Johnsen 1991). By restricting the amount of mutational states to two, they are able to construct and study the properties of rugged fitness landscapes, where the fitness of every possible genetic combination can be explicitly stated. Their approach offers some revealing insights into the self-ordered states which interacting evolving species can reach under selection from apparent chaos (Kauffman 1991), but it is not possible to replicate such an approach in a study of this kind due to the assumption of a very large number of mutational states.

5.4.4.5 Constraints on the evolution of polymorphisms

In population genetical representations of models of the maintenance of polymorphism (e.g. Spencer & Marks 1988), constraints on interactions are not required, since demographic parameters are not under selection. Constraints on evolutionary parameters may be required however. In their earlier models Spencer and Marks (Spencer & Marks 1988; Marks & Spencer 1991) observed that although polymorphisms of reasonable size could be maintained under selection, much larger polymorphisms (say thirty alleles) could be observed in nature. How were these maintained? In later work (Spencer & Marks 1992) they tried imposing correlations between fitnesses of the same allele as part of different diploid pairs, and found that much larger polymorphisms could be maintained. This is perhaps not surprising, because it indicates that alleles which have a relatively high fitness in combination with some other allele, are more likely to have a high fitness, and thus persist under selection, in combination with any other allele in the gene pool. Their assumption seems reasonable, in view of the occurrence of pleiotropic effects and incomplete dominance in nature. I did not include any such restrictions in the model presented here, in an effort to limit its complexity. It is possible that a modification of this kind could result in the maintenance of polymorphisms approximating better to the size and complexity of natural ones.

5.4.4.6 Conclusions

In comparison with the natural environment, it is perhaps surprising that any apparent polymorphism has been maintained at all in our system. I have postulated constant fitnesses as a result of a constant environment (except for the other species). I have assumed that the environment is uniform and thus that individuals of each species interact at random. All these assumptions are not satisfied in nature, where a great deal of genetic variation is maintained. What is more, polymorphisms should not be maintained in a single-species genetic model under these conditions.

In addition, I have assumed density-dependent selection, which would result in a fitness of zero at an ecological equilibrium. Analysis of the evolution of predator and prey at ecological equilibrium (Chapter 3) suggests that polymorphisms are unlikely to occur in such a system (R. Law, *pers. comm.*). On a more realistic fitness landscape, it would be reasonable to expect many local peaks of fitness, and hence allele polymorphisms might occur more frequently.

It appears that the limited evidence for polymorphisms occurring in this system is confounded with the effect of transient genetic dynamics, and the effect of the accumulation of similar alleles cannot be ruled out. However the use of the simulation does suggest some methodological improvements which could assist research on the topic in the future.

5.5 THE POPULATION DYNAMICAL CONSEQUENCES OF PREDATOR-PREY COEVOLUTION

5.5.1 Background

The population dynamics of predator-prey interactions have often been modelled through Lotka-Volterra equations (e.g. Svirezhev & Logofet 1983; Hofbauer & Sigmund 1988:40; Murray 1989:63). These equations have the disadvantage that they are non-linear, and thus when formulated in continuous time, are not soluble by the conventional techniques of calculus, for systems of linear equations (Simmons 1974). Instead analysis of the stability properties of the equilibria of such systems is often used (Simmons 1974:296). The corresponding difference equations (Hofbauer *et al.* 1987) are even less well understood analytically.

Local asymptotic stability (often called "local stability", after May 1973) analysis is often used in understanding ecological population models, but can be misleading, in that it only gives information about the small region near an equilibrium point for which a linear approximation to the nonlinear equations is appropriate (Wang & Guiterez 1980; Anderson *et al.* 1992; Law & Blackford 1992). Global measures of the stability of equilibria, such as permanence (also termed cooperativeness, permanent coexistence, uniform persistence or ecological stability; see Hofbauer *et al.* 1987) may be more appropriate (Hutson & Law 1985; Hofbauer *et al.* 1987; Hofbauer & Sigmund 1988; Anderson *et al.* 1992; Law & Blackford 1992; Law & Morton 1992). However there are problems in applying permanence to ecological systems of more than three species (Law & Blackford 1992; R. Law, *pers. comm.*).

The introduction of genotype densities into the population models described in previous chapters of this thesis effectively increases the dimensionality of the system and renders the technique of permanence ineffective. For this reason numerical simulation may be one of the few approaches that can be used to investigate the population dynamical consequences of predator-prey evolution away from the linear regions near equilibria.

What dynamics should be expected in evolving interacting populations is not clear. It is well-known that in continuous time, a system with a dimension of at least three is required for chaotic dynamics to occur, and for lower dimensions only limit cycles or point equilibria are found. In discrete time systems, no such result is known.

If we refer to the evidence from natural populations, it is easily to find evidence for populations spending most of the time away from equilibria (Wiens 1984), despite much of biological theory being based on the assumption that populations are at equilibrium. The simple discrete-time single-species models examined by May and others (May 1974, 1976; May & Oster 1976) showed that very complex dynamics could arise in mathematically very simple systems. Gilpin (1979), and Hastings and Powell (1992) show chaos in simple three-species systems.

The ease of observation of chaos in mathematical models led to a search for its occurrence in nature. Hassell *et al.* (1976) fitted parameters to insect populations but found only one located in the chaotic regime. Laboratory experiments (Thomas *et al.* 1980; Mueller *et al.* 1981; Stokes *et al.* 1988; Nisbet *et al.* 1989; but see Bellows & Hassell 1988) mostly seemed to suggest selection would act to produce stable parameter values. By contrast, attractor reconstruction has provided the best evidence for chaos in natural populations (Schaffer 1984, 1985; Schaffer & Kot 1985; Rand & Wilson 1991; Turchin & Taylor 1992). Whether chaos occurs in nature appears to be still an open question (against; Berrymann & Millstein 1989, see also Łomnicki 1989, Mani 1989, Nisbet *et al.* 1989; for; Godfray & Blythe 1990; Rand & Wilson 1991).

When evolution as well as population dynamics has to be considered, the situation becomes more complex. Evolution can result in changes in the dynamical properties of populations, which may affect the dynamical behaviour of the system (Nicholson 1957; Stokes *et al.* 1988). Thomas *et al.* (1980) argued that chaotic dynamics would be prevented by a kind of group selection. Nisbet *et al.* (1989), and Mani (1989), suggested evolution to stability could arise through conventional individual selection.

Metz and others (Metz 1992; Godfray *et al.* 1992; Metz & Godfray 1992) have used Lyapunov exponents (Metz *et al.* 1992) to examine the evolution of parameters in populations with complex dynamics. Some of their results predict evolution to parameter values corresponding to stable equilibria (Metz 1992; Metz & Godfray 1992) but such results are strongly affected by the constraints one places on such a model, and evolution from stable to chaotic dynamics, or to cyclic dynamics, or some other combination appears possible (*ibid.*; Godfray *et al.* 1992).

The difficulty of studying evolution in laboratory populations, and then fitting a mathematical model to the data obtained in order to predict the dynamical consequences of evolution makes simulation most appropriate to investigate this topic. In the following pages I will present time series of predator and prey population dynamics for the model described in the previous chapter, and contrast the type of dynamics that occurs after evolution with that occurring earlier in the time series. This should provide an indication of the dynamical consequences of the evolution of the predator-prey interaction.

The simulation programs described in Chapter 4 are used, both in continuous and discrete time implementations. Both the unconstrained (Model 1) and the constrained (Model 2) versions are used.

5.5.2 Results

What are the consequences of predator-prey coevolution for population dynamics? In order to answer this question I present a series of examples, intended to be representative of the behaviour of the system. The complexity of a simulation model sufficient to study this task means that not every combination of possible parameters could be examined.

Considering first the unconstrained system (Model 1), in discrete time, we might expect evolution to result in unstable non-equilibrium dynamics. However in many cases this does not occur, and the predator and prey converge to an equilibrium. Figure 5.5 shows an example. The position of the population dynamical equilibrium is continually changing, under selection, but the predator and prey manage to reach the new equilibrium each time. Selection acts to increase the equilibrium population density of the predator, and decrease that of the prey. We can account for this behaviour by considering the effect of selection on the ecological interaction terms (Figure 5.6). Selection acts on α_{11} to reduce it to near its minimum value, consistent with evolution of lack of self-limitation in the prey. α_{12} meanwhile evolves to a minimum absolute value while α_{21} evolves to a maximum. So the biologically paradoxical situation occurs of a predator evolving independence from predation, while the same predator evolved increased dependence on that species. This is a consequence of the independent evolution of α_{12} and α_{21} previously referred to.

The evolution of interactions causes the zero isoclines for predator and prey to change position on the predator-prey phase plane (Rosenzweig & MacArthur 1963; Rosenzweig 1973). The population dynamic equilibrium of the predator-prey system is at the intersection of the two isoclines, and so the equilibrium moves on the phase plane; Figure 5.7 shows this effect. The predator-prey system first reaches an equilibrium at about (0.5, 0.1), but selection then moves the equilibrium position towards the upper left of the diagram, where the predator density is higher and the prey density is lower. This occurs a number of times, and each time the populations converge to the new equilibrium.

Similar behaviour is found in the unconstrained continuous time system

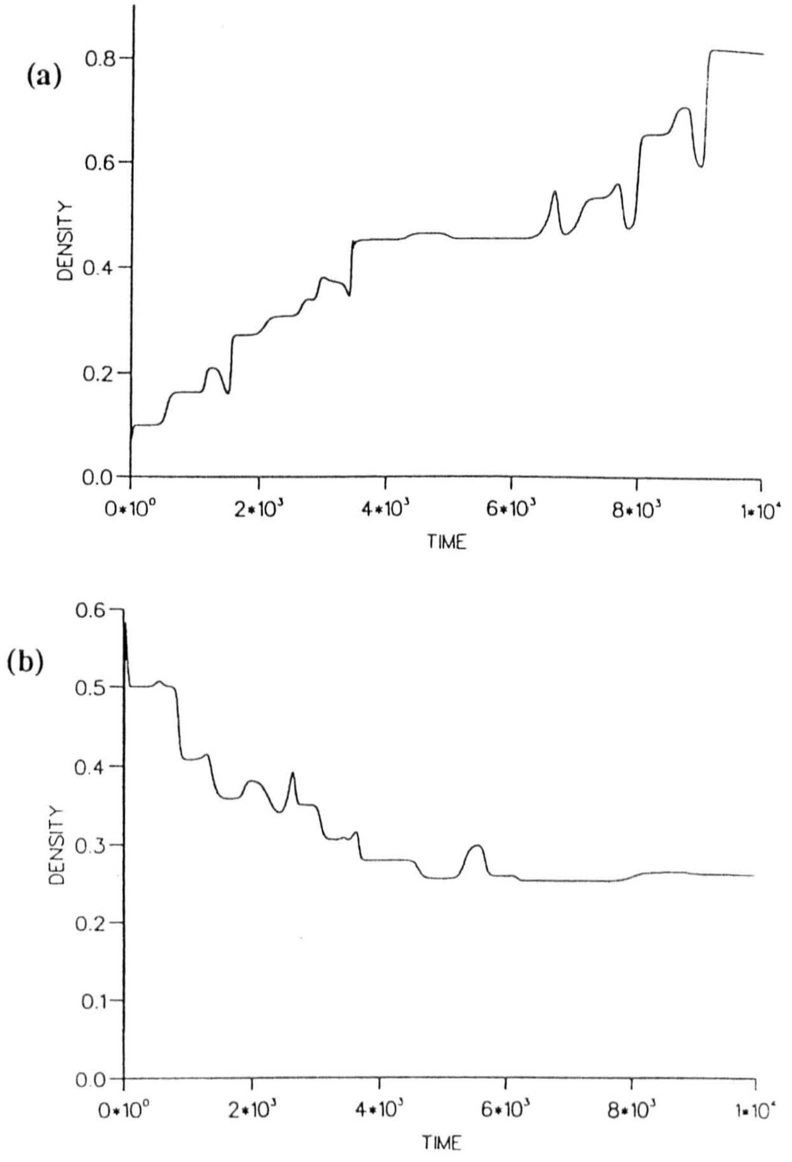


Figure 5.5. Evolution of population dynamical equilibria in predator and prey: Model 1, discrete time. (a) prey; (b) predator. Predator and prey converge to an equilibrium. Natural selection on interaction strengths changes the location of the equilibrium, then both populations converge to new equilibria. *Density* is total density of all genotypes in that species. *Time* refers to number of iterations completed.

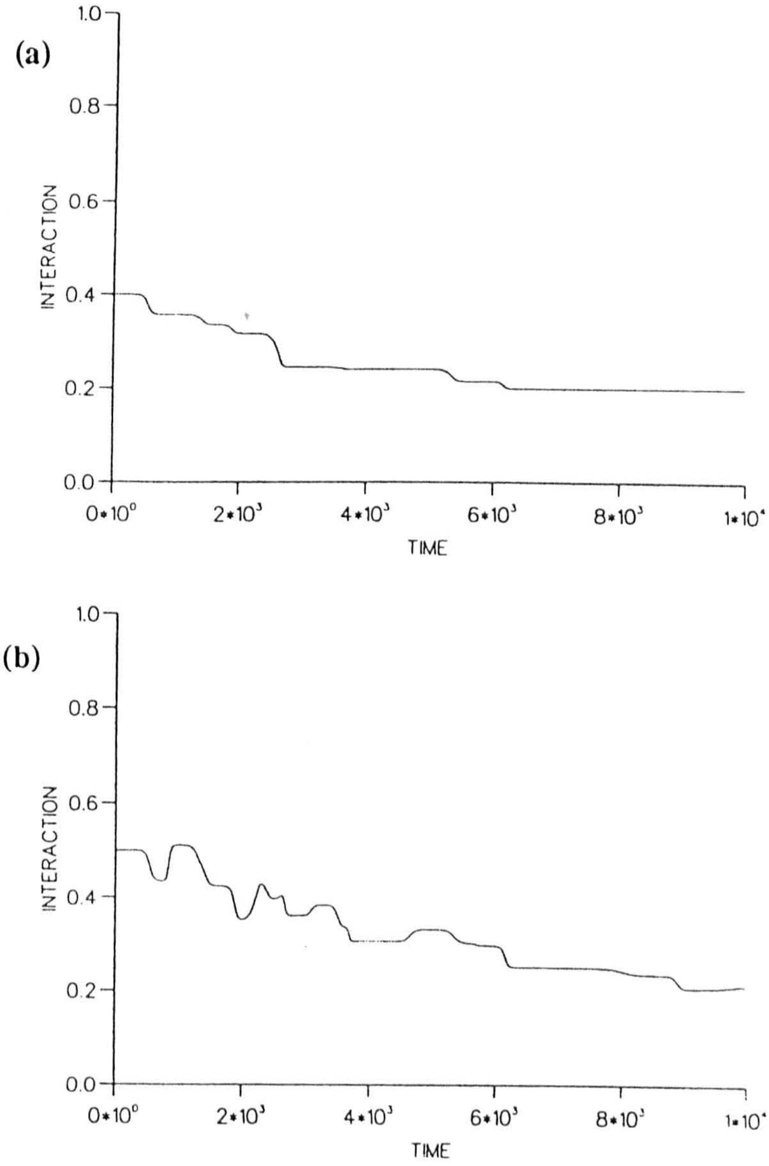


Figure 5.6. Evolution of interactions between predator and prey in the unconstrained model (Model 1). (a) α_{11}; (b) α_{12}; (c) α_{21}. The system corresponds to that of Figure 5.5. Population dynamics were evaluated in discrete time. *Interaction* denotes the weighted mean of the absolute value of the interaction intensity, weighted by the probability of occurrence of particular intergenotypic interactions, I_{ij} (calculated as in Equation 4.8). *Time* refers to the number of iterations completed. The simulation was run for ten thousand iterations.

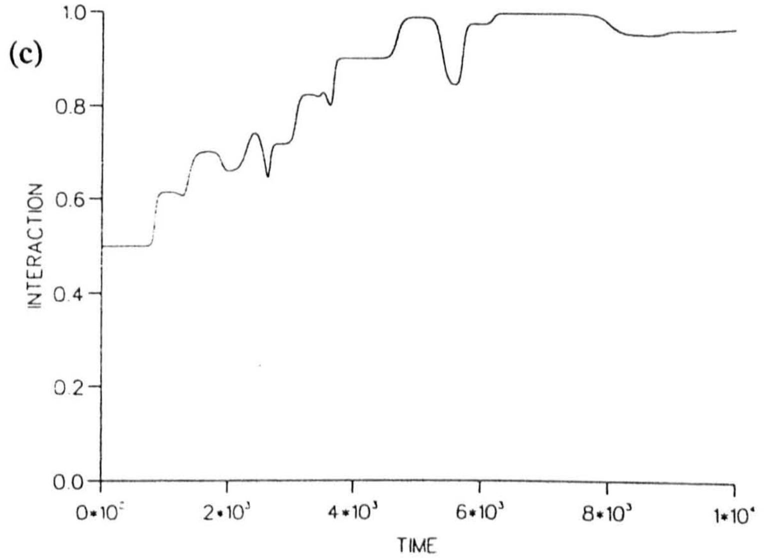


Figure 5.6 (continued)

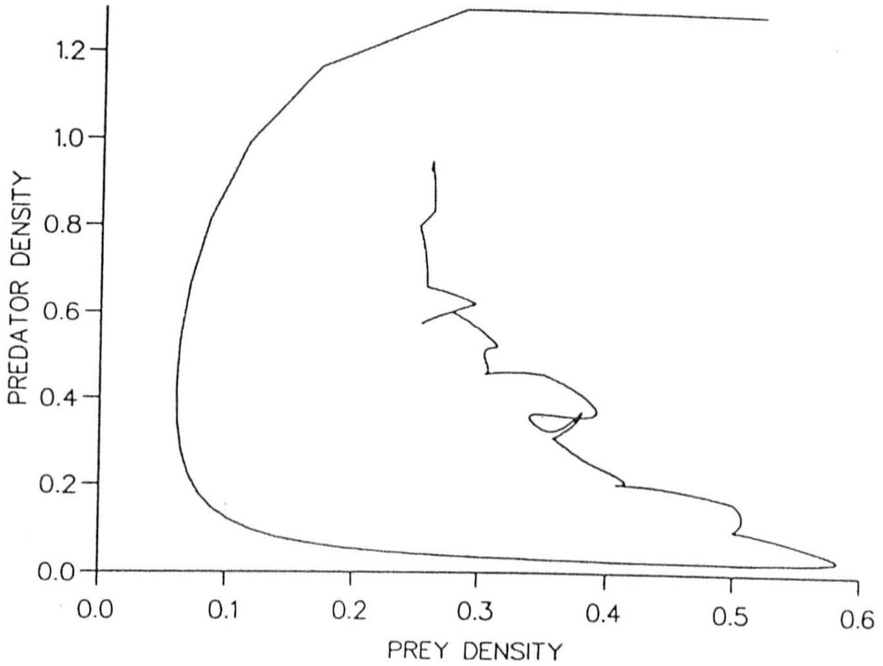


Figure 5.7. Phase plane of predator-prey population dynamics under Model 1 evolution, discrete time. The system is the same as Figure 5.5. Evolution causes the position of the predator and prey zero isoclines (not marked) to change so that the predator-prey equilibrium point moves to the upper left, where prey density is low and predator density is high. *Prey density* is the total density of all genotypes present in the prey species at each iteration; *predator density* is the corresponding value for the predator.

(Figure 5.8). Note that in this case the prey appears to be approaching an equilibrium density which is higher than that of the predator, more in line with what biological intuition would suggest. If this version of the model were run for longer (difficult, because of the great demands on computer time), one might find that the system eventually evolves to the situation in Figure 5.5.

This is not the only behaviour found in Model 1, however. Selection on interaction intensities can lead the system into regions of parameter space where cyclic dynamics occur (Figure 5.9), and chaotic dynamics can be produced for many combinations of parameters. It is possible that chaos did not occur in the examples shown here often due to the limits imposed on the values of the interactions ($0 < \alpha_{ij} <= 1$), and because the intrinsic growth rates r_i were not allowed to change. Higher intrinsic growth rates and stronger interactions are both likely to produce chaos.

Cyclic dynamics can also be unstable (Figure 5.10). In this example selection leads to an increase in the benefit the predator obtains per prey (α_{21}) and causes the predator and prey to cycle with ever-increasing amplitude, eventually forcing the prey to extinction ,and very soon afterwards, the predator. In many other cases extinction of the predator or both species occurs.

The constraints imposed on the separate coevolution of α_{12} and α_{21} by the incorporation of body sizes (s_i) in Model 2 might be expected to result in a system with more "well-behaved" dynamics. If we examine a particular Model 2 run (Figure 5.11), we find that population dynamics are relatively stable. The constraints on the interactions affect their evolution. α_{11} evolves to a minimum as the course of the simulation proceeds (Figure 5.12 (a)), as in Model 1. α_{12} and α_{21} by contrast (Figures 5.12 (b) and (c)), attain intermediate values, reflecting the opposing selection pressures on them, and the restrictions on their covariation.

Population dynamics often showed similar behaviour to Model 1; convergence to stable equilibrium, reflecting similar overall constraints on

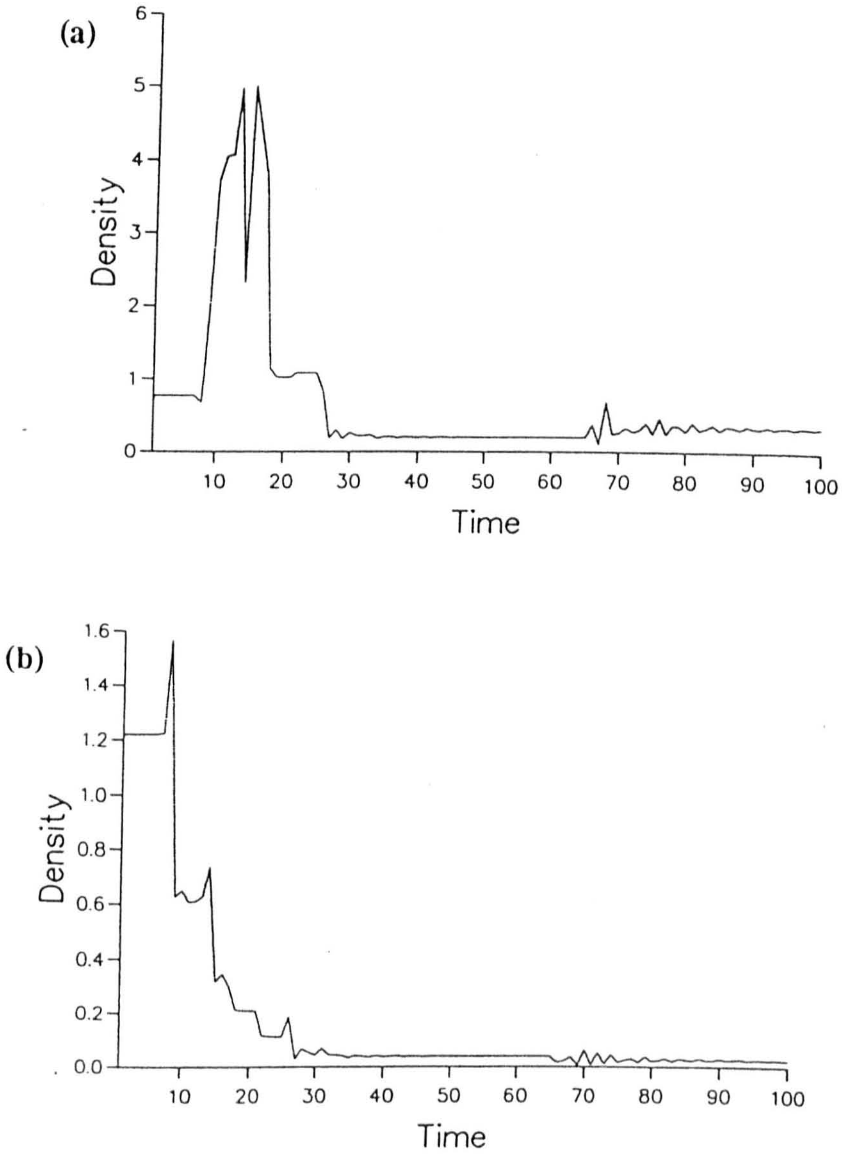
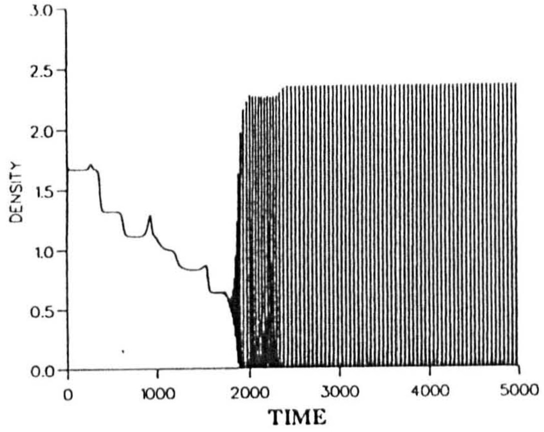


Figure 5.8. An example of the unconstrained (Model 1) evolution of population dynamics in continuous time. (a) prey; (b) predator. A period of unstable change near the start of the simulation converges towards an equilibrium. *Density* refers to the total density of each species. *Time* refers to the number of iterations completed. The simulation was run for one hundred iterations, due to the amount of computer time required.

(a)



(b)

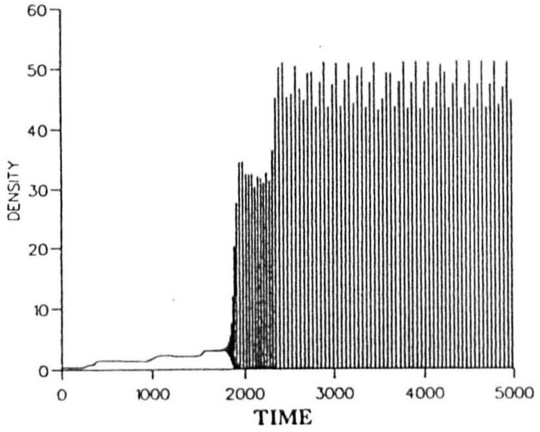


Figure 5.9. Evolution from equilibrium to limit cycles in predator and prey. The unconstrained (Model 1), discrete time model is used. (a) prey; (b) predator. Evolution of parameters leads to a succession of stable equilibria, followed by the system entering a zone of cyclic dynamics of gradually increasing amplitude. At the end of the simulation, the prey population dynamics appear to have attained a stable cycle, but it is not clear that this has occurred in the predator. *Density* refers to the total density of all genotypes in a particular species. *Time* refers to the number of iterations completed.

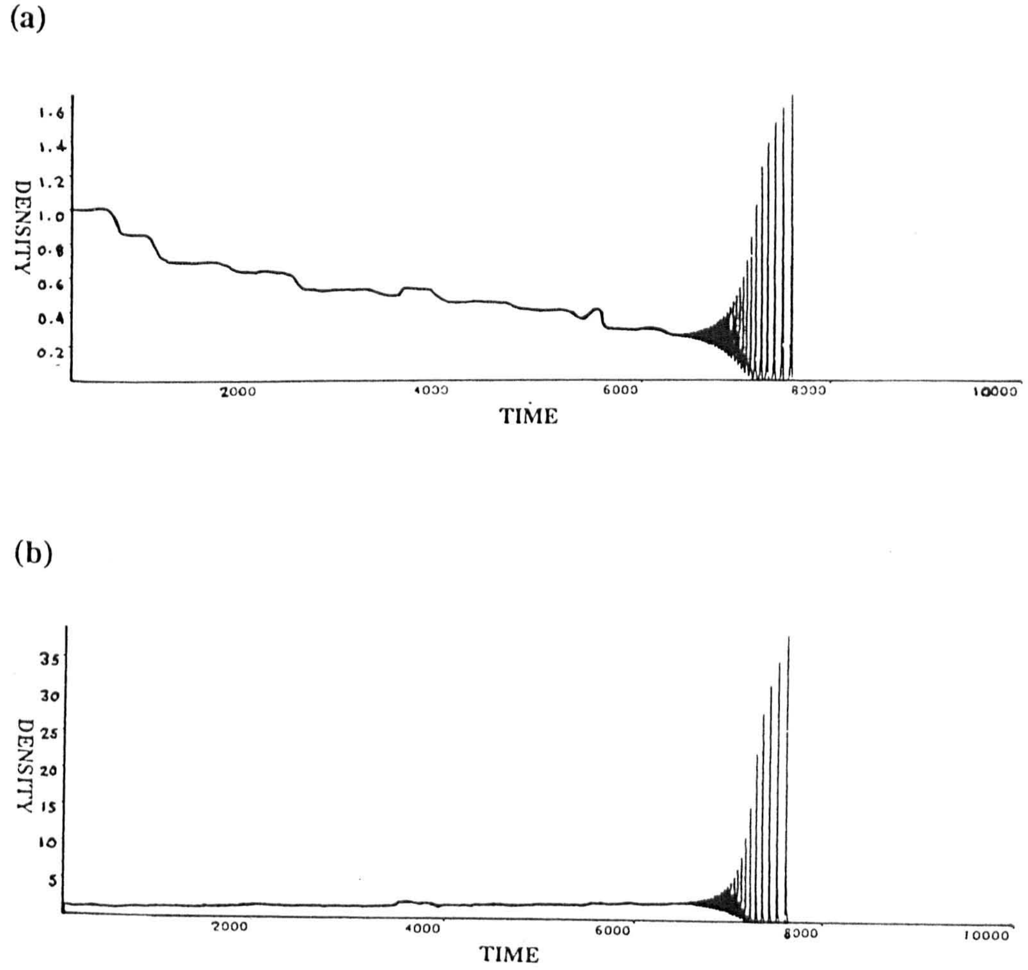


Figure 5.10. Evolution of unstable cycles in predator and prey. (a) prey; (b) predator. The discrete time, unconstrained (Model 1) model was used. Natural selection on interactions leads to an increase in the predator effect on prey (α_{21}), resulting in cyclical dynamics of increasing amplitude, eventually driving the prey to extinction, followed by the predator. *Density* refers to the total density of all genotypes in a particular species. *Time* refers to the number of iterations completed.

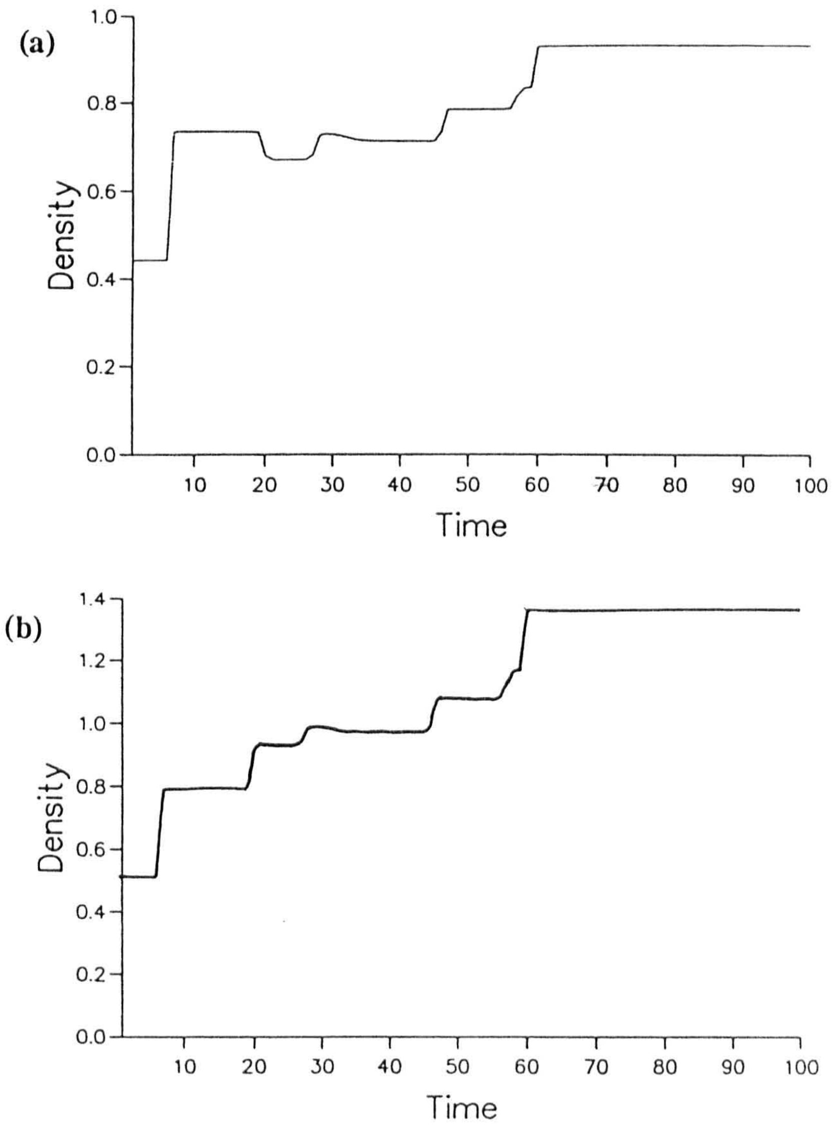
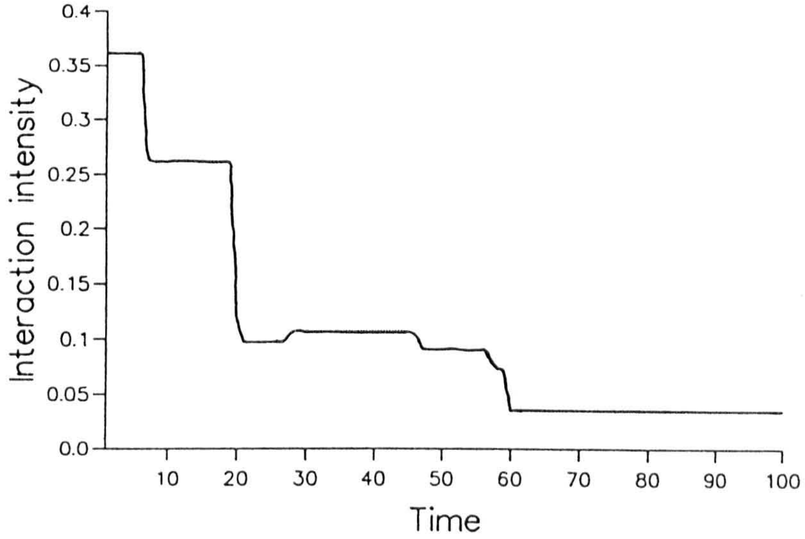


Figure 5.11. Evolution of population dynamics under constraint in predator and prey; Model 2, continuous time. (a) prey; (b) predator. Evolution leads to a different equilibrium for population density, at a greater density in both species than at the start of the simulation. *Density* refers to the total density of all genotypes in a particular species. *Time* refers to the number of iterations completed.

(a)



(b)

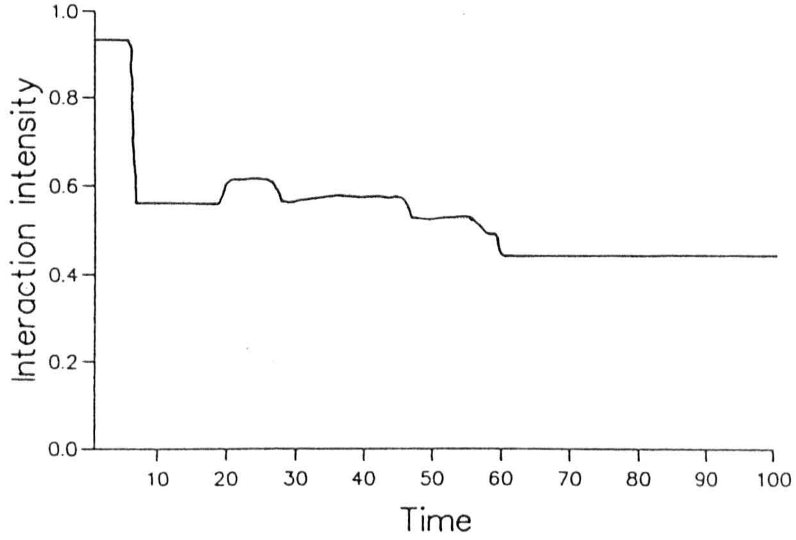


Figure 5.12. Evolution of interactions between predator and prey under constraint (Model 2), continuous time. (a) α_{11}; (b) α_{12}; (c) α_{21}. The system corresponds to that of Figure 5.11. *Interaction Intensity* refers to the arithmetic mean of the intergenotypic interactions, weighted by the probability of occurrence of each interaction (I_{ij} as Equation 4.8). *Time* refers to the number of iterations completed.

(c)

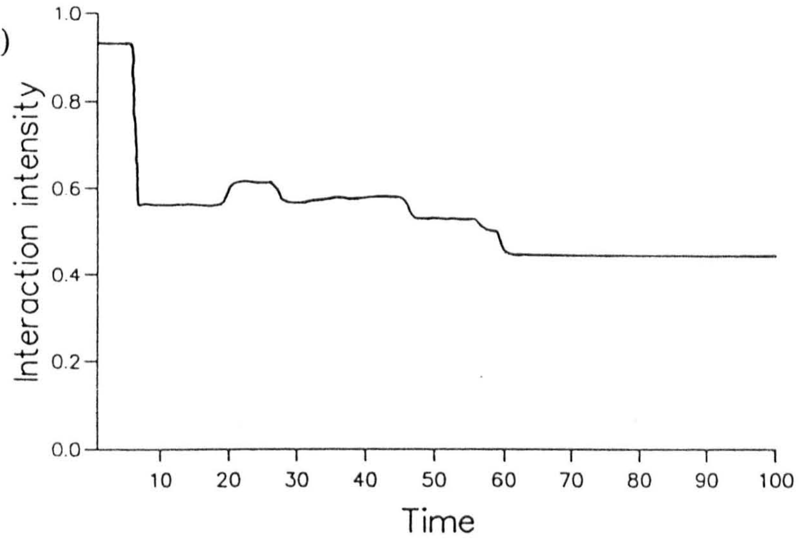


Figure 5.12 (continued)

parameter values. However, the lack of extreme values of predator effect on prey and *vice versa* in this model meant that extinction of the predator was observed only very rarely, and extinction of the prey leading to extinction of the whole system hardly ever. Unstable dynamics not resulting in convergence to an equilibrium was observed in this system, but frequently resulted in extinction of one or both species, and hence is not shown in the examples presented here.

In order to account fully for the behaviour of Model 2, we must examine also the values of s_i over time. Figures 5.13 (a) and (b) show the unweighted means for each species over time. We can see that s_1 declines to a very low level. It is probable, that, given sufficient variation, it would decline still further. The mean of s_2 reaches a value of about 0.5 at the same time. Looking at the values of interactions for each individual genotype (Table 5.10) shows considerable variation between genotypes, both in interaction values and densities, but such variation is to be expected in our model, reflecting evolutionary variation.

5.5.3 Discussion

The examples of population dynamics under evolutionary change shown here show that no single dynamical consequence can be attributed to predator-prey coevolution. Evolution can maintain populations within the stable equilibrium zone of parameter space, but it can also convert stable equilibrium dynamics into stable limit cycle behaviour, or unstable cyclic dynamics leading to extinction. Stable dynamical behaviour seems to be quite robust to evolutionary change of parameters. The lack (Model 1) or presence (Model 2) of evolutionary constraints via body size does not seem to seriously affect the conclusions. In addition, evolution from stability to chaos is plausible, although prevented in a number of cases considered here by assumptions about

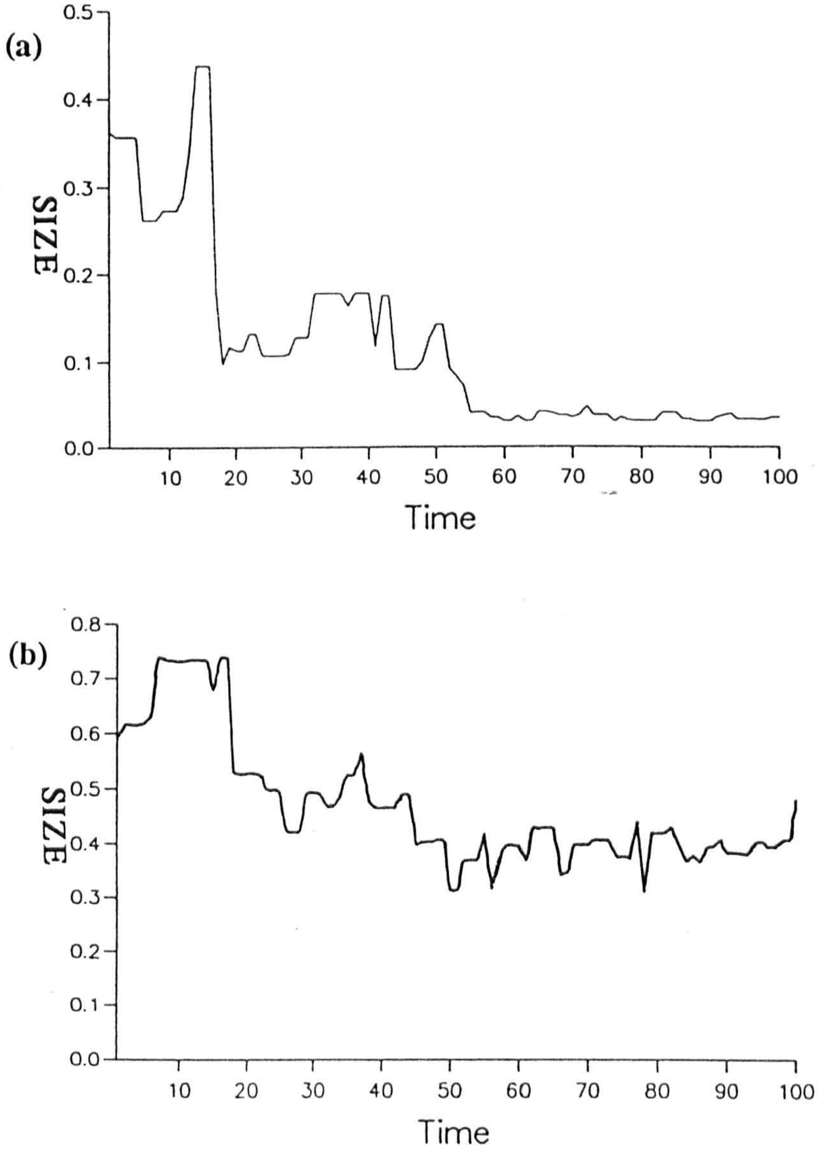


Figure 5.13. Evolution of sizes of predator and prey under constraint (Model 2). (a) prey; (b) predator. The continuous time version of the simulation model was used. *Size* refers to the arithmetic mean of the sizes of the different genotypes within that species. *Time* refers to the number of iterations completed.

Time	Prey		Predator	
	Density	Interactions	Density	Interactions
0	$x_{11} = 1.0$	$\alpha_{1111} = -0.1769$ $\alpha_{1211} = -0.6547$	$x_{21} = 1.0$	$\alpha_{2111} = 0.6547$
40	$x_{11} = 1.5915$	$\alpha_{1112} = -0.0217$ $\alpha_{1111} = -0.0217$ $\alpha_{1211} = -0.4439$ $\alpha_{1212} = -0.4423$ $\alpha_{1213} = -0.0141$	$x_{21} =$ 8.3E-5	$\alpha_{2111} = 0.4439$ $\alpha_{2112} = 0.4700$
	$x_{12} =$ 1.0E-6	$\alpha_{1121} = -0.0216$ $\alpha_{1122} = -0.0216$ $\alpha_{1221} = -0.4700$ $\alpha_{1222} = -0.4683$ $\alpha_{1223} = -0.0345$	$x_{22} =$ 1.7828	$\alpha_{2121} = 0.4423$ $\alpha_{2122} = 0.4683$
			$x_{23} =$ 1.0E-6	$\alpha_{2131} = 0.0141$ $\alpha_{2132} = 0.0345$
100	$x_{11} = 1.5857$	$\alpha_{1111} = -0.0217$ $\alpha_{1112} = -0.0217$ $\alpha_{1211} = -0.4439$ $\alpha_{1212} = -0.4423$ $\alpha_{1213} = -0.4441$ $\alpha_{1214} = -0.1122$	$x_{21} =$ 1.7702	$\alpha_{2111} = 0.4439$ $\alpha_{2112} = 0.5232$
	$x_{12} =$ 1.0E-6	$\alpha_{1121} = -0.0272$ $\alpha_{1122} = -0.0272$ $\alpha_{1221} = -0.5232$ $\alpha_{1222} = -0.5215$ $\alpha_{1223} = -0.5234$ $\alpha_{1224} = -0.1782$	$x_{22} =$ 0.0065	$\alpha_{2121} = 0.4423$ $\alpha_{2122} = 0.5215$
			$x_{23} =$ 1.0E-6	$\alpha_{2131} = 0.4441$ $\alpha_{2132} = 0.5234$
			$x_{24} =$ 1.0E-6	$\alpha_{2141} = 0.1122$ $\alpha_{2142} = 0.1782$

Table 5.10. Evolution of interspecific interactions over time in Model 2. The table displays the values of population densities and interaction terms at the start (time = 0), near the middle (time = 40), and at the end of a Model 2 run. The interaction terms are grouped on the same rows as the populations in which they have their effects. All non-zero interaction terms are given.

strength of interactions and intrinsic growth rates.

These results lend qualified support to theoretical (Heckel & Roughgarden 1980; Turelli & Petry 1980) and experimental (Thomas *et al.* 1980; Mueller & Ayala 1981) results which suggest that selection can maintain life histories such that population dynamics are stable. The qualification arises because the models I have investigated would not require much modification to produce chaotic dynamics for a wide range of parameters. In this they are similar to many relatively simple models of populations which can give rise to complex dynamics (May 1976; Godfray & Blythe 1990).

There are also problems with the method I have used which merit further attention. The complexity of the simulation model used meant that it was not possible to map exhaustively the model parameter space. If one considers only the evolving interactions, α_{11}, α_{12} and α_{21}, and allows one thousand possible different parameter values for each, then, taking all the possible intergenotypic interactions into account requires an impossible number of combinations of parameters (10^{900}), even when assuming all mutants are present and ignoring the initial state of the system, which is potentially variable. As a result it is difficult to assign quantitatively values to the relative importance of different types of dynamics that occur, and the analysis must remain descriptive.

Systematic variation of parameters in resilience tests would be useful way of judging the robustness of results observed, but could only be performed for limited ranges of parameters, and would still be extremely time-consuming and require intensive use of computing resources. Limitations on time prevented the carrying out of such a thorough analysis in this work.

Another problem concerns the lack of knowledge about the dynamics of individual genotypes these results give us. A very large amount of information would be required in order to be able to analyse this, but it would enable us to distinguish relatively stable population dynamics caused by the presence of one genotype at a high and relatively constant density, and many other genotypes at low but fluctuating densities, from a stable overall density made up of the continual cyclic turnover of alleles. Such modifications could be incorporated in future versions of models of this kind.

5.6 CONCLUSIONS: STUDYING COMPLEXITY BY SIMULATION

From these studies of different aspects of the predator-prey coevolutionary interaction, it can be seen that simulation modelling can shed light on questions which are difficult to address by conventional mathematical or experimental approaches. The three questions investigated here, although superficially very different, do bear common features in that they are all based on the same numerical models, and investigate different levels of the coevolutionary interaction, from the genetical to the ecological.

It will be seen that the studies presented in this chapter have not achieved all their objectives; where this is the case I have attempted to account for this and to suggest ways in which the methods used to could be improved to yield more reliable answers. Negative results, although they may not advance the study of the area of investigation very much, can be useful in showing paths for further research, as I have attempted to sketch here.

The various different problems with the simulation found in the different studies may in a large part, I suggest, be traced back to a central problem of the use of simulations to study complex theoretical models. This is that in order to represent natural complexity, the simulation model must itself become sufficiently complex as to preclude exhaustive testing, and thus limit the degree of understanding of the behaviour of the model. Biology presents some extremely interesting complex systems, about which much less is known than some other systems in other areas of the natural sciences, and computing power and accessability looks set to increase over the foreseeable future, but constructing more complex, more accurate models does not always imply greater understanding.

Despite this pessimistic note, it is difficult to see how simulation modelling can fail to become more significant in evolutionary biology, as the development of new computing equipment allows more and more questions to be investigated.

Chapter 6. GENERAL DISCUSSION

6.1 SUMMARY

The analytical, numerical and simulation models of evolution and dynamics in interacting populations, presented in preceding chapters, are discussed in two parts. The first part concentrates on evolution in interacting populations. The original aim of the project is discussed, and the reasons behind a more restricted focus, on evolution in predator-prey systems, are given. The implications of the models for predator-prey coevolution are considered. There are many problems in the theoretical study of predator-prey coevolution; and the evidence for such coevolution is examined in the light of these problems. Related questions in the field of parasite-host coevolution are also examined.

In the second part of the discussion the different types of dynamics that occur in predator-prey coevolution systems are examined. The word dynamics can be used to mean either evolutionary or ecological dynamics. I identify four distinct issues in connection with dynamics; evolutionary dynamics can be either genetic or phenotypic, while ecological dynamics presents the problems of avoiding the use of restrictive stability measures, and that of identifying the underlying dynamics of the predator-prey system. The success of the various techniques I have used in addressing these issues is discussed, and suggestions for further work are presented.

6.2 INTRODUCTION

At this point it seems appropriate to think back to the first page of this thesis; to the title of the project, *The evolution and dynamics of interacting populations.* The title can be split into two components. First, *Evolution of interacting populations*, and second, *Dynamics.* These provide a basis for consideration of the work presented in this thesis in two parts, which I shall follow here. First I shall consider how the research I have presented in the preceding chapters has addressed the topic of the evolution of interacting populations, then I shall go on to look at the meaning(s) of dynamics in this context. In the final section some of the many questions that arise out of this work, and inevitably, remain unanswered, will be considered.

6.3 EVOLUTION OF INTERACTING POPULATIONS

The phrase, *Evolution of interacting populations*, is more general than the topic I have actually considered in this project. What, for example, is the nature of the interaction between populations? One could assume that it was an ecological interaction, since populations are the stuff of population ecology, but there are many different such interactions (e.g. Begon *et al.* 1986). Due to the original intention to investigate the relationship between dynamical stability of food webs and ESSs (see Chapter 1, and section 6.5 below), I have considered only trophic interactions. The study of the evolution of trophically interacting populations implies examination of the evolution of food webs; in fact the models presented here have concentrated upon predator-prey interactions. Is this justified? In section 6.3.1 I shall consider this change of emphasis.

The study of predator-prey interactions and evolution means that one can address the topic of predator-prey coevolution. In section 6.3.2 I shall discuss the contribution the models I have studied have made to the understanding of predator-prey coevolution, and consider the relationship of the theory presented here to theoretical, experimental, palaeontological and field research on the same topic.

Predator-prey coevolution is a difficult phenomenon to define in nature however (Endler 1991), and it has been disputed whether or not it is actually coevolution *sensu stricto* (Janzen 1980). Mathematically closely related systems such as host-parasite (May & Anderson 1983b), or host-pathogen systems, may be more appropriate for the study of the evolution of interacting species. In section 6.3.3 I shall consider how the results of my research on predator-prey coevolution relate to studies in the related area of parasite-host coevolution, and whether some of the methods I have developed could be applied equally well to coevolutionary systems other than predator-prey ones.

6.3.1 Food webs and predator-prey interactions

In nature, every pair-wise trophic interaction is part of a web of multi-species interactions. Thus it would seem reasonable to study the evolution of interacting species at the level of the food web or the community rather than at the level of a pair-wise interaction between predator and prey. This has been the approach followed in a number of theoretical studies (e.g., Stenseth 1983; Stenseth & Maynard Smith 1984; Brown & Vincent 1987a). On the other hand this makes it difficult to take into account the interaction of population and evolutionary dynamics to any great extent. The models that I developed reflect the role of population dynamics in driving coevolutionary change more accurately, but they do so at the expense of greater difficulty in analysis and interpretation when many species are considered. For these reasons, it was necessary to focus my investigations on predator-prey interactions.

Two arguments provide some justification for restricting attention to predator-prey systems. First, in order to understand the evolution and dynamics of a trophic web, it is first necessary to comprehend fully the evolution of predator-prey interactions. This path to the analysis of multi-species evolution has been followed by a number of other workers (Rosenzweig & MacArthur 1963; Rosenzweig 1973; Schaffer & Rosenzweig 1978; Roughgarden 1983; Abrams 1986a, 1990, 1991). Second, there is evidence that strong interactions are rare in nature (Paine 1980, 1992; Hall & Raffaelli 1991). If many interactions have very little effect, the few that do have major effects on each species population dynamics may be similar to isolated pair-wise interactions.

6.3.2 Predator-prey coevolution

6.3.2.1 The models

In order to consider the implications of the results of previous chapters for predator-prey coevolution, I shall first examine the predictions of other theoretical models, and their implications for the styles of modelling I have used. Due to the observational difficulties involved in observing predator-prey coevolution (to which I shall return to later), much effort in this field has been concentrated upon theoretical studies (Rosenzweig & MacArthur 1963; Rosenzweig 1973; Schaffer & Rosenzweig 1978; Slatkin & Maynard Smith 1979; Roughgarden 1979, 1983; Abrams 1986a, 1990, 1991).

Much of this work has adopted the "arms race" analogy. This was introduced by Dawkins and Krebs (1979), but antagonistic coevolution of predator and prey had previously been referred to as a "rat race" by Rosenzweig (1973), and as an "evolutionary race" by Slobodkin (1974).

Parker (1983, 1985) discussed such a model in which the level of investment in predator and prey "armaments" was considered in an evolutionary game. Since I have defined the predator-prey interaction in terms of levels of investment in predatory and anti-predator traits (Marrow & Cannings 1992, Chapter 2; Marrow *et al.* 1992, Chapter 3; Chapter 4), the models I consider in preceding chapters may be considered as arms race models.

The arms race analogy has been used in several senses, for which the simple verbal definitions of Dawkins and Krebs (1979) are not sufficient to distinguish. Abrams (1986b) has pointed out that the arms race analogy may refer either to an alteration in the selection pressure for the incorporation of predation-related mutants as a response to a change in one species, or to an increased optimal level of investment in a predation-related trait as a result of the change. If the first alternative is considered then an increase in a predation-related trait in one species may not result in an increase in the other species of the level of a corresponding trait. This alternative is the sense in which the models I have considered are arms race models, since an increase in the investment, or body size, of one species, does not always produce an increase in the other.

The arms race analogy has been criticised (Abrams 1986a, b) for not reflecting the wide range of evolutionary behaviour that predator-prey systems can produce (Abrams 1986a, 1990, 1991). Such criticisms seem in part justified in the light of the wide variety of behaviour shown by the simple predator-prey models I have analysed in Chapters 2 and 3; ESSs, cyclical evolutionary change (Red Queen coevolution), as well as predator extinction are all possible. Only in certain systems (Marrow & Cannings 1992, Chapter 2; Marrow *et al.* 1992, Chapter 3) are directional coevolutionary change implied by the arms race analogy found.

Dawkins and Krebs (1979) derived the life-dinner principle from their assumptions about a predator-prey arms race. This suggests that there should be greater selection pressure upon the prey for anti-predator adaptations, than on the predator for predatory ones. This is one of a suite of observations that have been made of asymmetries in adaptation in predator and prey (reviewed by Endler 1991). The observation (Chapter 3; the loser-wins principle, Marrow *et al.* 1992) that the prey, although the loser in the ecological sense actually wins in the evolutionary interaction, by evolving to a state where the level of interaction with the predator is very weak, gives additional support to the idea of an asymmetry in predator-prey coevolution. This, due to the problems in applying the arms race analogy directly to predator-prey models (see above), may be its most important consequence for the evolution of predators and prey.

The coexistence of predator and prey is a biologically pleasing consequence of the models I have analysed, and occurs under a wide range of conditions. Such a conclusion agrees well with the intuitive notion that predator-prey interactions must have existed in nature for some time in order that we could observe them, as well as with theoretical models that have predicted this outcome (Rosenzweig 1973; Slobodkin 1974; Schaffer & Rosenzweig 1978).

Extinction of the predator, or predator overeating of the prey leading to the extinction of both species does occur with appreciable frequency: such results could be attributed to combinations of predators and prey that cannot occur in nature, but such an argument in the absence of a good empirical basis for the theory cannot be assessed adequately. It is very difficult to obtain data on the extinction of prey due to predator effects, due to the lack of evidence after the event. While it seems possible that predators could overeat their prey, in nature such a local extinction would probably occur in the context of a polyphagous predator, which could then switch to alternative prey.

The widespread occurrence of polyphagy is a fundamental problem for predator-prey models of two interacting species. Some attempts have been made to study the effects of other species on a predator-prey interaction (Abrams 1991), but even these models do not approach the complex food webs typical of natural trophic interactions (Cohen *et al.* 1990a). Although many trophic interactions may be so weak as not affect many species in the trophic web appreciably (Paine 1980, 1992; Hall & Raffaelli 1991; Hall *et al.* 1990a, b), there are many cases where strong interactions between more than two species can be found. In view of these difficulties with a theoretical approach, it is perhaps to the empirical evidence of predator-prey coevolution that we should look.

There remain, however, other problems with the models I have considered here, in particular. In basing the models upon the Lotka-Volterra food web equations, I have assumed linear functional responses (Holling 1961). In attempting to fit the models closer to reality, some form of non-linear functional response would be required (see, for example, Abrams 1986a, 1990, 1991). Functional responses of this form were not included in the models I consider here since they would render them intractable, or at least very resistant to analysis.

It is well-known that body size of organisms varies with age. Age structure was not considered in the models that I used because of the difficulties in analysis of the models that would then arise. A large body of theory has been developed using age-structured models, especially in the analysis of life histories (Charlesworth 1980; Stearns 1992). The incorporation of age structure would enable the evolutionary consequences of phenotypic evolution to be related more directly to life history traits which may be estimable in natural populations.

The weaknesses and advantages of the Lotka-Volterra equations as models of interacting populations are well-known, and I have discussed them elsewhere (e.g. Chapters 2, 3), so I shall not consider them in any detail here. One generalisation that can be made about the Lotka-Volterra equations is that they represent a population-level model. Individuals are assumed to interact at random, and individuals are uniform within populations. When genetic variation is introduced, individuals do not vary within genotypes, which ignores the occurrence of phenotypic plasticity (Lessells 1991). Yet predator-prey interactions are, fundamentally, interactions between individual predators (or small groups) and particular prey. It would be appropriate for a model of predator-prey coevolution to be based upon interactions between individuals and reflect individual variation (Łomnicki 1988). In addition the inclusion of a more complex, possibly diploid, genetic system would be advisable. One possible way that this could be done is via a Monte Carlo simulation model, recording the fates of individuals. Such a simulation would be very time-intensive, and as a result one might wish to look for natural evidence of predator-prey coevolution as an alternative.

6.3.2.2 The evidence

In the case of predator-prey coevolution, the difficulty of modelling a realistic situation means that we must look for broad agreement with empirical data rather than specific fits between a model and data. DeAngelis *et al.* (1984, 1985) provide the exception to this: they developed a model of a specific predator-prey interaction which they tested with data from the fossil record, but the greater complexity of their model meant that their conclusions were not as general as some of the models discussed above. Due to the long time scale of most evolutionary change, most of the data on predator-prey coevolution has come from the fossil record (Vermeij 1982, 1983, 1987; Vermeij & Covitch 1978; Kitchell *et al.* 1981; Bakker 1983; Stanley *et al.* 1983; West *et al.* 1991).

The evidence for predator-prey coevolution in the fossil record is not unequivocal. Vermeij (1982, 1983, 1987; Vermeij & Covitch 1978) has studied the effects of predators on hard-shelled molluscs, and found limited evidence for the kind of reciprocal adaptations that a strict definition of coevolution (Futuyma & Slatkin 1983a) requires. He suggested that the evolutionary interaction between predator and prey might more appropriately be described as "escalation" (Vermeij 1987). Bakker (1983) and Stanley *et al.* (1983) also consider the fossil record of the evolution of particular groups of predators and prey. Bakker (1983) found evolution of predator and prey occurred discontinuously, with lags in adaptation in one species in response to a change in others. Stanley *et al.* (1983) found established predator and prey species sufficiently stable to suggest that predator-prey coevolution only occurs very rapidly when the species first form.

These results do not produce clear predictions for the outcomes of theoretical models. The observations of Stanley *et al.* (1983) of, "slow, stuttering coevolution", could be taken as support for the occurrence of ESSs, but the predator-prey interaction occurs in a changing physical environment, and it may not be possible to define precisely an ESS in this context. The other prediction of continual coevolutionary change, or Red Queen coevolution (Marrow *et al.* 1992; Chapter 3), is not supported by studies of the fossil record of predator-prey interactions, but studies of larger communities and their evolution have given some support (Hoffman & Kitchell 1984; Hoffman 1991). The fossil record cannot give any details about intensity of selection, which would be useful in testing these hypotheses (Hoffman 1991).

In the absence of clear-cut evidence from the fossil record, models of predator-prey coevolution must rely upon biological plausibility for their justification. This justification underlies all the models I have considered here. In an ideal world experimental or field data could be used to back up evidence from palaeontological studies of coevolution. Unfortunately, the long time scale required means that experimental or observational studies of evolution in predator and prey can only address the problem peripherally. A number of studies have shown evolutionary responses in prey in response to predation (e.g., Reznick & Endler 1982; Edley & Law 1988) in field or laboratory experiments, but it is difficult to show the reciprocal effects of prey on predator which a narrow definition of coevolution would require (Futuyma & Slatkin 1983a).

In terms of their effect upon population densities, a predator-prey interaction is similar to a parasite-host or pathogen-host interaction, and indeed the interactions between parasitoids and their hosts can be considered as either. In the next section I shall consider the relationships between these types of antagonistic interactions.

6.3.3 Evolution of coevolutionary cycling: parasite-host interactions and the Red Queen

The observation of continuous evolutionary change, or Red Queen coevolution in simple predator-prey systems (Marrow *et al.* 1992, Chapter 3), is somewhat unexpected, and contrary to theoretical predictions (Rosenzweig *et al.* 1987) of the behaviour of coevolving communities. That Red Queen coevolution arises in such a simple system lends support to hypotheses of its occurrence in other systems, of similar or greater degrees of complexity. A great deal of attention in evolutionary biology has been focused upon the hypothesis that parasite-host interactions can generate Red Queen coevolution, and that this may be responsible for the selective maintenance of sexual reproduction (Hamilton 1980; Hutson & Law 1981; Bell 1982; Nee 1989; Hamilton *et al.* 1990). Models of the evolution of sex through parasite-host interaction require more complex assumptions about genetics than my models of predator-prey interactions have included. They require multi-locus control of the traits under selection, as well as a selective advantage to recombination of the alleles at these loci. Nevertheless, the results of the (much simpler) predator-prey models studied here imply that such a mechanism may be widespread in more complex systems.

Although at first sight, parasite-host or pathogen-host interactions are very different from predator-prey ones, they are similar in that they are all +/- ecological interactions, and can be modelled in similar ways (Hassell & Anderson 1989). It would be of interest to model the coevolutionary dynamics of a parasite-host interaction in a similar way to the models of predator-prey interactions I have considered here (Marrow *et al.* 1992; Chapter 3). Measures of virulence or resistance could be substituted for body size in the model. Such modelling might enable a more thorough understanding of the dynamics of parasite-host interactions and the frequency of occurrence of cyclic dynamics than is currently available.

6.4 DYNAMICS

The second major topic of this thesis can be denoted by the term *dynamics*. But the word dynamics can be interpreted in a number of different ways in the context of the evolution of interacting populations. These include; (1) the dynamics of genotypes within populations, (2) the dynamics of phenotypes, (3) population dynamics as considered by stability analysis, and (4) population dynamics resulting in non-equilibrium dynamical behaviour. I shall consider each of these alternatives in turn.

The dynamics of genotypes and of phenotypes are closely related in the systems I have considered, since they are based on a haploid genetic system. I shall distinguish between them by considering properties of the number and duration of genotypes as genetic dynamics, without direct reference to the characters they code for. I will then use the term *phenotype dynamics* to refer to changes in the traits encoded by the genotypes over time.

I consider population dynamics in the evolutionary models from two perspectives. The first is from the perspective of stability analysis, a widely-used technique for the understanding of non-linear differential equations (Simmons 1974:290). In population biology such analysis has depended frequently upon the assumption that populations remain close to ecological equilibria; this is the basis of the dynamical stability hypothesis of food web structure in particular (Pimm 1982). Since it is not clear that this assumption is satisfied in natural populations, it was intended that this study should avoid the use of local measures of stability about ecological equilibria, and if possible introduce global measures. This will be discussed in the first section on population dynamics.

The possible non-equilibrium behaviour of biological problems leads to another, more general, question about biological population dynamics; what type of dynamical behaviour arises in populations undergoing evolutionary change? Population dynamical systems could exhibit non-equilibrium behaviour as a result of lack of convergence to a stable equilibrium, but it could be that no such stable equilibrium occurs, and the only attractor present is a cyclic or chaotic attractor. This will be considered in the second section. The existence of non-equilibrium dynamics in population models is related to the fundamental question of the nature of dynamics found in natural populations. In the final section on ecological dynamics, I shall address this topic.

6.4.1 Evolutionary Dynamics

6.4.1.1 Genetic dynamics

I have considered the dynamics of genotypes in two contexts. First, the number of different genotypes maintained in each species over time. Second, the success rate of invasions of new genotypes. These approaches allowed consideration of important questions in population genetics, without some of the complexity of conventional population genetical models. The results of the two approaches are not unequivocal.

The simulation of the invasions of new genotypes into predator and prey (Chapter 5) gave minimal support to the hypothesis that polymorphisms could be maintained by predator-prey interactions at a haploid locus, but it was not possible to distinguish true polymorphism from confounding effects. The occurrence of polymorphism would be consistent with the genetic models of Spencer and Marks (1988, 1992; Marks & Spencer 1991). Conventional population genetics theory suggests that only one genotype should persist under density-dependent selection at a haploid locus in a single species.

If all the polymorphism observed is an artefact, then this may reflect the fact that a predator-prey interaction modelled in this way is not sufficient to maintain genetic variation. Work in progress (Marrow *et al.* 1992; R. Law, *pers. comm.*) suggests that polymorphisms may occur very rarely in predator-prey systems, for a restricted range of parameter values. The results observed may be a consequence of this. Antagonistic interactions are thought to be a cause of the maintenance of genetic variation in natural populations (Hamilton 1982; Cockburn 1991:50); it may be that the failure to detect their consequences in this model is a result of haploid genetics, and extension of the model in the incorporation of diploid genetics seems an appropriate task for future work.

The models of the invasions of mutants into predator and prey showed some evidence of decline in success rate of invaders through the progress of the simulation, but this was not clear-cut (Chapter 5; section 5.3). The build-up of resistance to invaders has been observed in the case of new species invading competition communities (Case 1990, 1991), or trophic webs (Drake 1990b). The method used in section 5.3 was not sufficient to isolate possible confounding factors, and the use of the haploid genetic system may prevent the occurrence of an effect which would be marked in a diploid system.

In the models of section 5.3 persistence of invaders was measured only one iteration after invasion had taken place. Açkakaya and Ginzburg (1989) measured the longevity of species invading a competition community. They found an approximately negative exponential distribution of longevity of invading species- with few species surviving for many invasion attempts (equivalent to iterations in my models), and a substantial number enduring for a few. It may be that a more accurate measure of the success of invading mutants in establishing themselves would be to look at the number remaining after some larger period of time. This was not measured in the simulations in chapter 5, and would be a topic for further work.

6.4.1.2 Phenotype dynamics

Phenotype-based modelling has been much used in evolutionary biology (e.g., Grafen 1991; Parker & Maynard Smith 1990), and the examination of the dynamics of phenotypes under selection has been an important theme of the work discussed here. I have studied phenotypic dynamics in several ways; (1) analytically (Chapter 2; Marrow & Cannings 1992), (2) numerically, based on analytical models (Chapter 3; Marrow *et al.* 1992), and (3) via numerical simulation (Chapters 4 and 5).

The methods of Chapters 2 and 3 have been very successful, generating a global description of the dynamics of phenotypes of predators and prey based upon the concept of the *phenotype space.* Notions similar to this concept have been used before; Lewontin (1974:13 ff.) characterized population genetics in terms of genotype and phenotype spaces; the use of character spaces to determine optimal life histories is a conventional technique in the study of life history evolution (e.g. Metz & Godfray 1992). Mirmirani and Oster (1978) described the ESS dynamics of optimal reproductive strategies in competing plants using a "strategy space"; while Maynard Smith and Brown (1986) examined the dynamics of the evolution of body sizes of competitors on a parameter space related to the sizes of different asexual genotypes. The work of Takada and Kigami (1991) probably comes closest to that described here-but their concern was primarily with the dynamics of evolutionary games, and they did not seek to include population dynamics. In that they include population dynamics, it appears that the models described in Chapters 2 and 3 give a more complete, more global description of the evolutionary dynamics of ecologically interacting species than has previously been available.

The results of the two models based upon the phenotype space present some interesting contrasts. The model of Chapter 2 (Marrow & Cannings 1992) does not produce ESSs except under exceptional conditions, but produces directional continuous evolutionary change (perhaps an "arms race", in the sense of Abrams [1986b], or "escalation", in the sense of Vermeij [1987]), and maintains coexisting predator and prey under selection. The latter result is biologically pleasing, corresponding both to biological intuition and the verbal (Slobodkin 1961) and theoretical (Slobodkin 1974) arguments predicting prudent predation (Taylor 1984:126). Directional evolutionary change to extreme phenotypes is more difficult to justify; but it must be pointed out that in the model of Chapter 2 the prey self-limitation is held constant, and it is found in chapter 3 that this is a key determinant of the evolutionary dynamics of the system. The results of chapter 2 are probably most significant in that they show that an ESS is by no means a certain outcome of predator-prey coevolution, which must call into question the considerable number of studies of the evolution of interacting species which are based upon deriving the conditions for an ESS, without determining whether it is attainable (e.g. Roughgarden 1979:464; Stenseth 1983; Reed & Stenseth 1984).

The models of Chapter 3 generate ESSs where predator and prey coexist, a biologically reasonable result for the same reasons as described in connection with the Chapter 2 models above. Multiple ESSs can also occur, an interesting result in view of the simplicity of the models used. The coexistence of multiple ESSs is theoretically plausible (Cannings & Vickers 1988; Vickers & Cannings 1988) and their occurrence in this system suggests that very interesting evolutionary consequences could be found in models of more complex communities. Such results suggest a role for evolution in the structuring of biological communities, in view of the observation of alternative stable states in ecosystems (Table 1.2).

The observation of Red Queen dynamics in this system is also of considerable interest, being unexpected both in the light of previous models (Rosenzweig *et al.* 1987), and in view of the simplicity of the model. That such a range of evolutionary dynamics can be isolated in this system suggests many potential directions in which this research could be developed. It would be possible to modify the numerical method of Chapter 3 to incorporate more interacting species, and there many be ways in which the reliance upon equilibrium population dynamics may be relaxed (see section 6.4.2.2 below). Also of interest would be to examine the phenotype dynamics of the system using the ecological interaction coefficients as variables directly, rather than looking at the body sizes. This would give a more general view of the dependence of ecological interaction upon genetic trait, although the model would be less directly related to a biologically proximate character, such as body size.

The simulations described in Chapters 4 and 5 were less directly successful in examining the dynamics of phenotypes. Constraints on computer time meant that only certain aspects of the computer models could be concentrated upon. It was possible to generalize about the evolution of interactions in Model 1 in terms of the movement of zero isoclines for population dynamics in this system (see Chapter 5; section 5.5.2). This conclusion is biologically unsatisfactory however, since it implies the paradoxical situation of a prey species evolving independence from predation while the predator simultaneously becomes more and more dependent upon it. Model 1 can be thought of as a null model against which the results of other evolutionary models with constraints can be compared.

Those aspects of phenotype dynamics that were observed were concerned with the evolution of interactions and body sizes over time; trends were observed in each, but it was not possible to incorporate these trends in a more general theory. Changes in average interaction intensity, or some related measure of interspecific interaction, have frequently been explored in models of community assembly and evolution (Ginzburg *et al.* 1988; Taylor 1988; Szathmáry *et al.* 1990; Vida *et al.* 1990), but the general behaviour of such systems has often also been not fully accounted for. A task for future work would be to reconstruct the attractors for interaction and size dynamics within the Model 2 system. The results from the simulations under Model 2 constraints show that ecological as well as evolutionary dynamics must be taken into account when the behaviour of models of evolving interacting species is considered.

6.4.2 Ecological dynamics

The models I have examined in the preceding chapters are all based upon the Lotka-Volterra models for population dynamics. Lotka-Volterra models despite their wide use present many problems in application, as has been mentioned in previous chapters. Central to the use of Lotka-Volterra equations as models of population dynamics are the issues of stability analysis as a method for understanding ecological dynamics, and the nature of the dynamical attractors underlying models of interacting populations.

6.4.2.1 Avoiding local stability

Local asymptotic stability (local stability; May 1973:13) analysis is a widely used technique in the study of models of biological populations. It enables an understanding of the behaviour of such models to be obtained despite their non-linearity. However it only gives information about a small region of phase space near an equilibrium point in which a linear approximation to the nonlinear equations is appropriate, and thus was thought to be misleading in the context of the evolution of interacting species. In this case there was thought to be no reason why the combined effects of evolutionary and ecological change would not perturb the ecological dynamics away from equilibrium.

The use of local asymptotic stability analysis was avoided in the simulation models (Chapters 4, 5) by evaluating the population dynamics directly, using numerical integration, and by allowing mutants to invade irrespective of whether populations had converged to equilibrium or not.

This was in contrast to many models of community assembly (Robinson & Valentine 1979; Drake 1983, 1990b; Post & Pimm 1983; Mithen & Lawton 1986; Case 1990, 1991), which assumed restrictive conditions about convergence to equilibrium at each stage. Thus the simulation models were "developmental" models in the sense of Taylor (1989).

The avoidance of local asymptotic stability analysis removed many of the problems associated with that technique, but introduced other problems preventing a general understanding of the behaviour of the simulation systems. In the absence of a complete exploration of the parameter space of the models, it was appropriate to use a global stability criterion to analyse the population dynamics of the evolving interacting populations. Permanence, as used by Law and Blackford (1992), in their models of food web assembly, seemed appropriate. Such a criterion is in a sense, more fundamental than one dealing with convergence to an equilibrium, since permanence addresses the question of the coexistence of populations through time, rather than the constancy of equilibrium densities (*ibid.*). There is no reason that convergence to a feasible (all densities positive) equilibrium should occur, in general.

Ideal although such a criterion might seem, there are problems in applying it to systems of more than three species. In the simulation models of Chapters 4 and 5, although I model only two species at a time, the introduction of genetic variation makes the model equivalent to a Lotka-Volterra system with up to twenty species. It is possible that permanence methods could be applied to the simulation models under conditions when only a few mutants were present, but there would always be the possibility of more mutants invading and causing the method to fail. Jansen (1987) has developed a criterion for permanence which can be applied to Lotka-Volterra systems of more than three species, but it is only a sufficient condition; i.e., it will identify permanent systems correctly but not all those systems which fail the criterion will *not* be permanent. Law and Blackford (1992) applied Janzen's criterion to certain Lotka-Volterra food web systems with greater than three species, and found no cases where the criterion failed to identify permanence correctly. However, their use of food web systems relied on Harrison's (1979) result (see below), and so cannot be regarded as a test of the use of the permanence criterion for general configurations of Lotka-Volterra systems.

For this reason, the analytical models of Chapters 2 and 3 are so constructed as to be able to rely upon the result of Harrison (1979), which states that a Lotka-Volterra food chain system, if it possesses a feasible interior equilibrium, will have the property of global asymptotic stability of that equilibrium. This means that, given sufficient time, all paths (also called orbits or trajectories in the literature) of the population dynamics in phase space will converge to the interior equilibrium, regardless of their starting points, providing those are positive. Global asymptotic stability also implies permanence. In the evolutionary models I considered, I regard sufficient time for convergence to equilibrium as being available, since mutations are assumed to occur rarely, with large amounts of ecological time in between each. So, in the case of these models there is no need to apply permanence criteria, or local asymptotic stability analysis, as global asymptotic stability, which is a more general condition than required by the latter method, applies.

6.4.2.2 Non-equilibrium dynamical behaviour

It would also be of interest to know of the evolutionary behaviour of the analytical models when population dynamics were not at equilibrium. Non-equilibrium behaviour could be due to transient lack of convergence to an equilibrium point, or to an underlying attractor which was not an equilibrium point. Although in both of these cases trajectories could occur leading to extinction of one or more populations, and so it would not be possible to infer conclusions about the coexistence of species, the type of dynamical behaviour exhibited by the evolutionary ecological models discussed here is of interest, since it would enable the better evaluation of the roles of mathematical models in relation to natural population dynamics. It might also be possible to draw conclusions about the type of dynamics present in natural populations.

The analytical models of Chapter 2 (and Marrow & Cannings 1992) required equilibrium population dynamics in order that their results could be evaluated explicitly. It is possible that non-equilibrium dynamics could be considered if the results were evaluated numerically across the phenotype space in the manner of Chapter 3 (Marrow *et al.* 1992); but it was not possible to investigate this in the time scale of the current project.

The results presented in Chapter 3 require equilibrium dynamics in order that measures of the invasion of new mutants can be evaluated. One possible way of investigating the invasion of new mutants into the system of chapter 3 would be through the use of Lyapunov exponents (Baker & Gollub 1990; Metz *et al.* 1992). Lyapunov exponents are frequently difficult to derive explicitly (*ibid.*), but, in the case of Lotka-Volterra systems, they can be obtained by making use of the property of the average density of the species to tend to the equilibrium density, given a sufficiently long time and as long as the densities are bounded away from zero and infinity (Hofbauer & Sigmund 1988:88). The Lyapunov exponent of a mutant is then its per capita growth rate at the equilibrium point (R. Law, *pers. comm.*). Thus it may be possible, in future work, to extend this method to populations with chaotic or cyclic population dynamics.

Some idea of the range of dynamical behaviour generated by the simulation models was obtainable by direct observation of the time series generated by numerical integration (Chapter 5; section 5.5). Non-equilibrium population dynamics was observed in this model, which made it more realistic in reflecting the possible dynamical behaviour of the system than many models of community assembly, which have tended to rely upon equilibrium behaviour (Robinson & Valentine 1979; Drake 1983, 1990b; Post & Pimm 1983; Mithen & Lawton 1986; Case 1990, 1991). However only limited understanding of the dynamical behaviour of the system was obtained from the number of simulation runs that it was possible to perform. The versatility of the simulation model so created, means that further exploration could be carried out without extra programming effort.

The use of the simulation model did run into problems caused by the complexity of the system under study. Complex evolving biological systems have attracted much attention from computer scientists, and others, interested in artificial representation of life-like processes (see Langton 1989a; Langton *et al.* 1991; and references therein). There seems to be, however, no clear consensus on what methods are most appropriate (Hogeweg 1989; Langton 1989b, 1991; Packard 1989; Taylor *et al.* 1989; Kauffman & Johnsen 1991; Lindgren 1991; Ray 1991). The complete description of the results of a computer simulation is a problem which different workers have adopted different approaches to, never being able to achieve the ideal (Drake 1985, 1990b; Taylor 1985, 1988; Szathmáry *et al.* 1990; Vida *et al.* 1990). The results described in this thesis give some indication of the nature of the effect of evolution on the population dynamics of interacting species, and provide a starting point for further work. Many problems remain to be addressed in this area.

6.4.2.3 Natural population dynamics

Questions about the underlying population dynamics of evolving interacting population models must remain of limited generality when the debate over the dynamics of natural populations is not yet resolved (Berryman & Millstein 1989; Godfray & Blythe 1990). What the models presented here do show, apart from new ways of understanding the evolutionary dynamics of interacting species, are that evolutionary and ecological dynamics are intertwined, and each has an effect on the other. A fuller understanding of the dynamics of natural populations will be possible when the effect of evolutionary change on ecological dynamics has been evaluated more completely.

6.5 THE FUTURE

In a work of this kind, it is inevitable that there remain a number of unanswered questions. In this section, I shall focus on some of the most important of those, in order to suggest some directions for future research.

6.5.1 Constraints on evolutionarily stable food webs

The original aim of this project was to examine evolution in food webs. For a number of reasons this was not carried out. But it remains the case that interesting analogies can be drawn between the work on patterns in food webs (Pimm 1982, 1991; Lawton 1989; Pimm *et al.* 1991), which set exclusion rules about configurations of food webs which are not observed, and work on patterns of coexisting ESSs (Cannings & Vickers 1988, 1989; Vickers & Cannings 1988), which establish exclusion results for configurations of multiple ESSs. If food web structure is affected by selection, as the results on predator-prey coevolution presented here imply, then could results on patterns of ESSs be used to place constraints on the structure of food webs that occurred under evolutionarily stable conditions? Combining the two areas of theory would enable the development of a theory of evolution in food webs more general than any yet developed.

6.5.2 Asymmetries in predator-prey coevolution and temporal variation in trophic structure

The models presented in Chapter 3 have provided evidence of asymmetries in predator-prey coevolution (the "loser wins" principle; Marrow *et al.* 1992) which are consistent with observations by other workers (Dawkins & Krebs 1979; Endler 1991). A great deal of attention has also been paid to spatial and temporal variation in food web structure (Kitching 1987; Warren 1989; Schoenly & Cohen 1991). It is tempting to regard some of the trends observed in temporal variation in food webs as due to selection acting on predator and prey, in the asymmetric fashion which many theoretical studies predict. Could food web structure, and variation in that structure, be accounted for in part by asymmetries in predator-prey coevolution? We are a long way from being able to answer this question at present; there is considerable disagreement about generalities of food web structure (Winemiller 1990b; Polis 1991), let alone the role of evolution in shaping it. The study of the way in which trophic webs vary over different timescales is still very descriptive. This is an area in which there is much scope for further work.

6.5.3 The life-history consequences of predator-prey coevolution

The problem of relating body sizes to ecological interactions has occurred in a number of contexts in the models considered here. Many organisms change size with age, and thus the incorporation of age structure into predator-prey evolution models would be a way to circumvent these problems. Including age structure would also be of interest in that it would enable evolution of interactions in predator-prey systems to be related to changes in life-history traits, with which body size will be strongly correlated. Age-structured models would thus enable the life-history consequences of predator-prey coevolution to be addressed, an area which has received little theoretical attention (Stearns 1992:210), but which may have significant practical applications in connection with evolution under harvesting (Reznick & Endler 1982; Edley & Law 1988; Law 1991).

6.5.4 Evolution in populations with complex dynamics

The results described in preceding chapters have shown that population dynamics can have complicated consequences for evolutionary change, and *vice versa*. Yet it has not been possible to address the question of evolution in populations with complex, non-equilibrium, population dynamics to any degree. This is in part due to the difficulty of identifying a sufficiently general measure of fitness, so that the invasion or otherwise of new mutants can be assessed. The use of the dominant Lyapunov exponent as a measure of fitness (Metz *et al.* 1992) has already been alluded to in previous chapters. This, and related techniques, may provide a way for theory about evolution and population dynamics to reflect the range of dynamical complexity that may occur in relatively simple population models. At the present time, results can mainly be obtained about single-species populations (Godfray *et al.* 1992; Metz & Godfray 1992; Metz *et al.* 1992). A suitable task for further research would be to extend this theory to interacting populations.

Chapter 7. CONCLUSION

The topic of evolution in interacting species was interpreted to focus upon predator-prey coevolution. This would enable a sound theoretical basis to be constructed for the analysis of evolution in larger systems, such as food webs. As a result all the systems explored in the project were predator-prey systems.

The use of analytical, numerical, and simulation models to study predator-prey coevolution has shown that there occur a variety of consequences for the ecological dynamics of evolving predator-prey systems. Evolutionary change can result in a wide range of dynamical behaviour, from stable equilibria to chaos. The consequences of natural selection need not be stability, as some single-species models and experiments have suggested. However, ecological dynamic stability is not required for evolutionary persistence.

The results obtained support arguments for the misleading nature of local asymptotic stability as a measure of the dynamics of ecological systems. However, it was not found possible to use permanence as an alternative to local asymptotic stability, as had been the original intention.

Results from the simulation models showed that convergence to ecological equilibrium was not necessarily to be expected in systems of evolving interacting species, in contrast to many models of community assembly and evolution. The size of the potential parameter space of the simulation models meant that not all the dynamical behaviour of these models could be explored in the time scale of the project.

The analytical models I developed enabled an exploration of evolutionary and ecological dynamics more thoroughly than the simulation models, and compensated for the limited understanding of the simulation systems. A wide range of evolutionary dynamics, such as ESSs and Red Queen coevolution, were seen to be produced from very simple systems, implying that more complex systems, such as food webs, would have much more interesting evolutionary consequences. The use of "phenotype space" based techniques enabled a more global understanding of the evolutionary and ecological dynamics of predator-prey interactions than had previously been possible.

In general, the results supported the contentions that both ecological and evolutionary dynamics need to be taken into consideration when studying the evolution of interacting species; and that ecological interactions need to be considered in evolutionary models. The techniques I used to address these questions have potential applications in future research.

Appendix A. SIMULATION MODEL: TECHNICAL NOTES.

In this appendix are presented some details of the implementation of the simulation models that were omitted from Chapter 4, due to their not being of central importance to the understanding of the model used. They are included here for purposes of record.

A.1 LANGUAGE REQUIREMENTS

The programs used to implement the simulation models were written in VAX Pascal (Digital Equipment Corporation 1985). External routines in Fortran were also included to perform numerical integration and generate graphics. The programs therefore required a Pascal compiler with the capability to link external Fortran code, and a Fortran compiler.

A.2 ADDITIONAL SOFTWARE REQUIREMENTS

The programs used the NAG library for numerical integration, and the Simpleplot library for graphics output. Execution of the programs required the presence of the NAG Fortran library (Numerical Algorithms Group 1990), and the Simpleplot graphics library (BUSS Ltd. 1985). The Uniras graphics applications package (Uniras Ltd. 1989) was used to generate most of the graphics output shown in this thesis. The Minitab statistical package (Minitab, Inc. 1989) was used in analysis of the numerical data generated on numbers of invasions into interacting species.

A.3 STORAGE REQUIREMENTS

The program required a large amount of memory both for execution of the program and storage of the results. The amounts required varied according to the length of the simulation being run, the time type chosen, and the complexity of the dynamics generated. Estimates of the amount of storage space required are given below in Table A.1. In addition the program required a considerable amount of working space, and execution would be severely hindered if only a small amount was available.

A.4 PROCESSING TIME REQUIREMENTS

The programs were very time intensive. The amount of CPU (central processing unit) time required was approximately proportional to the product of the number of species multiplied by the number of mutants in each species multiplied by the number of iterations. It was not possible to predict precisely the amount of time required by a particular run, but some typical values are as follows (taken from the series of numerical experiments in invasions into interacting species; section 5.3).

A predator-prey system (two species), with ten mutants in each species, run for ten thousand iterations in discrete time required 120 CPU seconds. The same predator-prey system, also with up to ten mutants in each species, and run for the same number of iterations in continuous time required 1500 CPU seconds, or 25 CPU minutes. So continuous time runs were about twelve times as slow as discrete time equivalents. The amount of time taken by a continuous time run was very dependent on the complexity of the numerical dynamics generated, and more complex dynamics could result in processes using rather more CPU time than their estimated values. The converse was also possible if rather simple dynamics were found.

A.5 HARDWARE REQUIREMENTS

The programs were run on VAX 8650 and 8550 computers. Additional items of hardware that were required were a Calcomp pen plotter, to produce graphical output, and a Silicon Graphics Indigo work station running Uniras to

Program files	
MODEL*.PAS (Source code)	50
*.PAS (Included files)	300
MODEL*.EXE (Executable image)	360
*.COM (Batch process command file)	10
Output files	
DATA.PLT (Graphical output)	c. 500-2000
INVSOUT.DAT (Invasion counting output)	c. 5-20
UNIGR.DAT (Numerical output)	c. 1550
SIMPLE.LOG (Simpleplot log file)	5
*.LOG (Batch process log file)	c. 10
TOTAL	c. 2790-4300

Table A.1. Memory requirements for Model 1 or 2. All requirements are given in VAX/VMS blocks, approximately equivalent to 0.5 kilobytes. Values were derived mainly from the numerical experiments on the maintenance of allele polymorphism (section 5.4). A * indicates that the name of the file varies, or, in the case of the included files for the source code, that a number of different files are considered. The names of the included files holding parts of the source code are given in Appendix B. Memory requirements for Model 1 and Model 2 were similar, but both could fluctuate considerably depending on the type of run anticipated.

generate the higher quality graphical output presented in this thesis, from the numerical output of the program.

A.6 NON-STANDARD FEATURES

The programs incorporated a number of non-standard features which were not part of Standard Pascal (Findlay & Watt 1985). Because the programs were so long (1500 lines), a large amount of the source code was not included in the main program file but in other files, which are referenced in the main program by the command `%INCLUDE`, which enforces compilation of included files. This is specific to VAX Pascal.

The programs included Fortran external routines. VAX Pascal enables Fortran routines to be called in a Pascal program, providing the variables are passed correctly. The non-standard VAX Pascal directive `%IMMED` enables parameters to be passed from Fortran routines to a Pascal program and *vice versa*. This was used to incorporate the numerical integration routines into the program. Another non-standard VAX Pascal directive, `%STDESCR`, was used to pass strings to the routines generating graphical output.

These were the main non-standard features of the program; there may be others depending on the type of system it is desired to implement the programs on. Limitations of time and space prevent an exhaustive description of the program here.

Appendix B. SIMULATION MODEL: SOURCE CODE

B.1 MODEL 1

Described in the source code as Model 7 for historical reasons. The lines of the program are shown in `Courier` typeface. Reformatting of the source code has caused some lines to run on, not a feature of the original program. The program is structured in the following way. At the start a series of comments record the modification of the program: they are not essential for program function. This is followed by declarations of the variables used by the program, and then by a series of `% INCLUDE` statements referring to files where the rest of the source code is stored. Finally, at `BEGIN {Main Program}` program execution begins. This listing was generated by the VAX Pascal compiler program. The comments to the left of each line are not part of the source code but indicate the line number (e.g. 00001), included code (I), or comments (C), and the level of procedural nesting (PL) and of statement nesting (SL). For more information see Digital Equipment Corporation (1985).

```
-LINE-IDC-PL-SL-

00001        0  0 PROGRAM Model7 (input, output, control, invsout, unigr);
00002     C  0  0   {This program models species interacting in a trophic
web, under repeated
00003     C  0  0    invasions of mutants.}
00004     C  0  0   {version: definitive Discrete time/DOUBLE precision}
00005     C  0  0   {reconstructed (9/11/90) from (27/7/90)}
00006     C  0  0   {edited (30/4/91) to conform to specifications for
interaction generation}
00007     C  0  0   {2 species; 20000 generations; NORMINT(0.1) mutation}
00008     C  0  0   {modification for continuous time from (1/5/91) onwards
as MODEL7}
00009     C  0  0   {user-defined parameters added (10/5/91)}
00010     C  0  0   {direct input/output and invasion counting added
(13/6/91)}
00011     C  0  0   {user-defined fraction added (6/1/92)}
00012        0  0
00013     C  0  0   {Author: Paul Marrow                }
00014     C  0  0   {         Department of Biology     }
00015     C  0  0   {         University of York        }
00016     C  0  0   {         York  YO1 5DD  UK         }
00017        0  0
00018        0  0   CONST  {Global constants}
00019        0  0     web=2;                   {number of species in food
web}
00020        0  0     variation=10;            {number of mutant niches
per species}
00021        0  0     terminus=5000;           {Number of time steps}
```

```
00022       0  0
00023       0  0    TYPE  {Definitions}
00024       0  0      initialtype=ARRAY [1..web] OF double;
00025       0  0      strtype=VARYING [80] OF char;
00026       0  0      species=ARRAY [1..web, 1..variation] OF double;
00027       0  0      matrix=ARRAY [1..web, 1..web, 1..variation,
1..variation] OF double;
00028       0  0      array2=ARRAY [1..web, 1..terminus] OF double;
00029       0  0      array3=ARRAY [1..web, 1..web, 1..terminus] OF double;
00030       0  0
00031       0  0    VAR  {Global variables}
00032       0  0      codestr:strtype;           {experimnetal code}
00033       0  0      control:text;              {text file for program
control}
00034       0  0      startpopn:initialtype;     {initial population size}
00035       0  0      invadepop:double;          {invading population size}
00036       0  0      extinct:double;            {extinction threshold}
00037       0  0      minselflimit:double;       {minimum self-limitation in
producer}
00038       0  0      mutation_rate:double;      {mutation rate (density^1)}
00039       0  0      ia:integer;                {counter}
00040       0  0      choice:double;             {random/nonrandom
initialisation}
00041       0  0      ttype:double;              {discrete/continuous time}
00042       0  0      step:double;               {step length for numerical
integration}
00043       0  0      tolerance:double;          {error tolerance for
numerical integration}
00044       0  0      replicates:double;         {number of replicate runs
with same parameters}
00045       0  0      mean:double;               {mean of negative
exponential distribution}
00046       0  0      fraction:double;           {standard deviation of
normal distribution}
00047       0  0      repl:integer;              {replicate loop counter}
00048       0  0      a:matrix;                  {interaction strengths}
00049       0  0      sign:matrix;               {trophic constraints on
interaction strengths}
00050       0  0      b:species;                 {growth rates}
00051       0  0      x:species;                 {population sizes}
00052       0  0      xic:species;               {invasion counter marker}
00053       0  0      count:integer;             {time counter}
00054       0  0      constraints:species;       {constraints on species
characteristics}
00055       0  0      generation_time:integer;         {dummy time counter}
00056       0  0      mean_interaction:array3;         {mean interaction
storage}
00057       0  0      population_over_time:array2;     {population time
series}
00058       0  0      coexisting_mutants:array2;       {number of coexisting
mutants}
00059       0  0      v:array2;                        {variance of allele
frequency}
00060       0  0      i,j,m,n:integer;                 {*debugging counters*}
00061       0  0      unigr:text;                      {results store}
00062    C  0  0      {Extra variables for invasion counting}
00063       0  0      incs:integer;                    {invasion counter}
00064       0  0      inct:integer;                    {successful invasion
counter}
00065       0  0      cstep:integer;                   {number of steps in
invasion counting}
00066       0  0      stint:integer;                   {step length in
invasion counting}
00067       0  0      invsout:text;                    {output file for
invasions results}
00068       0  0
00069       0  0    %INCLUDE 'nagrandu.pas /LIST'
00070 I     0  0    FUNCTION G05caf (x:double):double; EXTERN;
00071 I C   0  0      {This NAG routine produces pseudo-random numbers from
a uniform
```

```
00072 I C  0  0   distribution on (0,1).  x is a dummy parameter required
by FORTRAN
00073 I C  0  0   syntax.)
00074      0  0
00075      0  0   %INCLUDE 'nagrandn.pas /LIST'
00076 I    0  0   FUNCTION G05ddf (a, b:double):double; EXTERN;
00077 I C  0  0     (This function produces a random variate from a
Normal distribution, mean a
00078 I C  0  0      standard deviation b.)
00079      0  0
00080      0  0   %INCLUDE 'nagrandx.pas /LIST'
00081 I    0  0   FUNCTION G05dbf (a:double):double; EXTERN;
00082 I C  0  0     (This function generates a pseudo-random real number
taken from a
00083 I C  0  0   negative exponential distribution.  See NAG Fortran
Library manual
00084 I C  0  0   for details.)
00085      0  0
00086      0  0   %INCLUDE 'unrepeat.pas /LIST'
00087 I    0  0   PROCEDURE G05ccf; EXTERN;
00088 I C  0  0     (This NAG routine sets the random number generator to
an unrepeatable
00089 I C  0  0   initial state.)
00090 I    0  0
00091      0  0
00092      0  0   %INCLUDE 'inputcontrol.pas /LIST'
00093 I    1  0   PROCEDURE InputControl (lineno:integer; VAR
vinput:double);
00094 I C  1  0     (This procedure reads from CONTROL.DAT at a specified
line, and writes
00095 I C  1  0   result to an integer control parameter which is then
passed back to main
00096 I C  1  0   program.  If line number specified is out of range, an
error message is
00097 I C  1  0   displayed.)
00098 I    1  0
00099 I    1  0     VAR
00100 I    1  0       i:integer;  (counter)
00101 I    1  0
00102 I    1  0
00103 I    1  1     BEGIN  { InputControl }
00104 I    1  1
00105 I    1  1       IF lineno > 1 THEN
00106 I    1  2         BEGIN
00107 I    1  2           FOR i:=1 TO (lineno-1) DO
00108 I    1  3             BEGIN
00109 I    1  3               IF Eof (control)=false THEN
00110 I    1  3                 Readln (control)
00111 I    1  3             END  (i-loop)
00112 I    1  1         END;  (IF loop)
00113 I    1  1       IF (Eof (control)=true) OR (lineno < 1) THEN
00114 I    1  2         BEGIN
00115 I    1  2           Writeln ('Error in reading from Control: line
number out of range');
00116 I    1  2           vinput:=0
00117 I    1  2         END
00118 I    1  1       ELSE
00119 I    1  1         Readln (control, vinput);
00120 I    1  1       Reset (control)
00121 I    1  1
00122 I    0  0     END;  { InputControl }
00123      0  0
00124      0  0   %INCLUDE 'initial_sign.pas /LIST'
00125 I    1  0   PROCEDURE Initial_Sign (VAR sign:matrix);
00126 I C  1  0     (This procedure reads the values of the sign matrix
from terminal
00127 I C  1  0   into the program array.)
00128 I    1  0
00129 I    1  0   VAR
00130 I    1  0     i,j,k,m,n:integer;  (counters)
```

```
I     1  0     signm:double;     {sign constraint dummy variable}
I     1  0
I     1  0
I     1  1   BEGIN { Initial_Sign }
I     1  1
I C   1  1     {Defining wild-types}
I     1  1     k:=0;
I     1  1     m:=1;
I     1  1     n:=1;
I     1  1     FOR i:=1 TO web DO
I     1  2       BEGIN
I     1  2         FOR j:=1 TO web DO
I     1  3           BEGIN
I     1  3             k:=k + 1;
I     1  3             Writeln ('Input sign constraint for species
',i,' effect on species ',j);
I     1  3             Readln (signm);
I     1  3             sign[i,j,m,n]:=signm
I     1  3           END   {j-loop}
I     1  1       END;  {i-loop}
I     1  1
I C   1  1   {Defining outer rows and columns of mutant sign
matrices}
I     1  1   FOR n:=2 TO variation DO
I     1  2     BEGIN
I     1  2       FOR i:=1 TO web DO
I     1  3         BEGIN
I     1  3           FOR j:=1 TO web DO
I     1  3             sign[i,j,m,n]:=sign[i,j,1,1];
I     1  2         END;  {i-loop}
I     1  1     END;  {n-loop}
I     1  1   n:=1;
I     1  1   FOR m:=2 TO variation DO
I     1  2     BEGIN
I     1  2       FOR i:=1 TO web DO
I     1  3         BEGIN
I     1  3           FOR j:=1 TO web DO
I     1  3             sign[i,j,m,n]:=sign[i,j,1,1];
I     1  2         END;  {i-loop}
I     1  1     END;  {m-loop}
I     1  1
I C   1  1   {Defining mutant sign matrices}
I     1  1   FOR i:=1 TO web DO
I     1  2     BEGIN
I     1  2       FOR j:=1 TO web DO
I     1  3         BEGIN
I     1  3           FOR m:=2 TO variation DO
I     1  4             BEGIN
I     1  4               FOR n:=2 TO variation DO
I     1  4                 sign[i,j,m,n]:=sign[i,j,1,1];
I     1  4             END  {m-loop}
I     1  3         END  {j-loop}
I     1  2     END  {i-loop}
I     1  2
I     0  0   END; { Initial_Sign }
      0  0
      0  0   %INCLUDE 'initial_pop.pas /LIST'
I     1  0   PROCEDURE Initial_Pop (VAR popn:species);
I C   1  0     {Input is undefined population matrix from either R
or NRInitial; for m=1
I C   1  0   population values are set to StartPopn (global
variable), for m<>1 population
I C   1  0   values are set to 0.  Defined population matrix is
returned to appropriate
I C   1  0   initialisation procedure, and thus to main program.}
I     1  0
I     1  0     VAR
I     1  0       i,m:integer;
I     1  0
I     1  1     BEGIN
```

```
00196 I     1  1        m:=1;
00197 I     1  1        FOR i:=1 TO web DO
00198 I     1  1          popn[i,m]:=StartPopn[i];
00199 I     1  1        FOR m:=2 TO variation DO
00200 I     1  2          BEGIN
00201 I     1  2            FOR i:=1 TO web DO
00202 I     1  2              popn[i,m]:=0
00203 I     1  2          END  {m-loop}
00204 I     0  0      END;  { Initial_Pop }
00205 I     0  0
00206       0  0
00207       0  0    %INCLUDE 'initial_zero.pas /LIST'
00208 I     1  0    PROCEDURE Initial_Zero (VAR grwth:species; VAR
interact:matrix);
00209 I C   1  0      {Inputs are partially defined growth rate and
interaction matrices;
00210 I C   1  0    for m>1 values are set to 0 and returned to
initialisation procedures
00211 I C   1  0    and thus to main program.  This prepares the way for
mutant invasion.}
00212 I     1  0
00213 I     1  0      VAR
00214 I     1  0        i,j,m,n:integer;
00215 I     1  0
00216 I     1  0
00217 I     1  1      BEGIN  { Initial_Zero }
00218 I     1  1
00219 I     1  1        FOR i:=1 TO web DO
00220 I     1  2          BEGIN
00221 I     1  2            FOR m:=2 TO variation DO
00222 I     1  3              BEGIN
00223 I     1  3                grwth[i,m]:=0;
00224 I     1  3                FOR j:=1 TO web DO
00225 I     1  4                  BEGIN
00226 I     1  4                    FOR n:=2 TO variation DO
00227 I     1  4                      interact[i,j,m,n]:=0;
00228 I     1  4                    n:=1;
00229 I     1  4                    interact[i,j,m,n]:=0;
00230 I     1  4                  END  {j-loop}
00231 I     1  3              END  {m-loop}
00232 I     1  2          END  {i-loop}
00233 I     1  2
00234 I     0  0        END;  { Initial_Zero }
00235       0  0
00236       0  0    %INCLUDE 'nri.pas /LIST'
00237 I     1  0  PROCEDURE NonRandom_Initial (VAR sgn:matrix; VAR
population, growth:species;
00238 I     1  0                                 VAR alpha:matrix);
00239 I C   1  0    {This procedure establishes initial values for
parameters as input by user.}
00240 I     1  0
00241 I     1  0    VAR
00242 I     1  0      i, j:integer;  {Counting variables}
00243 I     1  0
00244 I     2  0    PROCEDURE NRInitial_Growth (VAR growth_rate:species;
sign_m:matrix;
00245 I     2  0                                  no:integer);
00246 I C   2  0      {This procedure establishes initial growth rates as
input by user.}
00247 I     2  0
00248 I     2  0      CONST
00249 I     2  0        m=1;
00250 I     2  0
00251 I     2  1      BEGIN  { NRInitial_Growth }
00252 I     2  1
00253 I     2  1        Writeln ('Input growth rate for species ',no);
00254 I     2  1        Readln (growth_rate[no,m]);
00255 I C   2  1        {Temporary constraint to produce predator growth
rates: not fully general 17/10/91}
00256 I     2  1        IF (no>1) THEN growth_rate[no,m]:=
```

```
growth_rate[no,m] * (-1);
00257 I     2  1
00258 I     1  0     END;  { NRInitial_Growth }
00259 I     1  0
00260 I     2  0    PROCEDURE NRInitial_Interaction (VAR alphaint:matrix;
sign_m:matrix;
00261 I     2  0                                     p, q:integer);
00262 I C   2  0     {This procedure establishes the initial interaction
terms as input by the user.}
00263 I     2  0
00264 I     2  0     CONST
00265 I     2  0       m=1;
00266 I     2  0
00267 I     2  0     VAR
00268 I     2  0       n:integer;
00269 I     2  0
00270 I     2  1     BEGIN  { NRInitial_Interaction }
00271 I     2  1
00272 I     2  1       n:=1;
00273 I     2  1       Writeln ('Input the initial interaction term for
species ',q,' effect on species ',p);
00274 I     2  1       Readln (alphaint[p,q,m,n]);
00275 I     2  1       IF (p=q) AND (p=1) THEN
00276 I     2  2         BEGIN
00277 I     2  2           IF alphaint[p,q,m,n]<minselflimit THEN
00278 I     2  2             alphaint[p,q,m,n]:=minselflimit;
00279 I     2  2           alphaint[p,q,m,n]:= sign_m[p,q,m,n] *
alphaint[p,q,m,n];
00280 I     2  2           FOR n:=2 TO variation DO
00281 I     2  2             alphaint[p,q,m,n]:= alphaint[p,q,m,1];
00282 I     2  2         END
00283 I     2  1       ELSE
00284 I     2  1         alphaint[p,q,m,n]:=sign_m[p,q,m,n] *
alphaint[p,q,m,n];
00285 I     2  1
00286 I     1  0     END;  { NRInitial_Interaction }
00287 I     1  0
00288 I     1  1    BEGIN  { NonRandom_Initial }
00289 I     1  1
00290 I     1  1      Initial_Pop (population);
00291 I     1  1      Initial_Sign (sgn);
00292 I     1  1      FOR i:=1 TO web DO
00293 I     1  1        NRInitial_Growth (growth, sgn, i);
00294 I     1  1      FOR i:=1 TO web DO
00295 I     1  2        BEGIN
00296 I     1  2          FOR j:=1 TO web DO
00297 I     1  2            NRInitial_Interaction (alpha, sgn, i, j)
00298 I     1  1        END; {i-loop}
00299 I     1  1      Initial_Zero (growth, alpha)
00300 I     1  1
00301 I     0  0    END;  { NonRandom_Initial }
00302       0  0
00303       0  0    %INCLUDE 'ri.pas /LIST'
00304 I     1  0    PROCEDURE RandomInitial (VAR sgn:matrix; VAR
population, growth:species;
00305 I     1  0                                VAR alpha:matrix);
00306 I C   1  0     {Initialises parameters not entered directly}
00307 I     1  0
00308 I     1  0     VAR
00309 I     1  0       i,j:integer;  {counting variables}
00310 I     1  0
00311 I     2  0     PROCEDURE RInitial_Growth (VAR growth_rate:species;
sign_m:matrix;
00312 I     2  0                                        no:integer);
00313 I     2  0
00314 I     2  0       CONST
00315 I     2  0         m=1;
00316 I     2  0
00317 I     2  1       BEGIN  { RInitial_Growth }
00318 I     2  1         growth_rate[no,m]:= g05dbf (mean);
```

```
I    2  1        IF no>1 THEN growth_rate[no,m]:=
-growth_rate[no,m];
I    1  0      END;  { RInitial_Growth }
I    1  0
I    2  0    PROCEDURE RInitial_Interaction (VAR alphaint:matrix;
sign_m:matrix;
I    2  0                                     p, q:integer);
I    2  0
I    2  0      CONST
I    2  0        m=1;
I    2  0
I    2  0      VAR
I    2  0        n:integer;
I    2  0
I    2  1      BEGIN  { RInitial_Interaction }
I    2  1        n:=1;
I    2  1        IF (p=1) AND (q=1) THEN
I    2  2          BEGIN
I    2  2            alphaint[p,q,m,n]:= G05dbf(mean);
I    2  2            IF alphaint[p,q,m,n]<minselflimit THEN
I    2  2              alphaint[p,q,m,n]:=minselflimit;
I    2  2            alphaint[p,q,m,n]:= sign_m[p,q,m,n] *
alphaint[p,q,m,n];
I    2  2            FOR n:=2 TO variation DO
I    2  2              alphaint[p,q,m,n]:=alphaint[p,q,m,1];
I    2  2          END  {alpha11 generation}
I    2  1        ELSE
I    2  2          BEGIN
I    2  2            alphaint[p,q,m,n]:= G05dbf(mean);
I    2  2            alphaint[p,q,m,n]:= sign_m[p,q,m,n] *
alphaint[p,q,m,n];
I    2  1          END;  {interaction generation}
I    1  0      END;  { RInitial_Interaction }
I    1  0
I    1  1    BEGIN  { RandomInitial }
I    1  1      Initial_Pop (population);
I    1  1      IF ia=1 THEN
I    1  1        Initial_Sign (sgn);
I    1  1      FOR i:=1 TO web DO
I    1  1        RInitial_Growth (growth, sgn, i);
I    1  1      FOR i:=1 TO web DO
I    1  2        BEGIN
I    1  2          FOR j:=1 TO web DO
I    1  2            RInitial_Interaction (alpha, sgn, i, j);
I    1  1        END;  {i-loop}
I    1  1      Initial_Zero (growth, alpha);
I C  1  1      {Printing out initialised graphics}
I    1  1      Writeln ('Alpha11 = ',alpha[1,1,1,1]);
I    1  1      Writeln ('Alpha12 = ',alpha[1,2,1,1]);
I    1  1      Writeln ('Alpha21 = ',alpha[2,1,1,1]);
I    1  1      Writeln ('R1 = ',growth[1,1]);
I    1  1      Writeln ('R2 = ',growth[2,1]);
I    0  0    END;  { RandomInitial }
     0  0
     0  0  %INCLUDE 'invin.pas /LIST'
I    1  0  PROCEDURE InvIn (rep:integer; VAR popic:species; VAR
inkt,inks,kstep:integer);
I C  1  0    {This procedure sets up the invasion counting
routines}
I    1  0
I    1  0    CONST
I    1  0      m=1;
I    1  0
I    1  0    VAR
I    1  0      i:integer;  {counter}
I    1  0
I    1  1    BEGIN  { InvIn }
I    1  1      FOR i:=1 TO web DO
I    1  1        popic[i,m]:=1;
I    1  1      kstep:=0;
```

```
I     1  1      inkt:=0;
I     1  1      inks:=0;
I     1  1      Writeln ('Replicate ',rep);
I     1  1      Write ('CSTEP ');
I     1  1      Write ('INCT ');
I     1  1      Writeln ('INCS ');
I     0  0     END;  { InvIn }
      0  0
      0  0    %INCLUDE 'invasion.pas /LIST'
I     1  0    PROCEDURE Invasion (VAR alpha:matrix; VAR growth,
population:species;
I     1  0                        VAR constraint:species;
sign_m:matrix; mutationr:double;
I     1  0                        VAR fraction:double);
I C   1  0     {This procedure causes a random attempted invasion of
a mutant into the
I C   1  0    preexisting food web species.  The defined interaction,
growth rate, and
I C   1  0    population matrices are read from main program,and
passed to nested procedures
I C   1  0    which check that invasion is possible, and then
generate an invader with
I C   1  0    random characteristics at a random location.  The
altered values for the
I C   1  0    interaction, growth rate, and population matrices are
returned to the main
I C   1  0    program as output.}
I     1  0
I     1  0     VAR
I     1  0      site:integer;
I     1  0      xx:double;         {dummy for random number
generator}
I     1  0
I     1  0     %INCLUDE 'emptyniches.pas /LIST'
I     2  0    FUNCTION EmptyNiches (popn:species):Boolean;
I C   2  0     {This function is similar to CheckMutReg, but checks
whole matrix of
I C   2  0    population values, and only returns false if all
elements are non-zero.}
I     2  0
I     2  0     VAR
I     2  0      i,m:integer;  {element counters}
I     2  0      z:integer;    {empty niche counter}
I     2  0      t:Boolean;    {dummy variable for function}
I     2  0
I     2  0
I     2  1     BEGIN  { EmptyNiches }
I     2  1
I     2  1      z:=0;
I     2  1      FOR i:=1 TO web DO
I     2  2       BEGIN
I     2  2        FOR m:=2 TO variation DO
I     2  2         IF popn[i,m]=0 THEN z:=z + 1
I     2  1       END;  {i-loop}
I     2  1      IF z=0 THEN t:=false
I     2  1       ELSE t:=true;
I     2  1      EmptyNiches:=t
I     2  1
I     1  0     END;  { EmptyNiches }
I     1  0
I     1  0     %INCLUDE 'checkmutreg.pas /LIST'
I     2  0    FUNCTION CheckMutReg (popn:species;
level:integer):Boolean;
I C   2  0     {This function accepts the current population matrix
and a parameter
I C   2  0    representing the location of the intended invasion
(i.e. trophic level) as
I C   2  0    input from Invasion, and checks that not all the
elements of that species'
I C   2  0    sub-matrix are occupied, returning 'true' if this is
```

```
so, and 'false' if it
I C  2  0   is not.}
I    2  0
I    2  0     VAR
I    2  0       m:integer;  {element counter}
I    2  0       z:integer;  {empty element detector}
I    2  0       y:Boolean;  {dummy variable for result}
I    2  0
I    2  0
I    2  1     BEGIN  { CheckMutReg }
I    2  1
I    2  1       z:=0;
I    2  1       FOR m:=2 TO variation DO
I    2  1         IF popn[level,m]=0 THEN
I    2  1           z:=z + 1;
I    2  1       IF z=0 THEN y:=false
I    2  1         ELSE y:=true;
I    2  1       CheckMutReg:=y
I    2  1
I    1  0     END;  { CheckMutReg }
I    1  0
I    1  0     %INCLUDE 'invasionprob.pas /LIST'
I    2  0   FUNCTION InvasionProb (popul:species; level:integer;
mutrate:double):Boolean;
I C  2  0     {This function makes the mutation rate
density-dependent.  The total
I C  2  0   density of the species at the invasion level is counted
and the
I C  2  0   probability of invasion occuring (but not successful
establishment) is
I C  2  0   =density/50.}
I    2  0
I    2  0     VAR
I    2  0       x:double;              {dummy for random number
generator}
I    2  0       density:double;        {density of species at which
mutation occurs}
I    2  0       probability:Boolean;   {dummy for InvasionProb}
I    2  0       m:integer;             {counter}
I    2  0
I    2  1     BEGIN  { InvasionProb }
I    2  1
I    2  1       x:=0;
I    2  1       density:=0;
I    2  1       x:=G05caf (x);
I    2  1       FOR m:=1 TO variation DO
I    2  1         density:=density + popul[level,m];
I    2  1       IF density=0 THEN probability:=false
I    2  1         ELSE
I    2  1           IF x>=(density * mutrate) THEN
probability:=false
I    2  1             ELSE probability:=true;
I    2  1       InvasionProb:=probability;
I    2  1
I    1  0     END;  { InvasionProb }
I    1  0
I    1  0     %INCLUDE 'population_size.pas /LIST'
I    2  0   PROCEDURE Population_Size (VAR popul:species;
level:integer);
I C  2  0     {This procedure writes the starting population of an
invading mutant of a
I C  2  0   pre-existing species into the population matrix.  Input
is the population
I C  2  0   matrix and the location of the invasion, from Invasion.
The altered
I C  2  0   population matrix is returned to invasion.}
I    2  0
I    2  0     VAR
I    2  0       m:integer;  {element counter}
I    2  0
```

```
I     2  0
I     2  1    BEGIN  { Population_Size }
I     2  1
I     2  1      m:=0;
I     2  2      REPEAT
I     2  2        m:=m + 1
I     2  1      UNTIL popul[level,m]=0;
I     2  1      popul[level,m]:=invadepop
I     2  1
I     1  0    END;  { Population_Size }
I     1  0
I     1  0    %INCLUDE 'repet7.pas /LIST'
I     1  0
I     2  0    FUNCTION Repetition_Check (interactions:matrix;
I     2  0                                   locat:integer;
j,msite,n:integer):Boolean;
I C   2  0      {This function checks to see whether the new mutant
has some character(s)
I C   2  0    the same as any other cospecific mutant; if that is
so it returns a value
I C   2  0    of true, else; false.}
I     2  0
I     2  0      VAR
I     2  0        m:integer;  {counters}
I     2  0        repet:Boolean;  {dummy for function}
I     2  0
I     2  1      BEGIN  { Repetition_Check }
I     2  1        repet:=false;
I     2  1          FOR m:=1 TO variation DO
I     2  2            BEGIN
I     2  2              IF (msite<>m) THEN
I     2  2                IF Trunc (interactions[locat,j,m,n] *
1000) =
I     2  2                   Trunc (interactions[locat,j,msite,n] *
1000)
I     2  2                  THEN repet:=true;
I     2  1            END;  {m-loop}
I     2  1        Repetition_Check:=repet;
I     1  0      END;  { Repetition_Check }
I     1  0
I     1  0
I     1  0    %INCLUDE 'delet7.pas  /LIST'
I     2  0    PROCEDURE Delete_Mutant (VAR interactions:matrix;
I     2  0                                 locat,j,msite,n:integer);
I C   2  0      {If a repeated invasion has occured, this procedure
deletes the invader.}
I     2  0
I     2  0
I     2  1      BEGIN  { Delete_Mutant }
I C   2  1        {Delete interaction term}
I     2  1        interactions[locat,j,msite,n]:=0;
I     1  0      END;  { Delete_Mutant }
I     1  0
I     1  0    %INCLUDE 'mutchargen3.pas /LIST'
I     2  0  PROCEDURE MutCharGen (VAR inter:matrix; VAR
growth:species; location:integer;
I     2  0                          constraints, popul:species;
signm:matrix;
I     2  0                          VAR fraction:double);
I C   2  0    {This procedure generates the characteristics of the
invading mutants.
I C   2  0  Population size has already been set, and here the
intrinsic growth rate of
I C   2  0  the mutant is set to the same as the species from which
it is derived, and
I C   2  0  the interaction terms of the mutant are derived
randomly from a distribution
I C   2  0  with mean the interaction strength of the original
species.  The values of
I C   2  0  the interaction terms, and also the growth rates, may
```

```
be subject to
00553 I C  2  0   constraints.}
00554 I    2  0
00555 I    3  0      PROCEDURE Set_Constraints (VAR constr:species;
locat:integer);
00556 I C  3  0        {This procedure sets constraints upon the values of
mutant
00557 I C  3  0      characteristics.  No effect at present on overall
dynamics, since
00558 I C  3  0      all constraints are set to 1.}
00559 I    3  0
00560 I    3  0        VAR
00561 I    3  0          i,m:integer;  {counters}
00562 I    3  0
00563 I    3  0
00564 I    3  1        BEGIN  { Set_Constraints }
00565 I    3  1
00566 I    3  1          FOR i:=1 TO web DO
00567 I    3  2            BEGIN
00568 I    3  2              FOR m:=1 TO variation DO
00569 I    3  2                constr[i,m]:=1.0;
00570 I    3  2            END  {i-loop}
00571 I    3  2
00572 I    2  0        END;  { Set_Constraints }
00573 I    2  0
00574 I    2  0
00575 I    2  0
00576 I    3  0      PROCEDURE GrowthR_Gen (VAR g_rate:species;
populn:species; locat:integer);
00577 I C  3  0        {This procedure sets the growth rate of the
invading mutant to
00578 I C  3  0      that is its parent species.  [This may eventually be
subject to
00579 I C  3  0      constraint, but at present is only altered by a scale
factor].
00580 I C  3  0      Input is the growth rate matrix and the location of
the invasion,
00581 I C  3  0      (i.e. trophic level) from MutCharGen.  Output to
MutCharGen is the
00582 I C  3  0      altered growth rate matrix.}
00583 I    3  0
00584 I    3  0        CONST
00585 I    3  0          scale=1;  {scaling factor}
00586 I    3  0
00587 I    3  0        VAR
00588 I    3  0          i,m:integer;  {counters}
00589 I    3  0
00590 I    3  0
00591 I    3  1        BEGIN  { GrowthR_Gen }
00592 I    3  1
00593 I    3  1          m:=0;
00594 I    3  2          REPEAT
00595 I    3  2            m:=m + 1;
00596 I    3  1          UNTIL populn[locat,m]=invadepop;  {invadepop is a
global const.}
00597 I    3  1          g_rate[locat,m]:=g_rate[locat,1] * scale;
00598 I    3  1
00599 I    2  0        END;  { GrowthR_Gen }
00600 I    2  0
00601 I    2  0
00602 I    2  0
00603 I    2  0
00604 I    2  0
00605 I    2  0
00606 I    2  0
00607 I    2  0
00608 I    3  0      PROCEDURE Interaction_Gen (VAR interactions:matrix;
constr,
00609 I    3  0                                      populn:species;
locat:integer;
```

```
00610 I     3  0                                    signs:matrix; VAR
fraction:double);
00611 I C  3  0      (This procedure generates interaction terms for the
invading mutant.
00612 I C  3  0     Input are the interaction, constraints and population
matrices, and
00613 I C  3  0     the location of the invasion, from MutCharGen.  The
procedure detects
00614 I C  3  0     the mutant element at which invasion takes place and
then goes through
00615 I C  3  0     all [j*n] interaction terms for this element,
producing new values related
00616 I C  3  0     to the parental values but multiplied by the
constraint matrix and by
00617 I C  3  0     random factors.  The interaction terms are then
checked in order that
00618 I C  3  0     conform to the constraints of the sign matrix, and
passed back to
00619 I C  3  0     MutCharGen.  Note: count and mean_interaction are
Global variables.}
00620 I     3  0
00621 I     3  0       VAR
00622 I     3  0         i,j,k,m,n:integer;  {counters}
00623 I     3  0         a,b:double;       {intermediates for random
number generator}
00624 I     3  0         x:double;         {random variate}
00625 I     3  0
00626 I     3  0
00627 I     4  0       PROCEDURE Normean (VAR x:double; i:integer;
j:integer; count:integer;
00628 I     4  0                                fraction:double;
interact:matrix);
00629 I C  4  0        {This procedure generates mutant characters from
a normal distribution,
00630 I C  4  0       mean the initial interaction strength, standard
deviation a fraction of
00631 I C  4  0       this.}
00632 I     4  0
00633 I     4  0         VAR
00634 I     4  0           a,b:double;
00635 I     4  0
00636 I     4  1         BEGIN { Normean }
00637 I     4  1           a:=Abs (interact[i,j,1,1]);
00638 I     4  1           b:=Abs (interact[i,j,1,1]/10);
00639 I     4  1           IF (interact[i,j,1,1]<>0) THEN
00640 I     4  2             BEGIN   {generator}
00641 I     4  3               REPEAT
00642 I     4  3                 x:=G05ddf (a,b);
00643 I     4  2               UNTIL (x>0);
00644 I     4  1             END;    {generator}
00645 I     3  0         END;  { Normean }
00646 I     3  0
00647 I     3  0
00648 I     4  0       PROCEDURE Normint (VAR x:double; i:integer;
j:integer; count:integer;
00649 I     4  0                                fraction:double);
00650 I C  4  0        {This procedure generates mutant characters from
a normal distribution,
00651 I C  4  0       mean the mean interaction term, standard deviation
a fraction of this.}
00652 I     4  0
00653 I     4  0         VAR
00654 I     4  0          a,b:double;
00655 I     4  0
00656 I     4  1         BEGIN { Normint }
00657 I C  4  1           {Random  number generator NORMINT}
00658 I     4  1           IF mean_interaction[i,j,count-1]<>0 THEN
00659 I     4  2             BEGIN
00660 I     4  2               a:=Abs (mean_interaction[i,j,count-1]);
00661 I     4  2               b:=Abs
```

```
(mean_interaction[i,j,count-1]/fraction);
00662 I    4  3              REPEAT
00663 I    4  3                x:=G05ddf (a,b);
00664 I    4  2              UNTIL (x>0);
00665 I    4  2            END  {If..Then}
00666 I    4  1          ELSE
00667 I    4  1            Normean (x, i, j, count, fraction,
interactions)
00668 I    3  0        END;  { Normint }
00669 I    3  0
00670 I    3  0
00671 I    3  1      BEGIN  { Interaction_Gen }
00672 I    3  1
00673 I    3  1        x:=0;
00674 I    3  1        FOR m:=1 TO variation DO
00675 I    3  2          BEGIN
00676 I    3  2            IF populn[locat,m]=invadepop THEN
00677 I    3  3              BEGIN  {generate new interaction terms}
00678 I    3  3                 FOR j:=1 TO web DO
00679 I    3  4                  BEGIN
00680 I    3  4                    FOR n:=1 TO variation DO
00681 I    3  5                      BEGIN  {generate effects of self on
others}
00682 I    3  5                        IF (locat=1) AND (j=1) THEN
00683 I    3  6                          BEGIN
00684 I    3  6                            K:=0;
00685 I    3  7                            REPEAT
00686 I    3  7                              k:=k + 1;
00687 I    3  7                              IF count=1 THEN
00688 I    3  7                                Normint (x, locat, j,
count+1, fraction)
00689 I    3  7                              ELSE
00690 I    3  7                                Normint (x, locat, j,
count, fraction);
00691 I    3  7                              interactions[locat,j,m,n]:=
constr[locat,1] *
00692 I    3  7                                                         x
* signs[locat,j,1,1];
00693 I    3  7                          IF Abs
(interactions[locat,j,m,n]) < minSelfLimit THEN
00694 I    3  7
interactions[locat,j,m,n]:=minSelfLimit * (-1);
00695 I    3  7                              IF n<>1 THEN
interactions[locat,j,m,n]:=
00696 I    3  7
interactions[locat,j,m,1];
00697 I    3  7                              IF Repetition_Check
00698 I    3  7                                 (interactions, locat, j,
m, n) = true THEN
00699 I    3  7                                Delete_Mutant
(interactions, locat, j, m, n);
00700 I    3  7                            UNTIL
00701 I    3  7                            (Repetition_Check
(interactions,locat,j,m,n)
00702 I    3  6                              = false) OR (k=50);
00703 I    3  6                          END  {generate alphal1}
00704 I    3  5                        ELSE
00705 I    3  5                          IF populn[j,n]<>0 THEN
00706 I    3  6                            BEGIN{check population
exists}
00707 I    3  6                              k:=0;
00708 I    3  7                              REPEAT
00709 I    3  7                                k:=k + 1;
00710 I    3  7                                IF count=1 THEN
00711 I    3  7                                  Normint (x, locat, j,
count+1, fraction)
00712 I    3  7                                ELSE
00713 I    3  7                                  Normint (x, locat, j,
count, fraction);
00714 I    3  7
```

```
interactions[locat,j,m,n]:= constr[locat,1] *
I    3  7                                                       x
* signs[locat,j,1,1];
I    3  7                                 IF Repetition_Check
(interactions,locat,j,m,n)
I    3  7                                   = true THEN
I    3  7                                   Delete_Mutant
(interactions,locat,j,m,n);
I    3  7                               UNTIL (Repetition_Check
(interactions,locat,j,m,n)
I    3  6                                 = false) OR (k=50);
I    3  6                             END  {check existence}
I    3  5                       END   {generating effects of self
on others}
I    3  3                   END;  {j-loop}
I    3  3                 FOR j:=1 TO web DO
I    3  4                   BEGIN  {generating effects of others on
self}
I    3  4                     FOR n:=1 TO variation DO
I    3  5                       BEGIN
I    3  5                         IF populn[j,n]<>0 THEN
I    3  6                           BEGIN  {check not extinct}
I    3  6                             IF (locat<>1) OR (j<>1) THEN
I    3  7                               BEGIN
I    3  7                                 k:=0;
I    3  8                                 REPEAT
I    3  8                                   k:=k + 1;
I    3  8                                   IF count=1 THEN
I    3  8                                     Normint (x, locat, j,
count+1, fraction)
I    3  8                                   ELSE
I    3  8                                     Normint (x, locat, j,
count, fraction);
I    3  8
interactions[j,locat,n,m]:= constr[j,1] *
I    3  8                                                   x *
signs[j,locat,1,1];
I    3  8                                   IF Repetition_Check
(interactions,locat,j,m,n)
I    3  8                                     = true THEN
I    3  8                                     Delete_Mutant
(interactions,locat,j,m,n);
I    3  8                                 UNTIL (Repetition_Check
(interactions,locat,j,m,n)
I    3  7                                   = false) OR (k=50);
I    3  7                               END  {check not alphall}
I    3  6                           END  {check not extinct}
I    3  5                       END  {n-loop}
I    3  4                   END  {generating effects of others on
self}
I    3  3               END  {generate new interaction terms}
I    3  2           END  {m-loop}
I    3  2
I    2  0       END;  { Interaction_Gen }
I    2  0
I    2  0
I    2  0
I    2  1     BEGIN  { MutCharGen }
I    2  1
I C  2  1       {Set constraints, where they exist.}
I    2  1       Set_Constraints (constraints, location);
I    2  1
I C  2  1       {Set growth rate of mutant}
I    2  1       GrowthR_Gen (growth, popul, location);
I    2  1
I C  2  1       {Set interaction terms for mutant}
I    2  1       Interaction_Gen (inter, constraints, popul,
location, signm, fraction);
I    2  1
I    1  0     END;  { MutCharGen }
```

```
00769 I    1  0
00770 I    1  0
00771 I    1  1     BEGIN  { Invasion }
00772 I    1  1
00773 I    1  1       IF EmptyNiches (population)=true THEN
00774 I    1  2         BEGIN  {try each species independently}
00775 I    1  2           FOR site:=1 TO web DO
00776 I    1  3             BEGIN
00777 I    1  3               IF CheckMutReg (population, site)=true THEN
00778 I    1  4                 BEGIN  {body of routine}
00779 I    1  4
00780 I    1  4                   IF (count>0) AND (count<>1) THEN
00781 I    1  4                     IF population_over_time[site,
count-1]<>0 THEN
00782 I    1  4                       IF InvasionProb (population, site,
mutationr)=true THEN
00783 I    1  5                         BEGIN {check species has not gone
extinct}
00784 I C  1  5                           {Establish mutant population}

00785 I    1  5                           Population_Size (population,
site);
00786 I C  1  5                           {Establish mutant
characterisitics}
00787 I    1  5                           MutCharGen (alpha, growth,
site,
00788 I    1  5                                       constraint,
population, sign_m, fraction)
00789 I    1  4                         END;  { invading }
00790 I    1  4
00791 I    1  4                   IF (count=0) OR (count=1) THEN
00792 I    1  4                     IF InvasionProb (population, site,
mutationr)=true THEN
00793 I    1  5                       BEGIN
00794 I    1  5                         Population_Size (population,
site);

00795 I    1  5                         MutCharGen (alpha, growth, site,
00796 I    1  5                                     constraint,
population, sign_m, fraction)
00797 I    1  4                       END;  { invading at start }
00798 I    1  4
00799 I    1  3                 END;  {body of routine}
00800 I C  1  3              {Check that invasions are not repeated}
00801 I    1  3
00802 I    1  2             END;  {sites}
00803 I    1  1         END;
00804 I    0  0     END;  { Invasion}
00805      0  0
00806      0  0   %INCLUDE 'invcount.pas /LIST'
00807 I    1  0   PROCEDURE InvCount (popn:species; VAR popic:species;
VAR inkt, inks, kstep:integer);
00808 I C  1  0     {This procedure counts the number of invasions and
successful invasions
00809 I C  1  0   {ones which actually manage to establish themselves}
over certain times.}
00810 I    1  0
00811 I    1  0     VAR
00812 I    1  0       i,m:integer;  {counters}
00813 I    1  0       dv:double;    {dummy variable}
00814 I    1  0
00815 I    1  1     BEGIN  { InvCount }
00816 I    1  1       dv:=(count/stint);
00817 I    1  1       IF count > 0 THEN
00818 I    1  1         IF (dv - Trunc (dv)) < Abs (1.0D-8) THEN
00819 I    1  2           BEGIN  {Resetting}
00820 I    1  2             kstep:=kstep + 1;
00821 I    1  2             IF kstep=1 THEN
00822 I    1  2               inks:=inks - web;
00823 I    1  2             IF inks < 0 THEN
00824 I    1  2               inks:=0;
```

```
I C  1  2            {Write output}
I    1  2            Write (kstep,' ');
I    1  2            Write (inkt,' ');
I    1  2            Writeln (inks);
I C  1  2            {Reset counters}
I    1  2            inkt:=0;
I    1  2            inks:=0;
I    1  1          END;  {Resetting}
I    1  1      FOR i:=1 TO web DO
I    1  2        BEGIN
I    1  2          FOR m:=1 TO variation DO
I    1  3            BEGIN
I    1  3              IF popn[i,m] = invadepop THEN
I    1  4                BEGIN
I    1  4                  inkt:=inkt + 1;
I    1  4                  popic[i,m]:=count;
I    1  3                END;
I    1  3              IF popn[i,m] = 0 THEN
I    1  3                popic[i,m]:=0;
I    1  3              IF popic[i,m] = count - 1 THEN
I    1  3                IF popn[i,m] <> 0 THEN
I    1  3                  inks:=inks + 1;
I    1  2            END;  {m-loop}
I    1  1        END;  {i-loop}
I    0  0    END;  { InvCount }
     0  0
     0  0  %INCLUDE 'time_series.pas /LIST'
I    1  0  PROCEDURE Time_series (alpha:matrix;
population:species;
I    1  0                                t:integer; VAR meanint:array3;
I    1  0                                VAR popnsum, nummut:array2);
I C  1  0    {This procedure calculates the mean interaction
strengths for the different
I C  1  0     species at a particular time and stores the result
for use in graphics.}
I    1  0
I    1  0    TYPE
I    1  0       arrayts=ARRAY [1..web, 1..web, 1..variation] OF
double;
I    1  0
I    1  0    VAR
I    1  0      alphasum:arrayts;       {intermediate in
interaction strength calc.}
I    1  0      i,j,m,n:integer;        {counters}
I    1  0
I    1  0
I    1  1    BEGIN  { Time_series }
I    1  1
I C  1  1      {Calculate interaction intensities}
I    1  1
I    1  1      FOR i:=1 TO web DO
I    1  2        BEGIN
I    1  2          FOR j:=1 TO web DO
I    1  3            BEGIN
I    1  3              meanint[i,j,t]:=0;
I    1  3              popnsum[i,t]:=0;
I    1  3              nummut[i,t]:=0;
I    1  3              FOR m:=1 TO variation DO
I    1  4                BEGIN
I    1  4                  alphasum[i,j,m]:=0;
I    1  4                  popnsum[j,t]:=0;
I    1  4                  FOR n:=1 TO variation DO
I    1  5                    BEGIN
I    1  5                      alphasum[i,j,m]:=alphasum[i,j,m] +
I    1  5                                                 (Abs
(alpha[i,j,m,n]) *
I    1  5
population[j,n]);
I    1  5                      popnsum[j,t]:=popnsum[j,t] +
I    1  5                                             population[j,n];
```

```
00888 I    1  4                      END;  {n-loop}
00889 I    1  4                    IF popnsum[j,t]<>0 THEN
00890 I    1  4
alphasum[i,j,m]:=alphasum[i,j,m]/popnsum[j,t]
00891 I    1  4                    ELSE
00892 I    1  4                      alphasum[i,j,m]:=0;
00893 I    1  4                    IF (population[i,m]<>0) THEN
00894 I    1  4                      nummut[i,t]:=nummut[i,t] + 1;
00895 I    1  4                    IF (i<>j) THEN
00896 I    1  4                      popnsum[i,t]:=popnsum[i,t] +
population[i,m];
00897 I    1  4                    meanint[i,j,t]:=meanint[i,j,t] +
(alphasum[i,j,m] *
00898 I    1  4                                   population[i,m]);
00899 I    1  3                  END;  {m-loop}
00900 I    1  3                IF popnsum[i,t]<>0 THEN
00901 I    1  3
meanint[i,j,t]:=meanint[i,j,t]/popnsum[i,t]
00902 I    1  3                ELSE
00903 I    1  3                  meanint[i,j,t]:=0;
00904 I    1  2              END;  {j-loop}
00905 I    1  1          END;  {i-loop}
00906 I    1  1
00907 I    0  0      END; { Time_series }
00908      0  0
00909      0  0    %INCLUDE 'allvar.pas /LIST'
00910 I    1  0    PROCEDURE Allvar (t:integer; population:species;
poptime, muttime:array2; VAR vari:array2);
00911 I C  1  0      {This procedure calculates the variance of allele
frequencies over time.}
00912 I    1  0
00913 I    1  0      VAR
00914 I    1  0        i, m:integer;       {counters}
00915 I    1  0        allfreq:species;    {frequencies of alleles}
00916 I    1  0        sumsq:initialtype;  {sum of squares for variance}
00917 I    1  0
00918 I    1  1      BEGIN  { Allvar }
00919 I    1  1        FOR i:=1 TO web DO
00920 I    1  2          BEGIN
00921 I    1  2            sumsq[i]:=0;
00922 I    1  2            FOR m:=1 TO variation DO
00923 I    1  3              BEGIN
00924 I    1  3                allfreq[i,m]:= 0;
00925 I    1  3                IF (poptime[i,t]<>0) THEN
00926 I    1  3                  allfreq[i,m]:=
(population[i,m]/poptime[i,t]);
00927 I    1  3                allfreq[i,m]:= Sqr (allfreq[i,m]);
00928 I    1  2              END;  {m-loop}
00929 I    1  1          END;  {i-loop}
00930 I    1  1        FOR i:=1 TO web DO
00931 I    1  2          BEGIN
00932 I    1  2            FOR m:=1 TO variation DO
00933 I    1  2              sumsq[i]:= sumsq[i] + allfreq[i,m];
00934 I    1  2            IF (muttime[i,t]<>0) THEN
00935 I    1  2              vari[i,t]:= sumsq[i] - (1/(muttime[i,t]));
00936 I    1  2            IF (muttime[i,t]>1) THEN
00937 I    1  2              vari[i,t]:= (vari[i,t]/(muttime[i,t] - 1))
00938 I    1  2            ELSE
00939 I    1  2              vari[i,t]:= 0;
00940 I    1  1          END;  {i-loop}
00941 I    0  0      END;  { Allvar }
00942 I    0  0
00943 I    0  0
00944 I    0  0
00945      0  0
00946      0  0    %INCLUDE 'iterate_discrete.pas /LIST'
00947 I    1  0    PROCEDURE Iterate_discrete (alphint:matrix;
growth_r:species;
00948 I    1  0                                VAR popn:species; VAR
gen:integer);
```

```
00949 I C  1  0     {Accepts old population values and times, as well as
defined growth rate
00950 I C  1  0    and interaction matrices from Iteration.  Iterates
difference equations,
00951 I C  1  0    increments time by 1, and returns new population values
to Iteration.}
00952 I     1  0
00953 I     1  0      CONST
00954 I     1  0        critical=32;  {to prevent overflow}
00955 I     1  0
00956 I     1  0      VAR
00957 I     1  0        int:double;
00958 I     1  0        expon:double;
00959 I     1  0        i,j,m,n:integer;
00960 I     1  0        oldpopn:species;
00961 I     1  0
00962 I     1  0
00963 I     1  1      BEGIN  { Iterate_discrete }
00964 I     1  1
00965 I     1  1        int:=0;
00966 I     1  1        oldpopn:=popn;
00967 I     1  1        FOR i:=1 TO web DO
00968 I     1  2          BEGIN
00969 I     1  2            FOR m:=1 TO variation DO
00970 I     1  3              BEGIN
00971 I     1  3                FOR j:=1 TO web DO
00972 I     1  4                  BEGIN
00973 I     1  4                    FOR n:=1 TO variation DO
00974 I     1  5                      BEGIN
00975 I     1  5                        int:=int + (alphint[i,j,m,n] *
oldpopn[j,n]);
00976 I     1  4                      END; {n-loop}
00977 I     1  3                  END;  {j-loop}
00978 I     1  3                expon:=growth_r[i,m] + int;
00979 I C   1  3                {Arithmetic overflow check}
00980 I     1  3                IF (growth_r[i,m] + int)>critical THEN
expon:=critical;
00981 I     1  3                popn[i,m]:=oldpopn[i,m] * EXP(expon);
00982 I C   1  3                {Extinction threshold}
00983 I     1  3                IF popn[i,m]<=extinct THEN popn[i,m]:=0;
00984 I C   1  3                {Maximum population density}
00985 I     1  3                IF popn[i,m]>1.000D24 THEN
popn[i,m]:=1.000D24;
00986 I     1  3                int:=0;
00987 I     1  3              END  {m-loop}
00988 I     1  2          END   {i-loop}
00989 I     1  2
00990 I     0  0      END;  { Iterate_discrete }
00991       0  0
00992       0  0    %INCLUDE 'i_c.pas /LIST'
00993 I     1  0    PROCEDURE Iterate_continuous (alphaint:matrix;
growth_r:species;
00994 I     1  0                                  VAR popn:species; stepd,
tol:double; gen:integer);
00995 I C  1  0     {Accepts old population values and times, as well as
defined growth rate
00996 I C  1  0    and interaction matrices from Iteration.  Solves
numerically differential
00997 I C  1  0    equation system using external NAG procedures for
time=t+interval and
00998 I C  1  0    returns solutions and time incremented by one unit to
Iteration.  Note that
00999 I C  1  0    the equations are stiff and thus must be solved by the
backward
01000 I C  1  0    differentiation formulae, rather than easier
Runge-Kutta or Adams-predictor
01001 I C  1  0    corrector methods.}
01002 I     1  0
01003 I     1  0      TYPE
01004 I     1  0        workarray=ARRAY [1..web*variation] OF double;
```

```
I     1  0        storearray=ARRAY [1..1500] OF double;
I     1  0        jacobarray=ARRAY [1..web*variation,
1..web*variation] OF double;
I     1  0
I     1  0      VAR
I     1  0        xx,xend:double;  {time parameters for NAG}
I     1  0        n,system:integer;  {dimension parameters for NAG}
I     1  0        i,m:integer;  {counters}
I     1  0        y:workarray;  {results store}
I     1  0        w:storearray; {working space}
I     1  0        iw:integer;   {dimension of working space}
I     1  0        ifail:integer;{error report caller}
I     1  0
I     1  0
I     2  0      [unbound] PROCEDURE Fcn (VAR t:double; VAR
y:workarray; VAR f:workarray);
I C   2  0        {NAG user-supplied procedure... evaluates dx/dt for
specific t}
I C   2  0        {Uses non-local variables defined in
Iterate_continuous}
I     2  0
I     2  0        VAR
I     2  0          i,j,m,q:integer;  {counters}
I     2  0          sys:integer;  {output counter}
I     2  0          int:double;  {accumulator}
I     2  0          acc:double;  {accumulator}
I     2  0          oldpopn:species;  {temporary store}
I C   2  0          {Note a:matrix b:species Global variables}
I     2  0
I     2  1        BEGIN  { Fcn }
I     2  1          int:=0;
I     2  1          acc:=0;
I     2  1
I C   2  1          {Initialise oldpopn}
I     2  1
I     2  1          sys:=1;
I     2  1          FOR i:=1 TO web DO
I     2  2            BEGIN
I     2  2              FOR m:=1 TO variation DO
I     2  3                BEGIN
I     2  3                  oldpopn[i,m]:=y[sys];
I     2  3                  sys:=sys + 1;
I     2  3                END  {m-loop}
I     2  1            END;  {i-loop}
I     2  1
I C   2  1          {Calculate derivative}
I     2  1
I     2  1          sys:=1;
I     2  1          FOR i:=1 TO web DO
I     2  2            BEGIN
I     2  2              FOR m:=1 TO variation DO
I     2  3                BEGIN
I     2  3                  FOR j:=1 TO web DO
I     2  4                    BEGIN
I     2  4                      FOR q:=1 TO variation DO
I     2  4                        int:=int + (a[i,j,m,q] *
oldpopn[j,q]);
I     2  4                      acc:=acc + int;
I     2  4                      int:=0;
I     2  3                    END;  {j-loop}
I     2  3                  f[sys]:=oldpopn[i,m] * (b[i,m] + acc);
I     2  3                  acc:=0;
I     2  3                  sys:=sys + 1;
I     2  3                  IF sys=((web * variation) + 1) THEN
sys:=1;
I     2  3                END  {m-loop}
I     2  2            END   {i-loop}
I     1  0        END;  { Fcn }
I     1  0
I     2  0      PROCEDURE d02eaf (VAR x:double; xend:double;
```

```
n:integer; VAR y:workarray;
01069 I    2  0                     VAR tol:double;
01070 I    2  0                     %IMMED [UNBOUND] PROCEDURE fcn (VAR
t:double;
01071 I    2  0                                                   VAR
y:workarray;
01072 I    2  0                                                   VAR
f:workarray);
01073 I    1  0                     VAR w:storearray; iw:integer; VAR
ifail:integer); EXTERN;
01074 I    1  0
01075 I C  1  0       {Note functions in procedural specification must be
forced with %IMMED}
01076 I C  1  0       {NAG procedure which, "..integrates a stiff system
of first-order ODEs
01077 I C  1  0      over a range with suitable initial conditions, using
a variable-order,
01078 I C  1  0      variable-step method implementing the Backward
Differentiation Formulae."}
01079 I C  1  0       {(see NAG User Guide FORTRAN routine summary)}
01080 I    1  0
01081 I    1  0
01082 I    1  1      BEGIN  { Iterate_continuous }
01083 I    1  1        xx:=Dble (gen);
01084 I    1  1        xend:=xx + stepd;
01085 I    1  1        iw:=1500;
01086 I    1  1        ifail:=0;
01087 I    1  1        n:=web * variation;
01088 I C  1  1        {Initialise y}
01089 I    1  1        system:=1;
01090 I    1  1        FOR i:=1 TO web DO
01091 I    1  2          BEGIN
01092 I    1  2            FOR m:=1 TO variation DO
01093 I    1  3              BEGIN
01094 I    1  3                y[system]:=popn[i,m];
01095 I    1  3                system:=system + 1;
01096 I    1  3              END  {m-loop}
01097 I    1  1          END;  {i-loop}
01098 I    1  1        d02eaf (xx, xend, n, y, tol, Fcn, w, iw, ifail);
01099 I    1  1        system:=1;
01100 I    1  1        FOR i:=1 TO web DO
01101 I    1  2          BEGIN
01102 I    1  2            FOR m:=1 TO variation DO
01103 I    1  3              BEGIN
01104 I    1  3                popn[i,m]:=y[system];
01105 I C  1  3                {Extinction threshold}
01106 I    1  3                IF popn[i,m]<=extinct THEN popn[i,m]:=0;
01107 I C  1  3                {Maximum population density}
01108 I    1  3                IF popn[i,m]>1.000D24 THEN
popn[i,m]:=1.000D24;
01109 I    1  3                system:=system +1;
01110 I    1  3              END  {m-loop}
01111 I    1  2          END  {i-loop}
01112 I    0  0      END;  { Iterate_continuous }
01113      0  0
01114      0  0    %INCLUDE 'graphics7 .pas /LIST'
01115 I    1  0    PROCEDURE Graphics7 (meanint:array3; popnsum,
nummut:array2; v:array2; coden:strtype);
01116 I C  1  0     {This procedure uses Simpleplot graphics library to
produce graphical
01117 I C  1  0    plots of the results of evolution of interacting
species for long runs.}
01118 I    1  0
01119 I    1  0      TYPE
01120 I    1  0        storage=ARRAY [1..terminus] OF real;
01121 I    1  0        lab=VARYING [80] OF char;
01122 I    1  0        axlab=VARYING [50] OF char;
01123 I    1  0        stringtype=PACKED ARRAY [1..11] OF char;
01124 I    1  0        string2=PACKED ARRAY [1..35] OF char;
01125 I    1  0        time_array=ARRAY [1..web] OF storage;
```

```
I     1  0
I     1  0      VAR
I     1  0        meanintstr:storage;       {mean interaction strength over time}
I     1  0        timearray:storage;        {time variable store}
I     1  0        poptime:storage;          {population time series}
I     1  0        muttime:storage;          {coexisting mutants time series}
I     1  0        vtime:storage;            {variance of allele frequency time series}
I     1  0        timestr,datestr:stringtype;  {strings to write current date and time}
I     1  0        strstr,codestr:lab;       {intermediate for title writing}
I     1  0        ymin, ymax:real;          {limits of axes}
I     1  0        mi:double;                {intermediate for type conversion}
I     1  0        i,j,m,n,t:integer;        {counters}
I     1  0
I C   1  0      {Simpleplot procedures for graphics}
I     1  0
I     1  0      PROCEDURE Devno (i:integer); FORTRAN;
I     1  0
I     1  0      PROCEDURE Papinc (cms:real); FORTRAN;
I     1  0
I     1  0      PROCEDURE Page (xcms, ycms:real); FORTRAN;
I     1  0
I     1  0      PROCEDURE Boxpag (tof:Boolean); FORTRAN;
I     1  0
I     1  0      PROCEDURE Group (nhoriz, nvert:integer); FORTRAN;
I     1  0
I     1  0      PROCEDURE Picsiz (xlen, ylen:real); FORTRAN;
I     1  0
I     1  0      PROCEDURE Limexc (varr:storage; nv:integer; VAR vmin,vmax:real); FORTRAN;
I     1  0
I     2  0      PROCEDURE Scales (xmin, xmax:real; xtype:integer; ymin, ymax:real;
I     1  0                                ytype:integer); FORTRAN;
I     1  0
I     1  0      PROCEDURE Axes7 (Xtitle, Ytitle:axlab); FORTRAN;
I     1  0
I     1  0      PROCEDURE Cvtype (ntype:integer); FORTRAN;
I     1  0
I     1  0      PROCEDURE Drawcv (xarr, yarr:storage; npts:integer); FORTRAN;
I     1  0
I     1  0      PROCEDURE Setpns (ipen1, ipen2, ipen3, ipen4:integer); FORTRAN;
I     1  0
I     1  0      PROCEDURE Pen (ipen:integer); FORTRAN;
I     1  0
I     1  0      PROCEDURE Title7 (vert, horiz:char; title:lab); FORTRAN;
I     1  0
I     1  0      PROCEDURE Endplt; FORTRAN;
I     1  0
I     1  0
I     1  1      BEGIN  { Graphics7 }
I     1  1
I C   1  1        {Choose output device}
I     1  1
I     1  1        Devno (1);
I     1  1
I C   1  1        {Set up graph}
I     1  1
I     1  1        Papinc (28.0 * web);
I     1  1        FOR i:=1 TO web DO
I     1  2          BEGIN
I     1  2            Setpns (1,2,3,4);
```

```
I     1  2            Pen (1);
I     1  2            Page (21.0, 29.7);
I     1  2            Boxpag (true);
I     1  2            Group (1,web + 3);
I     1  2            Picsiz (20.0, 5.0);
I     1  2
I C   1  2            {Draw graph}
I     1  2            j:=1;
I     1  2            FOR t:=1 TO terminus DO
I     1  3              BEGIN
I     1  3                timearray[t]:=t;
I     1  3                mi:=popnsum[i,t];
I     1  3                poptime[t]:=Sngl (mi)
I     1  2              END;  {t-loop}
I     1  2            Limexc (poptime, terminus, ymin, ymax);
I     1  2            Scales (0.0, terminus, 1, 0.0, ymax, 1);
I     1  2            Axes7 (%STDESCR('Time'), %STDESCR('Population
density'));
I     1  2            Cvtype (3);
I     1  2            Drawcv (timearray, poptime, terminus);
I     1  2
I     1  2            FOR t:=1 TO terminus DO
I     1  3              BEGIN
I     1  3                mi:=nummut[i,t];
I     1  3                muttime[t]:=Sngl (mi)
I     1  2              END;  {t-loop}
I     1  2            Scales (0.0, terminus, 1, 0, 10, 1);
I     1  2            Axes7 (%STDESCR('Time'), %STDESCR('Number of
Alleles'));
I     1  2            Cvtype (3);
I     1  2            Drawcv (timearray, muttime, terminus);
I     1  2
I     1  2            FOR t:=1 TO terminus DO
I     1  3              BEGIN
I     1  3                mi:=v[i,t];
I     1  3                vtime[t]:=Sngl (mi)
I     1  2              END;  {t-loop}
I     1  2            Limexc (vtime, terminus, ymin, ymax);
I     1  2            Scales (0.0, terminus, 1, 0, ymax, 1);
I     1  2            Axes7 (%STDESCR('Time'), %STDESCR('Variance of
Allele Frequency'));
I     1  2            Cvtype (3);
I     1  2            Drawcv (timearray, vtime, terminus);
I     1  2
I     1  2            FOR j:=1 TO web DO
I     1  3              BEGIN
I     1  3                FOR t:=1 TO terminus DO
I     1  4                  BEGIN
I     1  4                    mi:=meanint[i,j,t];
I     1  4                    meanintstr[t]:=Sngl (mi)
I     1  3                  END;
I     1  3                Scales (0.0, terminus, 1, 0.0, 1.0, 2);
I     1  3                Axes7 (%STDESCR('Time'), %STDESCR('Mean
interaction intensity'));
I     1  3                Cvtype (3);
I     1  3                Drawcv (timearray, meanintstr, terminus)
I     1  2              END;
I     1  2
I C   1  2            {Change pen colour}
I     1  2
I     1  2            Pen (2);
I     1  2
I C   1  2            {Write current time}
I C   1  2            { & experimental code}
I     1  2
I     1  2            Time (timestr);
I     1  2            Date (datestr);
I     1  2            strstr:=timestr + ' ' + datestr;
I     1  2            codestr:='Experiment ' + coden;
I     1  2
```

```
I C  1  2           {Add titles}
I    1  2
I    1  2           Title7 (%STDESCR('H'),%STDESCR('C'),
%STDESCR('MODEL7'));
I    1  2           Title7 (%STDESCR('H'),%STDESCR('C'),
%STDESCR(strstr));
I    1  2           Title7 (%STDESCR('H'),%STDESCR('C'),
%STDESCR(codestr));
I    1  2
I    1  1         END;  {i-loop}
I    1  1
I C  1  1       {End graphics}
I    1  1
I    1  1       Endplt
I    1  1
I    0  0     END; { Graphics7 }
     0  0
     0  0   %INCLUDE 'file_store7.pas /LIST'
I    1  0   PROCEDURE File_Store7 (meanint:array3;
popnsum,nummut,v:array2);
I C  1  0     {This procedure writes results to files for input
into interactive UNIRAS.
I C  1  0   This version for use with MODEL7.}
I    1  0
I    1  0     TYPE
I    1  0       storage=ARRAY [1..terminus] OF real;
I    1  0
I    1  0     VAR
I    1  0       meanintstr:storage;
I    1  0       timearray:storage;
I    1  0       poptime:storage;
I    1  0       muttime:storage;
I    1  0       vtime:storage;
I    1  0       mi:double;
I    1  0       i,j,t:integer;
I    1  0
I    2  0     PROCEDURE File_Write (results:array2; VAR
timestore:storage;
I    2  0                               VAR filename:text;
ii,tt:integer);
I C  2  0       {This procedure writes results from array to a text
file.}
I    2  0
I    2  0       VAR
I    2  0         mi:double;
I    2  0
I    2  1       BEGIN  { File_Write }
I    2  1         mi:=results[ii,tt];
I    2  1         timestore[tt]:=Sngl (mi);
I    2  1         Write (filename, timestore[tt]);
I    1  0       END;  { File_Write }
I    1  0
I    1  1     BEGIN  { File_Store7 }
I    1  1       Rewrite (unigr);
I    1  1         FOR t:=1 TO terminus DO
I    1  2           BEGIN
I    1  2             timearray[t]:=t;
I    1  2             Write (unigr, timearray[t]);
I    1  2             FOR i:=1 TO web DO
I    1  2               File_Write (popnsum, poptime, unigr, i, t);
I    1  2             FOR i:=1 TO web DO
I    1  2               File_Write (nummut, muttime, unigr, i, t);
I    1  2             FOR i:=1 TO web DO
I    1  2               File_Write (v, vtime, unigr, i, t);
I    1  2             FOR i:=1 TO web DO
I    1  3               BEGIN
I    1  3                 FOR j:=1 TO web DO
I    1  4                   BEGIN
I    1  4                     mi:=meanint[i,j,t];
I    1  4                     meanintstr[t]:=Sngl(mi);
```

```
I    1  4            Write (unigr, meanintstr[t]);
I    1  4            IF (i=web) AND (j=web) THEN
I    1  4              Writeln (unigr);
I    1  3          END;  {j-loop}
I    1  2        END;  {i-loop}
I    1  1      END;  {t-loop}
I    0  0   END;  { File_Store7 }
     0  0
     0  1  BEGIN {Main program}
     0  1
  C  0  1   {Inputing experimental code}
     0  1   Writeln ('Input code for experiment');
     0  1   Readln (codestr);
  C  0  1   {Inputing parameters as variables}
     0  1   FOR i:=1 TO web DO
     0  2     BEGIN
     0  2       Writeln ('Input initial density for species ',i);
     0  2       Readln (startpopn[i])
     0  1     END;  {i-loop}
     0  1   Writeln ('Input density of invading population');
     0  1   Readln (invadepop);
     0  1   Writeln ('Input extinction threshold');
     0  1   Readln (extinct);
     0  1   Writeln ('Input minimum self-limitation in prey');
     0  1   Readln (minselflimit);
     0  1   Writeln ('Input mutation rate (density^-1)');
     0  1   Readln (mutation_rate);
     0  1   Writeln ('Input SD of normal distribution as fraction
of mean ');
     0  1   Readln (fraction);
     0  1
  C  0  1   {Initialisation}
     0  1   Writeln ('Input type of initialisation required');
     0  1   Writeln ('Enter 0 for non-random initialisation, 1
for random initialisation');
     0  1   Readln (choice);
     0  1   IF (choice=1) THEN
     0  2     BEGIN
     0  2       Writeln ('Input mean of negative exponential
distribution');
     0  2       Readln (mean);
     0  2     END
     0  1   ELSE
     0  1     choice:=0;
     0  1   Writeln ('Input step length for invasion counting');
     0  1   Readln (stint);
     0  1
  C  0  1   {Running model}
  C  0  1   {Set up number of replicates}
     0  1   IF (choice = 1.0) OR (choice=0) THEN
     0  2     BEGIN
     0  2       Writeln ('Input the number of replicate runs
required');
     0  2       Readln (replicates);
     0  2       Writeln ('Random initialised system run for ',
replicates );
     0  2       Writeln (' runs.');
     0  2     END
     0  1     ELSE
     0  1       replicates:=1;
     0  1
  C  0  1   {Time type}
     0  1   Writeln ('Input the type of numerical system
required');
     0  1   Writeln ('Enter 0 for discrete time, 1 for continuous
time');
     0  1   Readln (ttype);
     0  1   IF (ttype=1) THEN
     0  2     BEGIN
     0  2       Writeln ('Input the step length for numerical
```

```
integration');
           0  2         Readln (step);
           0  2         Writeln ('Input the acceptable tolerance for
numerical integration');
           0  2         Readln (tolerance);
           0  1       END;  {numerical integration initialisation}
           0  1
        C  0  1     {Replicate loops}
           0  1     repl:=TRUNC(replicates);
           0  1     FOR ia:=1 TO repl DO
           0  2       BEGIN  {replicate loop}
        C  0  2         {Initialisation}
           0  2         G05ccf;
           0  2         IF (choice=0) THEN
           0  2           NonRandom_Initial (sign, x, b, a);
           0  2         IF (choice=1) THEN
           0  2           RandomInitial (sign, x, b, a);
           0  2         InvIn (ia, xic, inct, incs, cstep);
        C  0  2         {Population dynamics}
           0  2         generation_time:=0;
           0  2         IF ttype=0 THEN
           0  3           BEGIN  {discrete time}
           0  3             FOR count:=1 TO terminus DO
           0  4               BEGIN
           0  4                 Iterate_discrete (a, b, x,
generation_time);
           0  4                 Invasion (a, b, x, constraints, sign,
mutation_rate, fraction);
           0  4                 InvCount (x, xic, incs, inct, cstep);
           0  4                 Time_series (a, x, count,
mean_interaction,
           0  4                              population_over_time,
coexisting_mutants);
           0  4                 Allvar (count, x, population_over_time,
coexisting_mutants, v);
           0  3               END;  {time-counting}
           0  2           END;  {discrete time}
           0  2         IF ttype=1 THEN
           0  3           BEGIN  {continuous time}
           0  3             FOR count:=1 TO terminus DO
           0  4               BEGIN
           0  4                 Iterate_continuous (a, b, x, step,
tolerance, count);
           0  4                 Invasion (a, b, x, constraints, sign,
mutation_rate, fraction);
           0  4                 InvCount (x, xic, incs, inct, cstep);
           0  4                 Time_series (a, x, count,
mean_interaction,
           0  4                              population_over_time,
coexisting_mutants);
           0  4                 Allvar (count, x, population_over_time,
coexisting_mutants, v);
           0  3               END;  {time-counting}
           0  2           END;  {continuous time}
           0  1       END;  {Replication loop}
           0  1
        C  0  1     {Graphics...}
           0  1     Graphics7  (mean_interaction, population_over_time,
coexisting_mutants, v, codestr);
           0  1
        C  0  1     {File writing...}
           0  1     File_Store7 (mean_interaction, population_over_time,
coexisting_mutants, v);
           0  1
           0  0   END.  {Main program}
```

B.2 MODEL 2

For historical reasons described in the source code as Model 6. Lines of the program are shown in `Courier` typeface. Formatting of the source code in the preparation of this Appendix has caused some lines to run on; this does not occur in the original code. The program has a similar structure to the one above.

```
-LINE-IDC-PL-SL-

00001       0  0 PROGRAM Model6 (input, output, control, invsout, unigr);
00002    C  0  0   {This program models species interacting in a trophic
web, under repeated
00003    C  0  0    invasions of mutants.}
00004    C  0  0   {version: definitive DOUBLE precision}
00005    C  0  0   {reconstructed (9/11/90) from (27/7/90)}
00006    C  0  0   {reassembled from archive (27/11/90)
00007    C  0  0   {2 species; 5000 generations; NORMINT(0.1) mutation}
00008    C  0  0   {Explicit haploid genetic system with body size}
00009    C  0  0   {created (1/12/90)}
00010    C  0  0   {basic version without file writing or different random
sequences}
00011    C  0  0   {continuous time added (9/5/91)}
00012    C  0  0   {common self-limitation in prey added (4/7/91)}
00013    C  0  0   {invasion counting and output added (4/7/91)}
00014    C  0  0   {more user-defined parameters, allele variance, file
writing added (*/10/91)}
00015    C  0  0   {user-defined fraction added (6/1/92)}
00016    C  0  0   {discrete character states added (6/1/92)}
00017       0  0
00018    C  0  0   {Author: Paul Marrow                  }
00019    C  0  0   {         Department of Biology       }
00020    C  0  0   {         University of York          }
00021    C  0  0   {         York  Y01 5DD  UK           }
00022       0  0
00023       0  0   CONST  {Global constants}
00024       0  0     web=2;                       {number of species in food
web}
00025       0  0     variation=10;                {number of mutant niches
per species}
00026       0  0     terminus=5000;               {Number of time steps}
00027       0  0
00028       0  0   TYPE  {Definitions}
00029       0  0     initialtype=ARRAY [1..web] OF double;
00030       0  0     strtype=VARYING[80] OF char;
00031       0  0     species=ARRAY [1..web, 1..variation] OF double;
00032       0  0     matrix=ARRAY [1..web, 1..web, 1..variation,
1..variation] OF double;
00033       0  0     array2=ARRAY [1..web, 1..terminus] OF double;
00034       0  0     array3=ARRAY [1..web, 1..web, 1..terminus] OF double;
00035       0  0
00036       0  0   VAR  {Global variables}
00037       0  0     codestr:strtype;            {experimental code}
00038       0  0     control:text;               {text file for program
control}
00039    C  0  0     {Former constants as variables}
00040       0  0     startpopn:initialtype;      {starting population size}
00041       0  0     invadepop:double;           {invading population size}
00042       0  0     extinct:double;             {extinction threshold}
```

```
00043       0  0     minselflimit:double;       {minimum self-limitation in
producer}
00044       0  0     mutation_rate:double;      {mutation rate (density^1)}
00045       0  0     choice:double;             {random/nonrandom
initialisation}
00046       0  0     ttype:double;              {discrete/continuous time}
00047       0  0     step:double;               {step length in numerical
integration}
00048       0  0     tolerance:double;          {acceptable tolerance in
numerical integration}
00049       0  0     replicates:double;         {number of replicate runs
with same parameters}
00050       0  0     fraction:double;           {standard deviation of
mutanchargen normal distn.}
00051       0  0     repl:integer;              {replicate loop counter}
00052       0  0     a:matrix;                  {interaction strengths}
00053       0  0     sign:matrix;               {trophic constraints on
interaction strengths}
00054       0  0     b:species;                 {growth rates}
00055       0  0     x:species;                 {population sizes}
00056       0  0     xic:species;               {invasion counter marker}
00057       0  0     p:species;                 {phenotype=body size}
00058       0  0     v:array2;                  {variance of allele
frequency}
00059       0  0     count:integer;             {time counter}
00060       0  0     constraints:species;       {constraints on species
characteristics}
00061       0  0     generation_time:integer;       {dummy time counter}
00062       0  0     mean_interaction:array3;       {mean interaction
storage}
00063       0  0     population_over_time:array2;   {population time
series}
00064       0  0     coexisting_mutants:array2;     {number of coexisting
mutants}
00065       0  0     mean_size:array2;              {body size over time}
00066       0  0     i,j,m,n:integer;               {*debugging counters*}
00067       0  0     unigr:text;                    {results store}
00068       0  0     mean:double;                   {random distribution
parameter}
00069    C  0  0     {Extra variables for invasion counting}
00070       0  0     ia:integer;                    {counter}
00071       0  0     incs:initialtype;              {invasion counter}
00072       0  0     inct:initialtype;              {successful invasion
counter}
00073       0  0     pdm:initialtype;               {population density
counter}
00074       0  0     cstep:integer;                 {step number counter}
00075       0  0     ccount:integer;                {within step time
counter}
00076       0  0     stint:integer;                 {step length in
invasion counting}
00077       0  0     invsout:text;                  {output file for
invasions results}
00078       0  0
00079       0  0   %INCLUDE 'nagrandu.pas /LIST'
00080 I     0  0   FUNCTION G05caf (x:double):double; EXTERN;
00081 I C   0  0     {This NAG routine produces pseudo-random numbers from
a uniform
00082 I C   0  0   distribution on (0,1).  x is a dummy parameter required
by FORTRAN
00083 I C   0  0   syntax.}
00084       0  0
00085       0  0   %INCLUDE 'nagrandn.pas /LIST'
00086 I     0  0   FUNCTION G05ddf (a, b:double):double; EXTERN;
00087 I C   0  0     {This function produces a random variate from a
Normal distribution, mean a
00088 I C   0  0       standard deviation b.}
00089       0  0
00090       0  0   %INCLUDE 'nagrandx.pas /LIST'
00091 I     0  0   FUNCTION G05dbf (a:double):double; EXTERN;
```

```
00092 I C  0  0     {This function generates a pseudo-random real number
taken from a
00093 I C  0  0   negative exponential distribution.  See NAG Fortran
Library manual
00094 I C  0  0   for details.}
00095        0  0
00096        0  0   %INCLUDE 'unrepeat.pas /LIST'
00097 I      0  0   PROCEDURE G05ccf; EXTERN;
00098 I C  0  0     {This NAG routine sets the random number generator to
an unrepeatable
00099 I C  0  0   initial state.}
00100 I      0  0
00101        0  0
00102        0  0   %INCLUDE 'inputcontrol.pas /LIST'
00103 I      1  0   PROCEDURE InputControl (lineno:integer; VAR
vinput:double);
00104 I C  1  0     {This procedure reads from CONTROL.DAT at a specified
line, and writes
00105 I C  1  0   result to an integer control parameter which is then
passed back to main
00106 I C  1  0   program.  If line number specified is out of range, an
error message is
00107 I C  1  0   displayed.}
00108 I      1  0
00109 I      1  0     VAR
00110 I      1  0       i:integer;  {counter}
00111 I      1  0
00112 I      1  0
00113 I      1  1     BEGIN  { InputControl }
00114 I      1  1
00115 I      1  1       IF lineno > 1 THEN
00116 I      1  2         BEGIN
00117 I      1  2           FOR i:=1 TO (lineno-1) DO
00118 I      1  3             BEGIN
00119 I      1  3               IF Eof (control)=false THEN
00120 I      1  3                 Readln (control)
00121 I      1  3             END  {i-loop}
00122 I      1  1         END;  {IF loop}
00123 I      1  1       IF (Eof (control)=true) OR (lineno < 1) THEN
00124 I      1  2         BEGIN
00125 I      1  2           Writeln ('Error in reading from Control: line
number out of range');
00126 I      1  2           vinput:=0
00127 I      1  2         END
00128 I      1  1       ELSE
00129 I      1  1         Readln (control, vinput);
00130 I      1  1       Reset (control)
00131 I      1  1
00132 I      0  0     END;  { InputControl }
00133        0  0
00134        0  0   %INCLUDE 'initial_sign.pas /LIST'
00135 I      1  0   PROCEDURE Initial_Sign (VAR sign:matrix);
00136 I C  1  0     {This procedure reads the values of the sign matrix
from terminal
00137 I C  1  0   into the program array.}
00138 I      1  0
00139 I      1  0   VAR
00140 I      1  0     i,j,k,m,n:integer;  {counters}
00141 I      1  0     signm:double;     {sign constraint dummy variable}
00142 I      1  0
00143 I      1  0
00144 I      1  1   BEGIN { Initial_Sign }
00145 I      1  1
00146 I C  1  1     {Defining wild-types}
00147 I      1  1     k:=0;
00148 I      1  1     m:=1;
00149 I      1  1     n:=1;
00150 I      1  1     FOR i:=1 TO web DO
00151 I      1  2       BEGIN
00152 I      1  2         FOR j:=1 TO web DO
```

```
00153 I     1  3           BEGIN
00154 I     1  3             k:=k + 1;
00155 I     1  3             Writeln ('Input sign constraint for species
',i,' effect on species ',j);
00156 I     1  3             Readln (signm);
00157 I     1  3             sign[i,j,m,n]:=signm
00158 I     1  3           END   {j-loop}
00159 I     1  1       END;  {i-loop}
00160 I     1  1
00161 I C   1  1   {Defining outer rows and columns of mutant sign
matrices}
00162 I     1  1   FOR n:=2 TO variation DO
00163 I     1  2     BEGIN
00164 I     1  2       FOR i:=1 TO web DO
00165 I     1  3         BEGIN
00166 I     1  3           FOR j:=1 TO web DO
00167 I     1  3             sign[i,j,m,n]:=sign[i,j,1,1];
00168 I     1  2         END;  {i-loop}
00169 I     1  1     END;  {n-loop}
00170 I     1  1   n:=1;
00171 I     1  1   FOR m:=2 TO variation DO
00172 I     1  2     BEGIN
00173 I     1  2       FOR i:=1 TO web DO
00174 I     1  3         BEGIN
00175 I     1  3           FOR j:=1 TO web DO
00176 I     1  3             sign[i,j,m,n]:=sign[i,j,1,1];
00177 I     1  2         END;  {i-loop}
00178 I     1  1     END;  {m-loop}
00179 I     1  1
00180 I C   1  1   {Defining mutant sign matrices}
00181 I     1  1   FOR i:=1 TO web DO
00182 I     1  2     BEGIN
00183 I     1  2       FOR j:=1 TO web DO
00184 I     1  3         BEGIN
00185 I     1  3           FOR m:=2 TO variation DO
00186 I     1  4             BEGIN
00187 I     1  4               FOR n:=2 TO variation DO
00188 I     1  4                 sign[i,j,m,n]:=sign[i,j,1,1];
00189 I     1  4             END  {m-loop}
00190 I     1  3         END  {j-loop}
00191 I     1  2     END  {i-loop}
00192 I     1  2
00193 I     0  0   END;  { Initial_Sign }
00194       0  0
00195       0  0   %INCLUDE 'initial_pop.pas /LIST'
00196 I     1  0   PROCEDURE Initial_Pop (VAR popn:species);
00197 I C   1  0     {Input is undefined population matrix from either R
or NRInitial; for m=1
00198 I C   1  0   population values are set to StartPopn (global
variable), for m<>1 population
00199 I C   1  0   values are set to 0.  Defined population matrix is
returned to appropriate
00200 I C   1  0   initialisation procedure, and thus to main program.}
00201 I     1  0
00202 I     1  0     VAR
00203 I     1  0       i,m:integer;
00204 I     1  0
00205 I     1  1     BEGIN
00206 I     1  1       m:=1;
00207 I     1  1       FOR i:=1 TO web DO
00208 I     1  1         popn[i,m]:=StartPopn[i];
00209 I     1  1       FOR m:=2 TO variation DO
00210 I     1  2         BEGIN
00211 I     1  2           FOR i:=1 TO web DO
00212 I     1  2             popn[i,m]:=0
00213 I     1  2         END  {m-loop}
00214 I     0  0     END;  { Initial_Pop }
00215 I     0  0
00216       0  0
00217       0  0   %INCLUDE 'initial_zero.pas /LIST'
```

```
00218 I     1  0   PROCEDURE Initial_Zero (VAR grwth:species; VAR
interact:matrix);
00219 I C   1  0     {Inputs are partially defined growth rate and
interaction matrices;
00220 I C   1  0   for m>1 values are set to 0 and returned to
initialisation procedures
00221 I C   1  0   and thus to main program.  This prepares the way for
mutant invasion.}
00222 I     1  0
00223 I     1  0     VAR
00224 I     1  0       i,j,m,n:integer;
00225 I     1  0
00226 I     1  0
00227 I     1  1     BEGIN  { Initial_Zero }
00228 I     1  1
00229 I     1  1       FOR i:=1 TO web DO
00230 I     1  2         BEGIN
00231 I     1  2           FOR m:=2 TO variation DO
00232 I     1  3             BEGIN
00233 I     1  3               grwth[i,m]:=0;
00234 I     1  3               FOR j:=1 TO web DO
00235 I     1  4                 BEGIN
00236 I     1  4                   FOR n:=2 TO variation DO
00237 I     1  4                     interact[i,j,m,n]:=0;
00238 I     1  4                   n:=1;
00239 I     1  4                   interact[i,j,m,n]:=0;
00240 I     1  4                 END  {j-loop}
00241 I     1  3             END  {m-loop}
00242 I     1  2         END  {i-loop}
00243 I     1  2
00244 I     0  0       END;  { Initial_Zero }
00245       0  0
00246       0  0   %INCLUDE 'growth_gen.pas /LIST'
00247 I     1  0   PROCEDURE Growth_Gen (VAR growth_rate:species;
bsize:species; no,m:integer);
00248 I C   1  0     {This procedure calculates growth rates, given
initial phenotypes,
00249 I C   1  0     and subject to constraints.}
00250 I C   1  0     {Calls non-nested procedure InputControl.}
00251 I     1  0
00252 I     1  1     BEGIN  { Growth_Gen }
00253 I     1  1       IF bsize[no,m]<>0 THEN
00254 I     1  1         growth_rate[no,m]:=(1-bsize[no,m])
00255 I     1  1       ELSE
00256 I     1  1         growth_rate[no,m]:=0;
00257 I     1  1       IF no>1 THEN growth_rate[no,m]:= -growth_rate[no,m]
00258 I     0  0     END;  { Growth_Gen }
00259       0  0
00260       0  0   %INCLUDE 'selflimit1.pas /LIST'
00261 I     1  0     FUNCTION Self_limit (bsize:double):double;
00262 I C   1  0       {This function evaluates an interaction term for
self-limitation in
00263 I C   1  0     a producer species, or a consumer in a competition
community.}
00264 I     1  0
00265 I     1  0       CONST
00266 I     1  0         kt=1;
00267 I     1  0
00268 I     1  0       VAR
00269 I     1  0         it:double;  {dummy for function}
00270 I     1  0
00271 I     1  1       BEGIN  { Self_limit }
00272 I     1  1         it:=(kt * bsize);
00273 I     1  1         Self_limit:=it;
00274 I     0  0       END;  { Self_limit }
00275       0  0
00276       0  0   %INCLUDE 'pred_effect2.pas /LIST'
00277 I     1  0     FUNCTION Pred_effect (sizea,sizeb:double):double;
00278 I C   1  0       {This function evaluates an interaction term for
prey effect on predator.}
```

```
I    1  0
I    1  0       CONST
I    1  0         ka=1;
I    1  0         kb=1;
I    1  0         kc=1;
I    1  0         kd=1;
I    1  0
I    1  0       VAR
I    1  0         it:double;  (dummy for function)
I    1  0         kdiv:double;
I    1  0
I    1  1       BEGIN  { Pred_effect }
I    1  1         it:=((ka * Exp (-1.0 * kb * ((sizea - 0.5) *
(sizea - 0.5)))) *
I    1  1              (kc * Exp (-1.0 * kd * ((sizeb - 0.5) *
(sizeb - 0.5)))));
I    1  1         kdiv:=Exp (-1) * (Exp (1) - Exp (0.5));
I    1  1         it:=it/kdiv;
I    1  1         it:=it - 1.541494084;
I    1  1         IF it>1.0 THEN it:=1.0;
I    1  1         IF it<0.0 THEN it:=0.0;
I    1  1         Pred_effect:=it;
I    0  0       END;  { Pred_effect }
     0  0
     0  0   %INCLUDE 'prey_effect1.pas /LIST'
I    1  0     FUNCTION Prey_effect (sizea,sizeb:double):double;
I C  1  0       (This function evaluates an interaction term for
prey effect on predator.)
I    1  0
I    1  0       CONST
I    1  0         ka=1;
I    1  0         kb=1;
I    1  0         kc=1;
I    1  0         kd=1;
I    1  0
I    1  0       VAR
I    1  0         it:double;  (dummy for function)
I    1  0         kdiv:double;
I    1  0
I    1  1       BEGIN  { Prey_effect }
I    1  1         it:=((ka * Exp (-1.0 * kb * ((sizea - 0.5) *
(sizea - 0.5)))) *
I    1  1              (kc * Exp (-1.0 * kd * ((sizeb - 0.5) *
(sizeb - 0.5)))));
I    1  1         kdiv:=Exp (-1) * (Exp (1) - Exp (0.5));
I    1  1         it:=it/kdiv;
I    1  1         it:=it - 1.541494084;
I    1  1         IF it>1.0 THEN it:=1.0;
I    1  1         IF it<0.0 THEN it:=0.0;
I    1  1         Prey_effect:=it;
I    0  0       END;  { Prey_effect }
     0  0
     0  0   %INCLUDE 'interaction_gen.pas /LIST'
I    1  0   PROCEDURE Interaction_Gen (VAR alphaint:matrix;
sign_m:matrix;
I    1  0                                 bsize:species;
pp,q,m,n:integer);
I C  1  0     (This procedure generates interaction terms given
body sizes.)
I C  1  0     (Calls non-nested procedures for alpha11 (SelfLimit),
alpha12 (Prey_effect), and alpha21 (Pred_effect).)
I    1  0
I    1  0     VAR
I    1  0       ba,bc:double;  (mean size of prey accumulators)
I    1  0       h:integer;  (counter)
I    1  0
I    1  1     BEGIN  { Interaction_Gen }
I C  1  1       (Set all prey mutants to a common size)
I    1  1       ba:=0;
I    1  1       bc:=0;
```

```
00340 I    1  1       FOR h:=1 TO variation DO
00341 I    1  1           IF bsize[1,h]<>0 THEN
00342 I    1  2             BEGIN
00343 I    1  2               ba:=ba + bsize[1,h];
00344 I    1  2               bc:=bc +1;
00345 I    1  1             END;  {bsize accumulator}
00346 I    1  1       ba:=ba/bc;
00347 I    1  1
00348 I C  1  1       {Generate interaction terms}
00349 I    1  1       IF (pp>q) THEN
00350 I    1  1         alphaint[pp,q,m,n]:=Pred_effect
(bsize[pp,m],bsize[q,n]);
00351 I    1  1       IF (pp<q) THEN
00352 I    1  1         alphaint[pp,q,m,n]:=Prey_effect
(bsize[pp,m],bsize[q,n]);
00353 I    1  1       IF (pp=q) THEN
00354 I    1  1         alphaint[pp,q,m,n]:=Self_limit (ba);
{self-limitation generated from mean size}
00355 I    1  1       alphaint[pp,q,m,n]:=sign_m[pp,q,m,n] *
alphaint[pp,q,m,n];
00356 I    0  0     END;  { Interaction_Gen }
00357      0  0
00358      0  0   %INCLUDE 'nri.pas /LIST'
00359 I    1  0 PROCEDURE NonRandom_Initial (VAR sgn:matrix; VAR
population, growth,
00360 I    1  0                              size:species; VAR
alpha:matrix);
00361 I C  1  0    {This procedure establishes the initial values for
simulation parameters, as
00362 I C  1  0   input by the user.}
00363 I    1  0
00364 I    1  0   VAR
00365 I    1  0     i,j,m:integer;  {Counting variables}
00366 I    1  0
00367 I    2  0   PROCEDURE NRInitial_Size (VAR bsize:species;
no:integer);
00368 I C  2  0     {This procedure establishes the initial size as
entered by user.}
00369 I    2  0
00370 I    2  0     VAR
00371 I    2  0       m:integer;
00372 I    2  0
00373 I    2  1     BEGIN  { NRInitial_Size }
00374 I    2  1       m:=1;
00375 I    2  1       Writeln ('Input the initial trait (size) for
species ',no);
00376 I    2  1       Readln (bsize[no,m]);
00377 I    2  1       FOR m:=2 TO variation DO
00378 I    2  1         bsize[no,m]:=0;
00379 I    1  0     END;  { NRInitial_Size }
00380 I    1  0
00381 I    1  0
00382 I    1  1   BEGIN  { NonRandom_Initial }
00383 I    1  1
00384 I    1  1     Initial_Pop (population);
00385 I    1  1     Initial_Sign (sgn);
00386 I    1  1     FOR i:=1 TO web DO
00387 I    1  1       NRInitial_Size (size, i);
00388 I    1  1     FOR i:=1 TO web DO
00389 I    1  2       BEGIN
00390 I    1  2         FOR m:=1 TO variation DO
00391 I    1  3           BEGIN
00392 I    1  3             Growth_Gen (growth, size, i, m);
00393 I    1  3             FOR j:=1 TO web DO
00394 I    1  4               BEGIN
00395 I    1  4                 FOR n:=1 TO variation DO
00396 I    1  5                   BEGIN
00397 I    1  5                     IF (i=j) AND (i=1) THEN
00398 I    1  6                       BEGIN
00399 I    1  6                         Interaction_Gen (alpha, sgn,
```

```
size, i, j, m, n);
I    1  6                         IF
Abs(alpha[i,j,m,n])<minselflimit THEN
I    1  6                           alpha[i,j,m,n]:=minselflimit *
(-1.0);
I    1  6                       END  {alphall}
I    1  5                     ELSE
I    1  5                       IF population[j,n]<>0 THEN
I    1  5                         Interaction_Gen (alpha, sgn,
size, i, j, m, n);
I    1  4                   END;  {n-loop}
I    1  3               END;  {j-loop}
I    1  2           END;  {m-loop}
I    1  1       END; {i-loop}
I    1  1     Initial_Zero (growth, alpha)
I    1  1
I    0  0   END;  { NonRandom_Initial }
     0  0
     0  0   %INCLUDE 'ri.pas /LIST'
I    1  0 PROCEDURE Random_Initial (VAR sgn:matrix; VAR population,
growth,
I    1  0                              size:species; VAR
alpha:matrix;
I    1  0                              VAR constr:species);
I C  1  0   {This procedure defines initial parameters not entered
directly.}
I    1  0
I    1  0   VAR
I    1  0     i,j,m:integer;  {Counting variables}
I    1  0
I    2  0   PROCEDURE RInitial_Size (VAR bsize:species;
no:integer);
I C  2  0     {This procedure generates initial sizes at random.}
I    2  0
I    2  0     VAR
I    2  0       m:integer;
I    2  0
I    2  1     BEGIN  { RInitial_Size }
I    2  1       m:=1;
I    2  2       REPEAT
I    2  2         bsize[no,m]:= g05dbf (mean)
I    2  1       UNTIL (bsize[no,m]>0) AND (bsize[no,m]<1);
I    2  1       FOR m:=2 TO variation DO
I    2  1         bsize[no,m]:=0;
I    1  0     END;  { RInitial_Size }
I    1  0
I    1  0
I    1  1   BEGIN  { Random_Initial }
I    1  1
I    1  1     Initial_Pop (population);
I    1  1     IF ia=1 THEN
I    1  1       Initial_Sign (sgn);
I    1  1     FOR i:=1 TO web DO
I    1  1       RInitial_Size (size, i);
I    1  1     FOR i:=1 TO web DO
I    1  2       BEGIN
I    1  2         FOR m:=1 TO variation DO
I    1  3           BEGIN
I    1  3             constr[i,m]:=1;
I    1  3             Growth_Gen (growth, size, i, m);
I    1  3             FOR j:=1 TO web DO
I    1  4               BEGIN
I    1  4                 FOR n:=1 TO variation DO
I    1  5                   BEGIN
I    1  5                     IF (i=j) AND (i=1) THEN
I    1  6                       BEGIN
I    1  6                         Interaction_Gen (alpha, sgn,
size, i, j, m, n);
I    1  6                         IF
Abs(alpha[i,j,m,n])<minselflimit THEN
```

```
00460 I    1  6                     alpha[i,j,m,n]:=minselflimit *
(-1.0);
00461 I    1  6                   END  (all-generation)
00462 I    1  5                 ELSE
00463 I    1  5                   IF population[j,n]<>0 THEN
00464 I    1  5                     Interaction_Gen (alpha, sgn,
size, i, j, m, n);
00465 I    1  4               END;  (n-loop)
00466 I    1  3             END;  (j-loop)
00467 I    1  2           END;  (m-loop)
00468 I    1  1         END; (i-loop)
00469 I C  1  1        (Output initial parameters)
00470 I    1  1        Writeln ('Alpha11 = ', alpha[1,1,1,1]);
00471 I    1  1        Writeln ('Alpha12 = ', alpha[1,2,1,1]);
00472 I    1  1        Writeln ('Alpha21 = ', alpha[2,1,1,1]);
00473 I    1  1        Writeln ('R1 = ', growth[1,1]);
00474 I    1  1        Writeln ('R2 = ', growth[2,1]);
00475 I    1  1        Initial_Zero (growth, alpha);
00476 I    1  1
00477 I    0  0      END;  { Random_Initial }
00478      0  0
00479      0  0      %INCLUDE 'normean.pas /LIST'
00480 I    1  0         PROCEDURE Normean (VAR x:double; i:integer;
count:integer;
00481 I    1  0                               fraction:double; sizes:species);
00482 I C  1  0           (This procedure generates mutant characters from
a normal distribution,
00483 I C  1  0         mean the initial size, standard deviation a
fraction of this.)
00484 I    1  0
00485 I    1  0           VAR
00486 I    1  0             a,b:double;
00487 I    1  0
00488 I    1  1           BEGIN { Normean }
00489 I    1  1             a:=Abs (sizes[i,1]);
00490 I    1  1             b:=Abs (sizes[i,1]/10);
00491 I    1  1             IF (sizes[i,1]<>0) THEN
00492 I    1  2               BEGIN   (generator)
00493 I    1  3                 REPEAT
00494 I    1  3                   x:=G05ddf (a,b);
00495 I    1  2                 UNTIL (x>0) AND (x<1);
00496 I    1  1               END;    (generator)
00497 I    0  0           END;  { Normean }
00498      0  0
00499      0  0      %INCLUDE 'normint.pas /LIST'
00500 I    1  0         PROCEDURE Normint (VAR x:double; i:integer;
count:integer;
00501 I    1  0                               fraction:double);
00502 I C  1  0           (This procedure generates mutant characters from
a normal distribution,
00503 I C  1  0         mean the mean size, standard deviation a fraction
of this.)
00504 I    1  0
00505 I    1  0           VAR
00506 I    1  0            a,b:double;
00507 I    1  0
00508 I    1  1           BEGIN { Normint }
00509 I C  1  1             (Random  number generator NORMINT)
00510 I    1  1             IF mean_size[i,count-1]<>0 THEN
00511 I    1  2               BEGIN
00512 I    1  2                 a:=Abs (mean_size[i,count-1]);
00513 I    1  2                 b:=Abs (mean_size[i,count-1]/fraction);
00514 I    1  3                 REPEAT
00515 I    1  3                   x:=G05ddf (a,b);
00516 I    1  2                 UNTIL (x>0) AND (x<1);
00517 I    1  2               END  (If..Then)
00518 I    1  1             ELSE
00519 I    1  1               Normean (x, i, count, fraction, p);  (p is a
global variable)
00520 I    0  0           END;  { Normint }
```

```
       0  0
       0  0   %INCLUDE 'invin.pas /LIST'
I      1  0   PROCEDURE InvIn (rep:integer; VAR popn, popic:species;
VAR inkt,inks,ppdm:initialtype; VAR kstep, kcount:integer);
I C    1  0     {This procedure sets up the invasion counting
routines}
I      1  0
I      1  0     CONST
I      1  0       m=1;
I      1  0
I      1  0     VAR
I      1  0       i:integer;  {counter}
I      1  0
I      1  1     BEGIN  { InvIn }
I      1  1       FOR i:=1 TO web DO
I      1  2         BEGIN
I      1  2           popic[i,m]:=1;
I      1  2           inkt[i]:=0;
I      1  2           inks[i]:=0;
I      1  2           ppdm[i]:=popn[i,1];
I      1  1         END;  {i-loop}
I      1  1       kstep:=0;
I      1  1       kcount:=1;
I      0  0     END;  { InvIn }
       0  0
       0  0   %INCLUDE 'invasion.pas /LIST'
I      1  0   PROCEDURE Invasion (VAR alpha:matrix; VAR growth,
population, si:species;
I      1  0                       VAR constraint:species;
sign_m:matrix; populationtime:array2;
I      1  0                       mutationr:double; VAR
fraction:double);
I C    1  0     {This procedure causes a random attempted invasion of
a mutant into the
I C    1  0   preexisting food web species.  The defined interaction,
growth rate, and
I C    1  0   population matrices are read from main program,and
passed to nested procedures
I C    1  0   which check that invasion is possible, and then
generate an invader with
I C    1  0   random characteristics at a random location.  The
altered values for the
I C    1  0   interaction, growth rate, and population matrices are
returned to the main
I C    1  0   program as output.}
I      1  0
I      1  0     VAR
I      1  0       site:integer;
I      1  0       xx:double;        {dummy for random number
generator}
I      1  0
I      1  0     %INCLUDE 'emptyniches.pas /LIST'
I      2  0   FUNCTION EmptyNiches (popn:species):Boolean;
I C    2  0     {This function is similar to CheckMutReg, but checks
whole matrix of
I C    2  0   population values, and only returns false if all
elements are non-zero.}
I      2  0
I      2  0     VAR
I      2  0       i,m:integer;  {element counters}
I      2  0       z:integer;    {empty niche counter}
I      2  0       t:Boolean;    {dummy variable for function}
I      2  0
I      2  0
I      2  1     BEGIN  { EmptyNiches }
I      2  1
I      2  1       z:=0;
I      2  1       FOR i:=1 TO web DO
I      2  2         BEGIN
I      2  2           FOR m:=2 TO variation DO
```

```
00577 I     2  2             IF popn[i,m]=0 THEN z:=z + 1
00578 I     2  1           END;  {i-loop}
00579 I     2  1         IF z=0 THEN t:=false
00580 I     2  1           ELSE t:=true;
00581 I     2  1         EmptyNiches:=t
00582 I     2  1
00583 I     1  0       END;  { EmptyNiches }
00584 I     1  0
00585 I     1  0       %INCLUDE 'checkmutreg.pas /LIST'
00586 I     2  0     FUNCTION CheckMutReg (popn:species;
level:integer):Boolean;
00587 I C   2  0       (This function accepts the current population matrix
and a parameter
00588 I C   2  0     representing the location of the intended invasion
(i.e. trophic level) as
00589 I C   2  0     input from Invasion, and checks that not all the
elements of that species'
00590 I C   2  0     sub-matrix are occupied, returning 'true' if this is
so, and 'false' if it
00591 I C   2  0     is not.)
00592 I     2  0
00593 I     2  0       VAR
00594 I     2  0         m:integer;  (element counter)
00595 I     2  0         z:integer;  (empty element detector)
00596 I     2  0         y:Boolean;  (dummy variable for result)
00597 I     2  0
00598 I     2  0
00599 I     2  1       BEGIN  { CheckMutReg }
00600 I     2  1
00601 I     2  1         z:=0;
00602 I     2  1         FOR m:=2 TO variation DO
00603 I     2  1           IF popn[level,m]=0 THEN
00604 I     2  1             z:=z + 1;
00605 I     2  1         IF z=0 THEN y:=false
00606 I     2  1           ELSE y:=true;
00607 I     2  1         CheckMutReg:=y
00608 I     2  1
00609 I     1  0       END;  { CheckMutReg }
00610 I     1  0
00611 I     1  0       %INCLUDE 'invasionprob.pas /LIST'
00612 I     2  0     FUNCTION InvasionProb (popul:species; level:integer;
mutrate:double):Boolean;
00613 I C   2  0       (This function makes the mutation rate
density-dependent.  The total
00614 I C   2  0     density of the species at the invasion level is counted
and the
00615 I C   2  0     probability of invasion occuring (but not successful
establishment) is
00616 I C   2  0     =density/50.)
00617 I     2  0
00618 I     2  0       VAR
00619 I     2  0         x:double;               (dummy for random number
generator)
00620 I     2  0         density:double;         (density of species at which
mutation occurs)
00621 I     2  0         probability:Boolean;    (dummy for InvasionProb)
00622 I     2  0         m:integer;              (counter)
00623 I     2  0
00624 I     2  1       BEGIN  { InvasionProb }
00625 I     2  1
00626 I     2  1         x:=0;
00627 I     2  1         density:=0;
00628 I     2  1         x:=G05caf (x);
00629 I     2  1         FOR m:=1 TO variation DO
00630 I     2  1           density:=density + popul[level,m];
00631 I     2  1         IF density=0 THEN probability:=false
00632 I     2  1           ELSE
00633 I     2  1             IF x>=(density * mutrate) THEN
probability:=false
00634 I     2  1               ELSE probability:=true;
```

```
00635 I    2  1       InvasionProb:=probability;
00636 I    2  1
00637 I    1  0     END;  { InvasionProb }
00638 I    1  0
00639 I    1  0     %INCLUDE 'population_size.pas /LIST'
00640 I    2  0   PROCEDURE Population_Size (VAR popul:species;
level:integer);
00641 I C  2  0     {This procedure writes the starting population of an
invading mutant of a
00642 I C  2  0   pre-existing species into the population matrix.  Input
is the population
00643 I C  2  0   matrix and the location of the invasion, from Invasion.
The altered
00644 I C  2  0   population matrix is returned to invasion.}
00645 I    2  0
00646 I    2  0     VAR
00647 I    2  0       m:integer;  {element counter}
00648 I    2  0
00649 I    2  0
00650 I    2  1     BEGIN  { Population_Size }
00651 I    2  1
00652 I    2  1       m:=0;
00653 I    2  2       REPEAT
00654 I    2  2         m:=m + 1
00655 I    2  1       UNTIL popul[level,m]=0;
00656 I    2  1       popul[level,m]:=invadepop
00657 I    2  1
00658 I    1  0     END;  { Population_Size }
00659 I    1  0
00660 I    1  0     %INCLUDE 'repet6.pas /LIST'
00661 I    1  0
00662 I    2  0     FUNCTION Repetition_Check (bodysize,populn:species;
00663 I    2  0                                 locat:integer;
msite:integer):Boolean;
00664 I C  2  0       {This function checks to see whether the new mutant
has some character(s)
00665 I C  2  0     the same as any other cospecific mutant; if that is
so it returns a value
00666 I C  2  0     of true, else; false.}
00667 I    2  0
00668 I    2  0       VAR
00669 I    2  0         m:integer;  {counter}
00670 I    2  0         repet:Boolean;  {dummy for function}
00671 I    2  0
00672 I    2  1       BEGIN  { Repetition_Check }
00673 I    2  1         repet:=false;
00674 I    2  1                 FOR m:=1 TO variation DO
00675 I    2  2                   BEGIN
00676 I    2  2                     IF (msite<>m) THEN
00677 I    2  2                       IF Trunc (bodysize[locat,m] * 1000)
=
00678 I    2  2                          Trunc (bodysize[locat,msite] *
1000)
00679 I    2  2                         THEN repet:=true;
00680 I    2  1                   END;  {m-loop}
00681 I    2  1         Repetition_Check:=repet;
00682 I    1  0       END;  { Repetition_Check }
00683 I    1  0
00684 I    1  0
00685 I    1  0     %INCLUDE 'delet6.pas /LIST'
00686 I    2  0     PROCEDURE Delete_Mutant (VAR bodysize,populn:species;
00687 I    2  0                               locat,msite:integer);
00688 I C  2  0       {If a repeated invasion has occured, this procedure
deletes the invader.}
00689 I    2  0
00690 I    2  1       BEGIN  { Delete_Mutant }
00691 I C  2  1         {Delete body size}
00692 I    2  1         bodysize[locat,msite]:=0;
00693 I    1  0       END;  { Delete_Mutant }
00694 I    1  0
```

```
00695 I    1  0      %INCLUDE 'mutchargen6.pas /LIST'
00696 I    2  0    PROCEDURE MutCharGen (VAR inter:matrix; VAR
growth:species; location:integer;
00697 I    2  0                          constraints, popul:species; VAR
bsize:species;
00698 I    2  0                          signm:matrix; VAR
fraction:double);
00699 I C  2  0     {This procedure generates the characteristics of the
invading mutants.
00700 I C  2  0   Population size has already been set, and here the
intrinsic growth rate of
00701 I C  2  0   the mutant is set to the same as the species from which
it is derived, and
00702 I C  2  0   the interaction terms of the mutant are derived
randomly from a distribution
00703 I C  2  0   with mean the interaction strength of the original
species.  The values of
00704 I C  2  0   the interaction terms, and also the growth rates, may
be subject to
00705 I C  2  0   constraints.}
00706 I    2  0
00707 I    3  0     PROCEDURE Set_Constraints (VAR constr:species;
locat:integer);
00708 I C  3  0       {This procedure sets constraints upon the values of
mutant
00709 I C  3  0     characteristics.  No effect at present on overall
dynamics, since
00710 I C  3  0     all constraints are set to 1.}
00711 I    3  0
00712 I    3  0       VAR
00713 I    3  0         i,m:integer;  {counters}
00714 I    3  0
00715 I    3  0
00716 I    3  1       BEGIN  { Set_Constraints }
00717 I    3  1
00718 I    3  1         FOR i:=1 TO web DO
00719 I    3  2           BEGIN
00720 I    3  2             FOR m:=1 TO variation DO
00721 I    3  2               constr[i,m]:=1.0;
00722 I    3  2           END  {i-loop}
00723 I    3  2
00724 I    2  0       END;  { Set_Constraints }
00725 I    2  0
00726 I    3  0     PROCEDURE Size_Generator (VAR bodysize:species;
popul:species;
00727 I    3  0                                  loc, m:integer; VAR
fraction:double);
00728 I C  3  0       {This procedure generates new phenotypes (body
sizes), for an
00729 I C  3  0     invading mutant.}
00730 I    3  0
00731 I    3  0       VAR
00732 I    3  0         x:double;  {dummy for random number generator}
00733 I    3  0
00734 I    3  1       BEGIN  { Size_Generator }
00735 I    3  1         x:=0;
00736 I    3  1         m:=0;
00737 I    3  2         REPEAT
00738 I    3  2           m:=m + 1;
00739 I    3  1         UNTIL popul[loc,m]=invadepop;
00740 I    3  1         IF count=1 THEN
00741 I    3  1           Normint (x, loc, count+1, fraction)   {count is
a global variable}
00742 I    3  1         ELSE
00743 I    3  1           Normint (x, loc, count, fraction);
00744 I    3  1         bodysize[loc,m]:=x;
00745 I    2  0       END;  { Size_Generator }
00746 I    2  0
00747 I    3  0     PROCEDURE InteractionT_Gen (VAR interactions:matrix;
constr,
```

```
I    3  0                                     populn:species; VAR
bs:species;
I    3  0                                     locat:integer;
signs:matrix;
I    3  0                                     VAR fraction:double);
I C  3  0      {This procedure generates interaction terms for the
invading mutant.
I C  3  0    Input are the interaction, constraints and population
matrices, and
I C  3  0    the location of the invasion, from MutCharGen.  The
procedure detects
I C  3  0    the mutant element at which invasion takes place and
then goes through
I C  3  0    all [j*n] interaction terms for this element,
producing new values related
I C  3  0    to the parental values but multiplied by the
constraint matrix and by
I C  3  0    random factors.  The interaction terms are then
checked in order that
I C  3  0    conform to the constraints of the sign matrix, and
passed back to
I C  3  0    MutCharGen.  Note: count and mean_interaction are
Global variables.}
I    3  0
I    3  0      VAR
I    3  0        i,j,k,m,n,q:integer;  {counters}
I    3  0
I    3  1      BEGIN  { InteractionT_Gen }
I    3  1        m:=0;
I    3  2        REPEAT
I    3  2          m:=m + 1;
I    3  1        UNTIL populn[locat,m]=invadepop;
I C  3  1        {*** Discrete character states implementation
follows ***}
I    3  1        k:=0;
I    3  2        REPEAT
I    3  2          k:= k + 1;
I    3  2          Size_Generator (bs, populn, locat, m,
fraction);
I    3  2          IF Repetition_Check (bs, populn, locat, m) =
true THEN
I    3  2            Delete_Mutant (bs, populn, locat, m);
I    3  1        UNTIL (Repetition_Check (bs, populn, locat, m) =
false) OR (k=50);
I    3  1        FOR j:=1 TO web DO
I    3  2          BEGIN
I    3  2            FOR n:=1 TO variation DO
I    3  3              BEGIN
I    3  3                IF (locat=j) AND (locat=1) THEN
I    3  4                  BEGIN
I    3  4                    Interaction_Gen (interactions, signs,
bs, locat, j, m, n);
I    3  4                    IF Abs (interactions[locat,j,m,n]) <
minSelfLimit THEN
I    3  4
interactions[locat,j,m,n]:=minSelfLimit * (-1);
I    3  4                  END  {alpha11 generation}
I    3  3                ELSE
I    3  3                  IF  (populn[j,n]<>0) THEN
I    3  3                    Interaction_Gen (interactions, signs,
bs, locat, j, m, n);
I    3  2              END;  {interaction generation}
I    3  1          END; {j-loop}
I C  3  1        {Generate reciprocal interactions}
I    3  1        FOR i:=1 TO web DO
I    3  2          BEGIN
I    3  2            FOR q:=1 TO variation DO
I    3  3              BEGIN
I    3  3                IF (i<>locat) THEN
I    3  3                  IF (populn[i,q]<>0) THEN
```

SOURCE LISTING

```
I     3  3              Interaction_Gen (interactions, signs,
bs, i, locat, q, m);
I     3  2           END;  (q-loop)
I     3  1         END;  (i-loop)
I     2  0       END;  { InteractionT_Gen }
I     2  0
I     3  0      PROCEDURE GrowthR_Gen (VAR g_rate:species;
populn:species; locat:integer);
I C   3  0        {This procedure sets the growth rate of the
invading mutant to
I C   3  0      that is its parent species.  [This may eventually be
subject to
I C   3  0      constraint, but at present is only altered by a scale
factor].
I C   3  0      Input is the growth rate matrix and the location of
the invasion,
I C   3  0      (i.e. trophic level) from MutCharGen.  Output to
MutCharGen is the
I C   3  0      altered growth rate matrix.}
I     3  0
I     3  0       CONST
I     3  0         scale=1;  {scaling factor}
I     3  0
I     3  0       VAR
I     3  0         i,m:integer;  {counters}
I     3  0         x:double;     {dummy for random number generator}
I     3  0
I     3  1       BEGIN  { GrowthR_Gen }
I     3  1         x:=0;
I     3  1         m:=0;
I     3  2         REPEAT
I     3  2           m:=m + 1;
I     3  1         UNTIL populn[locat,m]=invadepop;  {invadepop is a
global variable.}
I     3  1         IF populn[locat,m]<>0 THEN
I     3  1           g_rate[locat,m]:=g_rate[locat,1] * scale
I     3  1         ELSE
I     3  2           BEGIN
I     3  2             G05caf (x);
I     3  2             g_rate[locat,m]:=x * scale;
I     3  1           END;  {else}
I     2  0       END;  { GrowthR_Gen }
I     2  0
I     2  1      BEGIN  { MutCharGen }
I     2  1
I C   2  1       {Set constraints, where they exist.}
I     2  1       Set_Constraints (constraints, location);
I     2  1
I C   2  1       {Set interaction terms for mutant}
I     2  1       InteractionT_Gen (inter, constraints, popul, bsize,
location, signm,
I     2  1                        fraction);
I     2  1
I C   2  1       {Set growth rate for mutant}
I     2  1       GrowthR_Gen (growth, popul, location);
I     2  1
I     1  0      END;  { MutCharGen }
I     1  0
I     1  0
I     1  1      BEGIN  { Invasion }
I     1  1
I     1  1       IF EmptyNiches (population)=true THEN
I     1  2         BEGIN  {try each species independently}
I     1  2           FOR site:=1 TO web DO
I     1  3             BEGIN
I     1  3               IF CheckMutReg (population, site)=true THEN
I     1  4                 BEGIN  {body of routine}
I     1  4
I     1  4                   IF (count>0) AND (count<>1) THEN
I     1  4                     IF populationtime[site, count-1]<>0
```

```
THEN
00860 I    1  4                     IF InvasionProb (population, site,
mutationr)=true THEN
00861 I    1  5                       BEGIN {check species has not gone
extinct}
00862 I C  1  5                         (Establish mutant population)

00863 I    1  5                         Population_Size (population,
site);
00864 I C  1  5                         {Establish mutant
characterisitics}
00865 I    1  5                         MutCharGen (alpha, growth,
site,
00866 I    1  5                                      constraint,
population, si, sign_m,
00867 I    1  5                                      fraction)
00868 I    1  4                       END;  ( invading )
00869 I    1  4
00870 I    1  4                 IF (count=0) OR (count=1) THEN
00871 I    1  4                   IF InvasionProb (population, site,
mutationr)=true THEN
00872 I    1  5                     BEGIN
00873 I    1  5                       Population_Size (population,
site);
00874 I    1  5                       MutCharGen (alpha, growth, site,
00875 I    1  5                                    constraint,
population, si, sign_m,
00876 I    1  5                                    fraction)
00877 I    1  4                     END;  { invading at start }
00878 I    1  4
00879 I    1  3               END;  {body of routine}
00880 I C  1  3            (Check that invasions are not repeated}
00881 I    1  3
00882 I    1  2           END;  {sites}
00883 I    1  1       END;
00884 I    0  0   END;  ( Invasion)
00885      0  0
00886      0  0   %INCLUDE 'invcount.pas /LIST'
00887 I    1  0   PROCEDURE InvCount (popn:species; VAR popic:species;
VAR inkt, inks, ppdm:initialtype; VAR kstep, kcount:integer);
00888 I C  1  0   {This procedure counts the number of invasions and
successful invasions
00889 I C  1  0   (ones which actually manage to establish themselves)
over certain times.}
00890 I    1  0
00891 I    1  0     VAR
00892 I    1  0       i,m:integer;  {counters}
00893 I    1  0       dv:double;    {dummy variable}
00894 I    1  0
00895 I    1  1     BEGIN  ( InvCount )
00896 I    1  1       dv:=(count/stint);
00897 I    1  1       IF count > 0 THEN
00898 I    1  1         IF (dv - Trunc (dv)) < Abs (1.0D-8) THEN
00899 I    1  2           BEGIN  {Resetting}
00900 I    1  2             kstep:=kstep + 1;
00901 I    1  2             FOR i:=1 TO web DO
00902 I    1  3               BEGIN
00903 I    1  3                 IF kstep=1 THEN
00904 I    1  3                   inks[i]:=inks[i] - web;
00905 I    1  3                 IF inks[i] < 0 THEN
00906 I    1  3                   inks[i]:=0;
00907 I C  1  3                 {Write output}
00908 I    1  3                 Write (invsout, Trunc (inkt[i]));
00909 I    1  3                 Write (invsout, Trunc (inks[i]));
00910 I    1  3                 Write (invsout, Sngl (ppdm[i]));
00911 I C  1  3                 {Reset counters}
00912 I    1  3                 inkt[i]:=0;
00913 I    1  3                 inks[i]:=0;
00914 I    1  3                 kcount:=1;
00915 I C  1  3                 {Reset population density mean}
```

```
I    1  3                 ppdm[i]:=0;
I    1  3                 FOR m:=1 TO variation DO
I    1  3                   ppdm[i]:=ppdm[i] + popn[i,m];
I    1  2               END;  {i-loop}
I    1  2               Writeln (invsout);
I    1  1           END;  {Resetting}
I    1  1       FOR i:=1 TO web DO
I    1  2         BEGIN
I    1  2           FOR m:=1 TO variation DO
I    1  3             BEGIN
I    1  3               IF popn[i,m] = invadepop THEN
I    1  4                 BEGIN
I    1  4                   inkt[i]:=inkt[i] + 1;
I    1  4                   popic[i,m]:=count;
I    1  3                 END;
I    1  3               IF popn[i,m] = 0 THEN
I    1  3                 popic[i,m]:=0;
I    1  3               IF popic[i,m] = count - 1 THEN
I    1  3                 IF popn[i,m] <> 0 THEN
I    1  3                   inks[i]:=inks[i] + 1;
I    1  2             END;  {m-loop}
I    1  2           ppdm[i]:=(ppdm[i] * (kcount-1));
I    1  2           FOR m:=1 TO variation DO
I    1  2             ppdm[i]:=ppdm[i] + popn[i,m];
I    1  2           IF kcount<>0 THEN
I    1  2             ppdm[i]:=(ppdm[i]/kcount);
I    1  1         END;  {i-loop}
I    1  1       kcount:=kcount + 1;
I    0  0     END;  { InvCount }
     0  0
     0  0   %INCLUDE 'time_series.pas /LIST'
I    1  0   PROCEDURE Time_series (alpha:matrix;
population:species;
I    1  0                                   t:integer; VAR meanint:array3;
I    1  0                                   VAR popnsum, nummut:array2);
I C  1  0     {This procedure calculates the mean interaction
strengths for the different
I C  1  0      species at a particular time and stores the result
for use in graphics.}
I    1  0
I    1  0     TYPE
I    1  0        arrayts=ARRAY [1..web, 1..web, 1..variation] OF
double;
I    1  0
I    1  0     VAR
I    1  0       alphasum:arrayts;       {intermediate in
interaction strength calc.}
I    1  0       i,j,m,n:integer;        {counters}
I    1  0
I    1  0
I    1  1     BEGIN  { Time_series }
I    1  1
I C  1  1       {Calculate interaction intensities}
I    1  1
I    1  1       FOR i:=1 TO web DO
I    1  2         BEGIN
I    1  2           FOR j:=1 TO web DO
I    1  3             BEGIN
I    1  3               meanint[i,j,t]:=0;
I    1  3               popnsum[i,t]:=0;
I    1  3               nummut[i,t]:=0;
I    1  3               FOR m:=1 TO variation DO
I    1  4                 BEGIN
I    1  4                   alphasum[i,j,m]:=0;
I    1  4                   popnsum[j,t]:=0;
I    1  4                   FOR n:=1 TO variation DO
I    1  5                     BEGIN
I    1  5                       alphasum[i,j,m]:=alphasum[i,j,m] +
I    1  5                                                   (Abs
(alpha[i,j,m,n]) *
```

```
00980 I    1  5
population[j,n]);
00981 I    1  5                       popnsum[j,t]:=popnsum[j,t] +
00982 I    1  5                                       population[j,n];
00983 I    1  4                     END;  {n-loop}
00984 I    1  4                   IF popnsum[j,t]<>0 THEN
00985 I    1  4
alphasum[i,j,m]:=alphasum[i,j,m]/popnsum[j,t]
00986 I    1  4                   ELSE
00987 I    1  4                     alphasum[i,j,m]:=0;
00988 I    1  4                   IF (population[i,m]<>0) THEN
00989 I    1  4                     nummut[i,t]:=nummut[i,t] + 1;
00990 I    1  4                   IF (i<>j) THEN
00991 I    1  4                     popnsum[i,t]:=popnsum[i,t] +
population[i,m];
00992 I    1  4                   meanint[i,j,t]:=meanint[i,j,t] +
(alphasum[i,j,m] *
00993 I    1  4                                  population[i,m]);
00994 I    1  3                 END;  {m-loop}
00995 I    1  3               IF popnsum[i,t]<>0 THEN
00996 I    1  3
meanint[i,j,t]:=meanint[i,j,t]/popnsum[i,t]
00997 I    1  3               ELSE
00998 I    1  3                 meanint[i,j,t]:=0;
00999 I    1  2             END;  {j-loop}
01000 I    1  1         END;  {i-loop}
01001 I    1  1
01002 I    0  0     END; { Time_series }
01003      0  0
01004      0  0   %INCLUDE 'allvar.pas /LIST'
01005 I    1  0   PROCEDURE Allvar (t:integer; population:species;
poptime, muttime:array2; VAR vari:array2);
01006 I C  1  0     {This procedure calculates the variance of allele
frequencies over time.}
01007 I    1  0
01008 I    1  0     VAR
01009 I    1  0       i, m:integer;        {counters}
01010 I    1  0       allfreq:species;     {frequencies of alleles}
01011 I    1  0       sumsq:initialtype;   {sum of squares for variance}
01012 I    1  0
01013 I    1  1     BEGIN  { Allvar }
01014 I    1  1       FOR i:=1 TO web DO
01015 I    1  2         BEGIN
01016 I    1  2           sumsq[i]:=0;
01017 I    1  2           FOR m:=1 TO variation DO
01018 I    1  3             BEGIN
01019 I    1  3               allfreq[i,m]:= 0;
01020 I    1  3               IF (poptime[i,t]<>0) THEN
01021 I    1  3                 allfreq[i,m]:=
(population[i,m]/poptime[i,t]);
01022 I    1  3               allfreq[i,m]:= Sqr (allfreq[i,m]);
01023 I    1  2             END;  {m-loop}
01024 I    1  1         END;  {i-loop}
01025 I    1  1       FOR i:=1 TO web DO
01026 I    1  2         BEGIN
01027 I    1  2           FOR m:=1 TO variation DO
01028 I    1  2             sumsq[i]:= sumsq[i] + allfreq[i,m];
01029 I    1  2           IF (muttime[i,t]<>0) THEN
01030 I    1  2             vari[i,t]:= sumsq[i] - (1/(muttime[i,t]));
01031 I    1  2           IF (muttime[i,t]>1) THEN
01032 I    1  2             vari[i,t]:= (vari[i,t]/(muttime[i,t] - 1))
01033 I    1  2           ELSE
01034 I    1  2             vari[i,t]:= 0;
01035 I    1  1         END;  {i-loop}
01036 I    0  0     END;  { Allvar }
01037 I    0  0
01038 I    0  0
01039 I    0  0
01040      0  0
01041      0  0   %INCLUDE 'iterate_discrete.pas /LIST'
```

```
I     1  0   PROCEDURE Iterate_discrete (alphint:matrix;
growth_r:species;
I     1  0                              VAR popn:species; VAR
gen:integer);
I C   1  0     {Accepts old population values and times, as well as
defined growth rate
I C   1  0   and interaction matrices from Iteration.  Iterates
difference equations,
I C   1  0   increments time by 1, and returns new population values
to Iteration.}
I     1  0
I     1  0     CONST
I     1  0       critical=32;  {to prevent overflow}
I     1  0
I     1  0     VAR
I     1  0       int:double;
I     1  0       expon:double;
I     1  0       i,j,m,n:integer;
I     1  0       oldpopn:species;
I     1  0
I     1  0
I     1  1     BEGIN  { Iterate_discrete }
I     1  1
I     1  1       int:=0;
I     1  1       oldpopn:=popn;
I     1  1       FOR i:=1 TO web DO
I     1  2         BEGIN
I     1  2           FOR m:=1 TO variation DO
I     1  3             BEGIN
I     1  3               FOR j:=1 TO web DO
I     1  4                 BEGIN
I     1  4                   FOR n:=1 TO variation DO
I     1  5                     BEGIN
I     1  5                       int:=int + (alphint[i,j,m,n] *
oldpopn[j,n]);
I     1  4                     END; {n-loop}
I     1  3                 END;  {j-loop}
I     1  3               expon:=growth_r[i,m] + int;
I C   1  3               {Arithmetic overflow check}
I     1  3               IF (growth_r[i,m] + int)>critical THEN
expon:=critical;
I     1  3               popn[i,m]:=oldpopn[i,m] * EXP(expon);
I C   1  3               {Extinction threshold}
I     1  3               IF popn[i,m]<=extinct THEN popn[i,m]:=0;
I C   1  3               {Maximum population density}
I     1  3               IF popn[i,m]>1.000D24 THEN
popn[i,m]:=1.000D24;
I     1  3               int:=0;
I     1  3             END  {m-loop}
I     1  2         END   {i-loop}
I     1  2
I     0  0     END;  { Iterate_discrete }
      0  0
      0  0   %INCLUDE 'i_c.pas /LIST'
I     1  0   PROCEDURE Iterate_continuous (alphaint:matrix;
growth_r:species;
I     1  0                                  VAR popn:species; stepd,
tol:double; gen:integer);
I C   1  0     {Accepts old population values and times, as well as
defined growth rate
I C   1  0   and interaction matrices from Iteration.  Solves
numerically differential
I C   1  0   equation system using external NAG procedures for
time=t+interval and
I C   1  0   returns solutions and time incremented by one unit to
Iteration.  Note that
I C   1  0   the equations are stiff and thus must be solved by the
backward
I C   1  0   differentiation formulae, rather than easier
Runge-Kutta or Adams-predictor
```

```
I C  1  0   corrector methods.}
I    1  0
I    1  0     TYPE
I    1  0       workarray=ARRAY [1..web*variation] OF double;
I    1  0       storearray=ARRAY [1..1500] OF double;
I    1  0       jacobarray=ARRAY [1..web*variation,
1..web*variation] OF double;
I    1  0
I    1  0     VAR
I    1  0       xx,xend:double;  {time parameters for NAG}
I    1  0       n,system:integer;  {dimension parameters for NAG}
I    1  0       i,m:integer;  {counters}
I    1  0       y:workarray;  {results store}
I    1  0       w:storearray; {working space}
I    1  0       iw:integer;   {dimension of working space}
I    1  0       ifail:integer;{error report caller}
I    1  0
I    1  0
I    2  0     [unbound] PROCEDURE Fcn (VAR t:double; VAR
y:workarray; VAR f:workarray);
I C  2  0       {NAG user-supplied procedure... evaluates dx/dt for
specific t}
I C  2  0       {Uses non-local variables defined in
Iterate_continuous}
I    2  0
I    2  0       VAR
I    2  0         i,j,m,q:integer;  {counters}
I    2  0         sys:integer;  {output counter}
I    2  0         int:double;  {accumulator}
I    2  0         acc:double;  {accumulator}
I    2  0         oldpopn:species;  {temporary store}
I C  2  0         {Note a:matrix b:species Global variables}
I    2  0
I    2  1       BEGIN  { Fcn }
I    2  1         int:=0;
I    2  1         acc:=0;
I    2  1
I C  2  1         {Initialise oldpopn}
I    2  1
I    2  1         sys:=1;
I    2  1         FOR i:=1 TO web DO
I    2  2           BEGIN
I    2  2             FOR m:=1 TO variation DO
I    2  3               BEGIN
I    2  3                 oldpopn[i,m]:=y[sys];
I    2  3                 sys:=sys + 1;
I    2  3               END  {m-loop}
I    2  1           END;  {i-loop}
I    2  1
I C  2  1         {Calculate derivative}
I    2  1
I    2  1         sys:=1;
I    2  1         FOR i:=1 TO web DO
I    2  2           BEGIN
I    2  2             FOR m:=1 TO variation DO
I    2  3               BEGIN
I    2  3                 FOR j:=1 TO web DO
I    2  4                   BEGIN
I    2  4                     FOR q:=1 TO variation DO
I    2  4                       int:=int + (a[i,j,m,q] *
oldpopn[j,q]);
I    2  4                     acc:=acc + int;
I    2  4                     int:=0;
I    2  3                   END;  {j-loop}
I    2  3                 f[sys]:=oldpopn[i,m] * (b[i,m] + acc);
I    2  3                 acc:=0;
I    2  3                 sys:=sys + 1;
I    2  3                 IF sys=((web * variation) + 1) THEN
sys:=1;
I    2  3               END  {m-loop}
```

```
01160 I     2  2          END   (i-loop)
01161 I     1  0       END;  ( Fcn )
01162 I     1  0
01163 I     2  0     PROCEDURE d02eaf (VAR x:double; xend:double;
n:integer; VAR y:workarray;
01164 I     2  0                    VAR tol:double;
01165 I     2  0                    %IMMED [UNBOUND] PROCEDURE fcn (VAR
t:double;
01166 I     2  0                                                      VAR
y:workarray;
01167 I     2  0                                                      VAR
f:workarray);
01168 I     1  0                    VAR w:storearray; iw:integer; VAR
ifail:integer); EXTERN;
01169 I     1  0
01170 I C   1  0       (Note functions in procedural specification must be
forçed with %IMMED)
01171 I C   1  0       (NAG procedure which, "..integrates a stiff system
of first-order ODEs
01172 I C   1  0     over a range with suitable initial conditions, using
a variable-order,
01173 I C   1  0     variable-step method implementing the Backward
Differentiation Formulae.")
01174 I C   1  0      ((see NAG User Guide FORTRAN routine summary))
01175 I     1  0
01176 I     1  0
01177 I     1  1     BEGIN  ( Iterate_continuous )
01178 I     1  1       xx:=Dble (gen);
01179 I     1  1       xend:=xx + stepd;
01180 I     1  1       iw:=1500;
01181 I     1  1       ifail:=0;
01182 I     1  1       n:=web * variation;
01183 I C   1  1       (Initialise y)
01184 I     1  1       system:=1;
01185 I     1  1       FOR i:=1 TO web DO
01186 I     1  2         BEGIN
01187 I     1  2           FOR m:=1 TO variation DO
01188 I     1  3             BEGIN
01189 I     1  3               y[system]:=popn[i,m];
01190 I     1  3               system:=system + 1;
01191 I     1  3             END  (m-loop)
01192 I     1  1         END;  (i-loop)
01193 I     1  1       d02eaf (xx, xend, n, y, tol, Fcn, w, iw, ifail);
01194 I     1  1       system:=1;
01195 I     1  1       FOR i:=1 TO web DO
01196 I     1  2         BEGIN
01197 I     1  2           FOR m:=1 TO variation DO
01198 I     1  3             BEGIN
01199 I     1  3               popn[i,m]:=y[system];
01200 I C   1  3               (Extinction threshold)
01201 I     1  3               IF popn[i,m]<=extinct THEN popn[i,m]:=0;
01202 I C   1  3               (Maximum population density)
01203 I     1  3               IF popn[i,m]>1.000D24 THEN
popn[i,m]:=1.000D24;
01204 I     1  3               system:=system +1;
01205 I     1  3             END  (m-loop)
01206 I     1  2         END  (i-loop)
01207 I     0  0     END;  ( Iterate_continuous )
01208       0  0
01209       0  0   %INCLUDE 'body_size.pas /LIST'
01210 I     1  0   PROCEDURE Body_Size (size:species; t:integer; VAR
mean:array2);
01211 I C   1  0     (This procedure calculates the mean body size for
each species at each time
01212 I C   1  0   step, and writes it to the mean size variable.)
01213 I     1  0
01214 I     1  0     VAR
01215 I     1  0       i,m,n:integer;  (counters)
01216 I     1  0       sum:double;     (accumulator)
01217 I     1  0
```

```
I     1  1      BEGIN  { Body_Size }
I     1  1        FOR i:=1 TO web DO
I     1  2          BEGIN
I     1  2            sum:=0;
I     1  2            n:=0;
I     1  2            FOR m:=1 TO variation DO
I     1  3              BEGIN
I     1  3                IF size[i,m]<>0 THEN
I     1  4                  BEGIN
I     1  4                    sum:=sum + size[i,m];
I     1  4                    n:=n + 1
I     1  3                  END;  {size non-zero}
I     1  2              END;  {summation}
I     1  2            mean[i,t]:=sum/n;
I     1  1          END;  {i-loop}
I     0  0      END;  { Body_Size }
      0  0
      0  0    %INCLUDE 'graphics4.pas /LIST'
I     1  0    PROCEDURE Graphics4 (meanint:array3; popnsum, nummut,
meansize:array2; v:array2; coden:strtype);
I C   1  0      {This procedure uses Simpleplot graphics library to
produce graphical
I C   1  0    plots of the results of evolution of interacting
species for long runs.}
I     1  0
I     1  0      TYPE
I     1  0        storage=ARRAY [1..terminus] OF real;
I     1  0        lab=VARYING [80] OF char;
I     1  0        axlab=VARYING [50] OF char;
I     1  0        stringtype=PACKED ARRAY [1..11] OF char;
I     1  0        string2=PACKED ARRAY [1..35] OF char;
I     1  0        time_array=ARRAY [1..web] OF storage;
I     1  0
I     1  0      VAR
I     1  0        meanintstr:storage;          {mean interaction
strength over time}
I     1  0        timearray:storage;           {time variable store}
I     1  0        poptime:storage;             {population time series}
I     1  0        muttime:storage;             {coexisting mutants time
series}
I     1  0        sizetime:storage;            {body size time series}
I     1  0        vtime:storage;               {variance of allele
frequency time series}
I     1  0        timestr,datestr:stringtype;  {strings to write
current date and time}
I     1  0        strstr,codestr:lab;          {intermediate for title
writing}
I     1  0        ymin, ymax:real;             {limits of axes}
I     1  0        mi:double;                   {intermediate for type
conversion}
I     1  0        i,j,m,n,t:integer;           {counters}
I     1  0
I C   1  0      {Simpleplot procedures for graphics}
I     1  0
I     1  0      PROCEDURE Devno (i:integer); FORTRAN;
I     1  0
I     1  0      PROCEDURE Papinc (cms:real); FORTRAN;
I     1  0
I     1  0      PROCEDURE Page (xcms, ycms:real); FORTRAN;
I     1  0
I     1  0      PROCEDURE Boxpag (tof:Boolean); FORTRAN;
I     1  0
I     1  0      PROCEDURE Group (nhoriz, nvert:integer); FORTRAN;
I     1  0
I     1  0      PROCEDURE Picsiz (xlen, ylen:real); FORTRAN;
I     1  0
I     1  0      PROCEDURE Limexc (varr:storage; nv:integer; VAR
vmin,vmax:real); FORTRAN;
I     1  0
I     2  0      PROCEDURE Scales (xmin, xmax:real; xtype:integer;
```

```
ymin, ymax:real;
I     1  0                        ytype:integer); FORTRAN;
I     1  0
I     1  0     PROCEDURE Axes7 (Xtitle, Ytitle:axlab); FORTRAN;
I     1  0
I     1  0     PROCEDURE Cvtype (ntype:integer); FORTRAN;
I     1  0
I     1  0     PROCEDURE Drawcv (xarr, yarr:storage; npts:integer);
FORTRAN;
I     1  0
I     1  0     PROCEDURE Setpns (ipen1, ipen2, ipen3,
ipen4:integer); FORTRAN;
I     1  0
I     1  0     PROCEDURE Pen (ipen:integer); FORTRAN;
I     1  0
I     1  0     PROCEDURE Title7 (vert, horiz:char; title:lab);
FORTRAN;
I     1  0
I     1  0     PROCEDURE Endplt; FORTRAN;
I     1  0
I     1  0
I     1  1     BEGIN  { Graphics3 }
I     1  1
I C   1  1       {Choose output device}
I     1  1
I     1  1       Devno (1);
I     1  1
I C   1  1       {Set up graph}
I     1  1
I     1  1       Papinc (28.0 * web);
I     1  1       FOR i:=1 TO web DO
I     1  2         BEGIN
I     1  2           Setpns (1,2,3,4);
I     1  2           Pen (1);
I     1  2           Page (21.0, 29.7);
I     1  2           Boxpag (true);
I     1  2           Group (1,web + 4);
I     1  2           Picsiz (20.0, 4.0);
I     1  2
I C   1  2           {Draw graph}
I     1  2           j:=1;
I     1  2           FOR t:=1 TO terminus DO
I     1  3             BEGIN
I     1  3               timearray[t]:=t;
I     1  3               mi:=popnsum[i,t];
I     1  3               poptime[t]:=Sngl (mi)
I     1  2             END;  {t-loop}
I     1  2           Limexc (poptime, terminus, ymin, ymax);
I     1  2           Scales (0.0, terminus, 1, 0.0, ymax, 1);
I     1  2           Axes7 (%STDESCR('Time'), %STDESCR('Population
density'));
I     1  2           Cvtype (3);
I     1  2           Drawcv (timearray, poptime, terminus);
I     1  2
I     1  2           FOR t:=1 TO terminus DO
I     1  3             BEGIN
I     1  3               mi:=nummut[i,t];
I     1  3               muttime[t]:=Sngl (mi)
I     1  2             END;  {t-loop}
I     1  2           Scales (0.0, terminus, 1, 0, 10, 1);
I     1  2           Axes7 (%STDESCR('Time'), %STDESCR('Number of
Alleles'));
I     1  2           Cvtype (3);
I     1  2           Drawcv (timearray, muttime, terminus);
I     1  2
I     1  2           FOR t:=1 TO terminus DO
I     1  3             BEGIN
I     1  3               mi:=v[i,t];
I     1  3               vtime[t]:=Sngl (mi)
I     1  2             END;  {t-loop}
```

```
I     1  2          Limexc (vtime, terminus, ymin, ymax);
I     1  2          Scales (0.0, terminus, 1, 0, ymax, 1);
I     1  2          Axes7 (%STDESCR('Time'), %STDESCR('Variance of
Allele Frequency'));
I     1  2          Cvtype (3);
I     1  2          Drawcv (timearray, vtime, terminus);
I     1  2
I     1  2
I     1  2          FOR t:=1 TO terminus DO
I     1  3            BEGIN
I     1  3              mi:=meansize[i,t];
I     1  3              sizetime[t]:=Sngl (mi)
I     1  2            END;
I     1  2          Scales (0.0, terminus, 1, 0, 10, 1);
I     1  2          Axes7 (%STDESCR('Time'), %STDESCR('Mean
Size'));
I     1  2          Cvtype (3);
I     1  2          Drawcv (timearray, sizetime, terminus);
I     1  2
I     1  2          FOR j:=1 TO web DO
I     1  3            BEGIN
I     1  3              FOR t:=1 TO terminus DO
I     1  4                BEGIN
I     1  4                  mi:=meanint[i,j,t];
I     1  4                  meanintstr[t]:=Sngl (mi)
I     1  3                END;
I     1  3              Scales (0.0, terminus, 1, 0.0, 1.0, 2);
I     1  3              Axes7 (%STDESCR('Time'), %STDESCR('Mean
interaction intensity'));
I     1  3              Cvtype (3);
I     1  3              Drawcv (timearray, meanintstr, terminus)
I     1  2            END;
I     1  2
I C   1  2          {Change pen colour}
I     1  2
I     1  2          Pen (2);
I     1  2
I C   1  2          {Write current time}
I C   1  2          { & experimental code}
I     1  2
I     1  2          Time (timestr);
I     1  2          Date (datestr);
I     1  2          strstr:=timestr + ' ' + datestr;
I     1  2          codestr:='Experiment ' + coden;
I     1  2
I C   1  2          {Add titles}
I     1  2
I     1  2          Title7 (%STDESCR('H'),%STDESCR('C'),
%STDESCR('MODEL6'));
I     1  2          Title7 (%STDESCR('H'),%STDESCR('C'),
%STDESCR(strstr));
I     1  2          Title7 (%STDESCR('H'),%STDESCR('C'),
%STDESCR(codestr));
I     1  2
I     1  1        END;  {i-loop}
I     1  1
I C   1  1      {End graphics}
I     1  1
I     1  1      Endplt
I     1  1
I     0  0    END; { Graphics3 }
      0  0
      0  0  %INCLUDE 'file_store6.pas /LIST'
I     1  0  PROCEDURE File_Store6 (meanint:array3;
popnsum,nummut,meansize, v:array2);
I C   1  0    {This procedure writes results to files for input
into interactive UNIRAS.
I C   1  0  This version for use with MODEL6.}
I     1  0
I     1  0    TYPE
```

```
I    1 0     storage=ARRAY [1..terminus] OF real;
I    1 0
I    1 0   VAR
I    1 0     meanintstr:storage;
I    1 0     timearray:storage;
I    1 0     poptime:storage;
I    1 0     muttime:storage;
I    1 0     sizetime:storage;
I    1 0     vtime:storage;
I    1 0     mi:double;
I    1 0     i,j,t:integer;
I    1 0
I    2 0   PROCEDURE File_Write (results:array2; VAR
timestore:storage;
I    2 0                VAR filename:text;
ii,tt:integer);
I C  2 0     {This procedure writes results from array to a text
file.}
I    2 0
I    2 0     VAR
I    2 0       mi:double;
I    2 0
I    2 1     BEGIN  { File_Write }
I    2 1       mi:=results[ii,tt];
I    2 1       timestore[tt]:=Sngl (mi);
I    2 1       Write (filename, timestore[tt]);
I    1 0     END;  { File_Write }
I    1 0
I    1 1   BEGIN  { File_Store4 }
I    1 1     Rewrite (unigr);
I    1 1       FOR t:=1 TO terminus DO
I    1 2         BEGIN
I    1 2           timearray[t]:=t;
I    1 2           Write (unigr, timearray[t]);
I    1 2           FOR i:=1 TO web DO
I    1 2             File_Write (popnsum, poptime, unigr, i, t);
I    1 2           FOR i:=1 TO web DO
I    1 2             File_Write (nummut, muttime, unigr, i, t);
I    1 2           FOR i:=1 TO web DO
I    1 2             File_Write (meansize, sizetime, unigr, i,
t);
I    1 2           FOR i:=1 TO web DO
I    1 2             File_Write (v, vtime, unigr, i, t);
I    1 2           FOR i:=1 TO web DO
I    1 3             BEGIN
I    1 3               FOR j:=1 TO web DO
I    1 4                 BEGIN
I    1 4                   mi:=meanint[i,j,t];
I    1 4                   meanintstr[t]:=Sngl(mi);
I    1 4                   Write (unigr, meanintstr[t]);
I    1 4                   IF (i=web) AND (j=web) THEN
I    1 4                     Writeln (unigr);
I    1 3                 END;  {j-loop}
I    1 2             END;  {i-loop}
I    1 1         END;  {t-loop}
I    0 0   END;  { File_Store6 }
     0 0
     0 0
     0 1 BEGIN {Main program}
     0 1
  C  0 1   {Inputing experimental codes}
     0 1   Writeln ('Input code for experiment');
     0 1   Readln (codestr);
  C  0 1   {Inputing parameters as variables}
     0 1   FOR i:=1 TO web DO
     0 2     BEGIN
     0 2       Writeln ('Input initial density for species ',i);
     0 2       Readln (startpopn[i])
     0 1     END;  {i-loop}
     0 1   Writeln ('Input density of invading population');
```

```
     0  1    Readln (invadepop);
     0  1    Writeln ('Input extinction threshold');
     0  1    Readln (extinct);
     0  1    Writeln ('Input minimum self-limitation in prey');
     0  1    Readln (minselflimit);
     0  1    Writeln ('Input mutation rate (density^1)');
     0  1    Readln (mutation_rate);
     0  1    Writeln ('Input SD of normal distribution as fraction
of mean ');
     0  1    Readln (fraction);
     0  1
  C  0  1    {Initialisation}
     0  1    Writeln ('Input type of initialisation required');
     0  1    Writeln ('Enter 0 for non-random initialisation, 1
for random initialisation');
     0  1    Readln (choice);
     0  1    IF (choice=1) THEN
     0  2      BEGIN
     0  2        Writeln ('Input mean of negative exponential
distribution');
     0  2        Readln (mean);
     0  2      END
     0  1    ELSE
     0  1      mean:=0;
     0  1    Writeln ('Input step length for invasion counting');
     0  1    Readln (stint);
     0  1
  C  0  1    {Running model}
  C  0  1    {Set up number of replicates}
     0  1    IF choice = 1.0 THEN
     0  2      BEGIN
     0  2        Writeln ('Input the number of replicate runs
required');
     0  2        Readln (replicates);
     0  2        Writeln ('Random initialised system run for ',
replicates );
     0  2        Writeln (' runs.');
     0  2      END
     0  1      ELSE
     0  1        replicates:=1;
     0  1
  C  0  1    {Time type}
     0  1    Writeln ('Input the type of numerical system
required');
     0  1    Writeln ('Enter 0 for discrete time, 1 for continuous
time');
     0  1    Readln (ttype);
     0  1    IF (ttype=1) THEN
     0  2      BEGIN
     0  2        Writeln ('Input the step length required for
numerical integration');
     0  2        Readln (step);
     0  2        Writeln ('Input the acceptable tolerance for
numerical integration');
     0  2        Readln (tolerance);
     0  1      END;  {numerical integration initialisation}
     0  1
  C  0  1    {Replicate loops}
     0  1    Rewrite (invsout);
     0  1    repl:=TRUNC(replicates);
     0  1    FOR ia:=1 TO repl DO
     0  2      BEGIN  {replicate loop}
  C  0  2        {Initialisation}
     0  2        g05ccf;
     0  2        IF (choice=0) THEN
     0  2          NonRandom_Initial (sign, x, b, p, a);
     0  2        IF (choice=1) THEN
     0  2          Random_Initial (sign, x, b, p, a, constraints);
     0  2        InvIn (ia, x, xic, inct, incs, pdm, cstep,
ccount);
```

```
01530   C  0  2          {Population dynamics}
01531      0  2          generation_time:=0;
01532      0  2          IF ttype=0 THEN
01533      0  3            BEGIN  {discrete time}
01534      0  3              FOR count:=1 TO terminus DO
01535      0  4                BEGIN
01536      0  4                  Iterate_discrete (a, b, x,
generation_time);
01537      0  4                  Invasion (a, b, x, p, constraints, sign,
population_over_time,
01538      0  4                            mutation_rate, fraction);
01539      0  4                  InvCount (x, xic, incs, inct, pdm, cstep,
ccount);
01540      0  4                  Time_series (a, x, count,
mean_interaction,
01541      0  4                               population_over_time,
coexisting_mutants);
01542      0  4                  Allvar (count, x, population_over_time,
coexisting_mutants, v);
01543      0  4                  Body_size (p, count, mean_size);
01544      0  3                END;  {time-counting}
01545      0  2            END;  {discrete time}
01546      0  2          IF ttype=1 THEN
01547      0  3            BEGIN  {continuous time}
01548      0  3              FOR count:=1 TO terminus DO
01549      0  4                BEGIN
01550      0  4                  Iterate_continuous (a, b, x, step,
tolerance, count);
01551      0  4                  Invasion (a, b, x, p, constraints, sign,
population_over_time,
01552      0  4                            mutation_rate, fraction);
01553      0  4                  InvCount (x, xic, incs, inct, pdm, cstep,
ccount);
01554      0  4                  Time_series (a, x, count,
mean_interaction,
01555      0  4                               population_over_time,
coexisting_mutants);
01556      0  4                  Allvar (count, x, population_over_time,
coexisting_mutants, v);
01557      0  4                  Body_size (p, count, mean_size);
01558      0  3                END;  {time counting}
01559      0  2            END;  {continuous time}
01560      0  2
01561   C  0  2          {Graphics...}
01562      0  2          Graphics4 (mean_interaction,
population_over_time, coexisting_mutants, mean_size, v, codestr);
01563      0  2
01564   C  0  2          {File writing...}
01565      0  2          File_Store6 (mean_interaction,
population_over_time, coexisting_mutants, mean_size, v);
01566      0  2
01567      0  1        END;  {Replication loop}
01568      0  1
01569      0  0    END.  {Main program.}
```

LIST OF SYMBOLS

The following list describes most of the symbols introduced in this thesis. Some common mathematical and statistical symbols have been omitted.

Symbol	Chapter	Description
a	5	Intercept of least-squares linear regression.
b	5	Slope of least-squares linear regression.
c_1, c_2	4	Constants of transformation of F_{21}.
F	5	F-ratio in analysis of variance.
F_{ij}	3,4	Function relating body size (investment in predatory or anti-predator traits) to interspecific interaction coefficient for species j effect on species i.
f_{ij}	2	See F_{ij} above.
I_{ij}	4	Weighted mean of intergenotypic interaction coefficients for interspecific interaction coefficient for species j effect on species i.
i	1-4	Subscript identifying particular species.
j	1-4	Subscript identifying particular species.
k_1, k_2, k_3, k_4	4	Constants defining form of F_{21} function.
k_5	4	Constant defining form of F_{11} function.
m	4	Subscript identifying particular mutant genotype within a species.
n	1,2,4	Any number.
n	4	Subscript denoting mutant genotype within a species with an effect on another genotype.
n	5	Number of observations.
p_1	3	Parameter controlling depth of F_{12} function.

SYMBOLS USED

Symbol	**Chapter**	**Description**
p_2	3	Parameter of cross-product term for F_{12}.
p_3	3	Parameter defining location of trough of F_{12}, with respect to s_1.
p_4	3	Parameter controlling degree of spread of F_{12}, with respect to s_1.
p_5	3	As p_3, but with respect to s_2.
p_6	3	As p_4, but with respect to s_2.
p_7	3	Parameter controlling height of F_{21} function.
p_8	3	Parameter of cross-product term for F_{21}.
p_9	3	Parameter defining location of peak of F_{21}, with respect to s_1.
p_{10}	3	Parameter controlling degree of spread of F_{21}, with respect to s_1.
p_{11}	3	As p_9, but with respect to s_2.
p_{12}	3	As p_{10}, but with respect to s_2.
p_{13}, p_{14}, p_{15}	3	Parameters defining F_{11} function.
r_i	1-4	Intrinsic growth rate of species *i*.
r_{im}	4	Intrinsic growth rate of mutant genotype *m* in species *i*.
s_i	2-5	Investment in predatory or anti-predator traits (as appropriate) for species *i*. Equivalent to body size of species *i*.
$\dot{s}_1$, $\dot{s}_2$	2	Partial derivative of s_1, s_2 with respect to time.
t	1-4	Time.
W_i	2,3	Fitness function of species *i*. (Per capita growth rate of species *i*).

SYMBOLS USED

Symbol	**Chapter**	**Description**
W_i'	3	Fitness function for mutant of species *i*.
W_{im}	4	Fitness function for genotype *m* of species *i*.
x_i	1-4	Population density of species *i*.
x_{im}	4	Genotype density of genotype *m* in species *i*.
x_{im}'	4	Discrete time density of genotype *m* of species *i* at time $t + 1$.
$\hat{x}_1$	2,3	Prey equilibrium density.
$\hat{x}_2$	2,3	Predator equilibrium density.
α_{ij}	1-5	Interspecific interaction coefficient for effect of species *j* on species *i*.
α_{ij}'	3	Interaction coefficient as above for mutant of species *i*.
α_{ijmn}	4	Intergenotypic interaction coefficient for effect of genotype *n* in species *j* on genotype *m* in species *i*.
γ_1, γ_2	2	Values of ρ at which predator equilibrium density is zero.
δ_1, δ_2	3	Symbols introduced for notational convenience in F_{12}.
δ_3, δ_4	3	Symbols introduced for notational convenience in F_{21}.
ε_i	3	Mutant effect on body size of species *i*.
θ	2	Maximum (turning point) of f_{12} and f_{21} when their two maxima are coincident.
θ_{ij}	2	Maximum (turning point) of f_{ij}.
ρ	2	Function relating body sizes of predator and prey to interspecific interaction coefficients.

REFERENCES

> Of making many books there is no end; and much study is a weariness of the flesh.
>
> Ecclesiastes 12:12

Abrams, P. A. 1986a. Adaptive responses of predators to prey and prey to predators: the failure of the arms race analogy. Evolution 40:1229-1247.

Abrams, P. A. 1986b. Is predator-prey coevolution an arms race? Trends in Ecology and Evolution 1:108-110.

Abrams, P. A. 1990. The evolution of anti-predator traits in prey in response to evolutionary change in predators. Oikos 59:147-156.

Abrams, P. A. 1991. The effects of interacting species on predator-prey coevolution. Theoretical Population Biology 39:241-262.

Abrams, P. A. 1992. Adaptive foraging by predators as a cause of predator-prey cycles. Evolutionary Ecology 6:56-72.

Akçakaya, H. R., and L. R. Ginzburg. 1989. Niche overlap and the evolution of competitive interactions. Pages 32-42 *in* A. Fontdevila, editor. Evolutionary biology of transient unstable populations. Springer-Verlag, Berlin, Germany.

Akçakaya, H. R., and L. R. Ginzburg. 1991. Community construction: speciation versus invasion. Trends in Ecology and Evolution 6:100-101.

Anderson, H. M., V. Hutson, and R. Law. 1992. On the conditions for permanence of species in ecological communities. American Naturalist 139:663-668.

Anderson, R. M., and R. M. May. 1982. Coevolution of hosts and parasites. Parasitology 85:411-426.

Baker, G. L., and J. P. Gollub. 1990. Chaotic dynamics: an introduction. Cambridge University Press, Cambridge, England.

Bakker, R. R. 1983. The deer flees, the wolf purses: incongruencies in predator-prey coevolution. Pages 350-382 *in* D. J. Futuyma, and M. Slatkin, editors. Coevolution. Sinauer, Sunderland, Mass., USA.

REFERENCES

Barkai, A., and C. McQuaid. 1988. Predator-prey reversal in a marine benthic system. Science 242:62-64.

Beaver, R. A. 1985. Geographical variation in food web structure in *Nepenthes* pitcher plants. Ecological Entomology 10:241-248.

Begon, M. E., J. L. Harper, and C. R. Townsend. 1986. Ecology: individuals, populations and communities. Blackwell Scientific, Oxford, England.

Bell, G. 1982. The masterpiece of nature: the evolution and genetics of sexuality. University of California Press, Berkeley, California, USA.

Bellows, T. S., Jr., and M. P. Hassell. 1988. The dynamics of age-structured host-parasitoid interactions. Journal of Animal Ecology 57:259-268.

Berryman, A. A., and J. A. Millstein. 1989. Are ecological systems chaotic-and if not, why not? Trends in Ecology and Evolution 4:26-28.

Bodmer, W. F., and L. L. Cavalli-Sforza. 1971. Variation in fitness and molecular evolution. Pages 225-275 *in* Proceedings of the 6th Berkeley symposium on mathematics, statistics and probability. Volume V: Darwinism, neo-Darwinism and non-Darwinian evolution. University of California Press, Berkeley, California, USA.

Briand, F. 1983. Environmental control of food web structure. Ecology 64:253-263.

Briand, F., and J. E. Cohen. 1984. Community food webs have scale-invariant structure. Nature 307:264-266.

Briand, F., and J. E. Cohen. 1987. Environmental correlates of food chain length. Science 238:956-960.

Briand, F., and J. E. Cohen. 1989. Habitat compartmentation and environmental correlates of food chain length. Science 243:239-240.

Brown, J. S., and T. L. Vincent. 1987a. Coevolution as an evolutionary game. Evolution 41:66-79.

Brown, J. S., and T. L. Vincent. 1987b. A theory for the evolutionary game. Theoretical Population Biology 31:140-166.

Burnet, M., and D. O. White. 1972. Natural history of infectious disease.

Cambridge University Press, Cambridge, England.

BUSS Ltd. 1985. Simpleplot mark 2 manual, 2nd edition. BUSS Ltd., Bradford, England.

Buss, L. W., and J. B. C. Jackson. 1979. Competitive networks: nontransitive competitive relationships in cryptic coral reef environments. American Naturalist **113**:223-234.

Calder, W. A. 1984. Size, function and life history. Harvard University Press, Cambridge, Mass., USA.

Cannings, C. 1990. Topics in the theory of ESSs. Pages 95-119 *in* S. Lessard, editor. Mathematical and statistical developments of evolutionary theory. Kluwer Academic, Dordrecht, The Netherlands.

Cannings, C., and G. T. Vickers. 1988. Patterns of ESSs II. Journal of Theoretical Biology **132**:409-420.

Cannings, C., and G. T. Vickers. 1989. Patterns and invasions of evolutionarily stable strategies. Applied Mathematics and Computation **32**:227-253.

Carroll, L. 1974. The philosopher's Alice. Alice's adventures in Wonderland and through the looking-glass. Academy Editions, London, England.

Case, T. J. 1990. Invasion resistance arises in strongly-interacting species-rich model competition communities. Proceedings of the National Academy of Sciences of the USA **87**:9610-9614.

Case, T. J. 1991. Invasion resistance, species build-up and community collapse in metapopulation models with interspecies competition. Biological Journal of the Linnean Society **42**:239-266.

Charlesworth, B. 1980. Evolution in age-structured populations. Cambridge University Press, Cambridge, England.

Cockburn, A. 1991. An introduction to evolutionary ecology. Blackwell Scientific, Oxford, England.

Cohen, J. E. 1977. Ratio of predators to prey in community food webs. Nature **270**:165-167.

REFERENCES

Cohen, J. E. 1978. Food webs and niche space. Princeton University Press, Princeton, New Jersey, USA.

Cohen, J. E. 1989. Food webs and community structure. Pages 181-202 *in* J. Roughgarden, R. M. May, and S. A. Levin, editors. Perspectives in ecological theory. Princeton University Press, Princeton, New Jersey, USA.

Cohen, J. E. 1990. A stochastic theory of community food webs. VI. Heterogeneous alternatives to the cascade model. Theoretical Population Biology 37:55-90.

Cohen, J. E., and F. Briand. 1984. Trophic links of community food webs. Proceedings of the National Academy of Sciences of the USA 81:4105-4109.

Cohen, J. E., F. Briand, and C. M. Newman. 1986. A stochastic theory of community food webs. III. Predicted and observed lengths of food chains. Proceedings of the Royal Society, London, Series B 228:317-353.

Cohen, J. E., F. Briand, and C. M. Newman. 1990a. Community food webs: data and theory. Springer-Verlag, Berlin, Germany.

Cohen, J. E., and T. Łuczak. 1992. Trophic levels in community food webs. Evolutionary Ecology 6:73-89.

Cohen, J. E., T. Łuczak, C. M. Newman, and Z.-M. Zhou. 1990b. Stochastic structure and nonlinear dynamics of food webs: qualitative stability in a Lotka-Volterra cascade model. Proceedings of the Royal Society, London, Series B 240:607-627.

Cohen, J. E., and C. M. Newman. 1985. A stochastic theory of community food webs. I. Models and aggregated data. Proceedings of the Royal Society, London, Series B 224:421-448.

Cohen, J. E., and C. M. Newman. 1988. Dynamic basis of food web organisation. Ecology 69:1655-1664.

Cohen, J. E., and C. M. Newman. 1991. Community area and food chain length: theoretical predictions. American Naturalist **138**:1542-1554.

Cohen, J. E., C. M. Newman, and F. Briand. 1985. A stochastic theory of community food webs. II. Individual webs. Proceedings of the Royal Society, London, Series B **224**:449-461.

Cohen, J. E., and Z. J. Palka. 1990. A stochastic theory of community food webs. V. Intervality and triangulation in the trophic-niche overlap graph. American Naturalist **135**:435-463.

Cole, B. J. 1983. Assembly of mangrove ant communities: colonization abilities. Journal of Animal Ecology **52**:349-355.

Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. Science **199**:1302-1310.

Dawkins, R. 1982. The extended phenotype. Oxford University Press, Oxford, England.

Dawkins, R., and J. R. Krebs. 1979. Arms races between and within species. Proceedings of the Royal Society, London, Series B **205**:489-511.

DeAngelis, D. L. 1975. Stability and connectance in food web models. Ecology **56**:238-243.

DeAngelis, D. L. 1980. Energy flow, nutrient cycling and ecosystem resilience. Ecology **61**:764-771.

DeAngelis, D. L., J. A. Kitchell, and W. M. Post. 1985. The influence of naticid predation on evolutionary strategies of bivalve prey- conclusions from a model. American Naturalist **126**:817-842.

DeAngelis, D. L., J. A. Kitchell, W. M. Post, and C. C. Travis. 1984. A model of naticid gastropod predator-prey coevolution. Pages 120-136 *in* S. A. Levin, and T. G. Hallam, editors. Mathematical ecology. Springer-Verlag, Berlin, Germany.

Dickinson, J. E., and J. V. Robinson. 1984. The assembly of microscopic communities: patterns of species importance. Transactions of the American Microscopical Society **103**:164-171.

Dickinson, J. E., and J. V. Robinson. 1985. Microcosms as islands: a test of the MacArthur-Wilson equilibrium theory. Ecology **66**:966-980.

Dickinson, J. E., and J. V. Robinson. 1986. The controlled assembly of microcosmic communities: the selective extinction hypothesis. Oecologia **71**:12-17.

Digital Equipment Corporation. 1985. Programming in VAX PASCAL. Digital Equipment Corporation, Maynard, Mass., USA.

Drake, J. A. 1983. Invasibility in Lotka-Volterra interaction webs. Pages 83-92 *in* D. L. DeAngelis, W. M. Post, and G. Sugihara, editors. Current trends in food web theory: report on a food web workshop. Oak Ridge National Laboratory, Oak Ridge, Tenn., USA.

Drake, J. A. 1985. Some theoretical and empirical explorations of structure in food webs. PhD thesis, Purdue University, Purdue, Indiana, USA.

Drake, J. A. 1990a. Communities as assembled structures: do rules govern pattern? Trends in Ecology and Evolution **5**:159-164.

Drake, J. A. 1990b. The mechanics of community assembly and succession. Journal of Theoretical Biology **147**:213-233.

Drake, J. A. 1991. Community-assembly mechanics and the structure of an experimental species ensemble. American Naturalist **137**:1-26.

Ebenman, B., and L. Persson, editors. 1988. Size-structured populations: ecology and evolution. Springer-Verlag, Berlin, Germany.

Edley, M. T., and R. Law. 1988. Evolution of life histories and yields in experimental populations of *Daphnia magna*. Biological Journal of the Linnean Society **34**:309-326.

Ellner, S., A. R. Gallant, D. McCaffrey, and D. Nychka. 1991. Convergence rates and data requirements for Jacobian-based estimates of Lyapunov exponents from data. Physics Letters A **153**:357-363.

Elton, C. 1927. Animal ecology. Sidgwick & Jackson, London, England.

Endler, J. A. 1986. Natural selection in the wild. Princeton University Press, Princeton, New Jersey, USA.

Endler, J. A. 1991. Interactions between predators and prey. Pages 169-196 *in*

J. R. Krebs, and N. B. Davies, editors. Behavioural ecology: an evolutionary approach. 3rd edition. Blackwell Scientific, Oxford, England.

Eshel, I. 1971. On evolution in a population with an infinite number of types. Theoretical Population Biology 2:209-236.

Findlay, W., and D. A. Watt. 1985. Pascal: an introduction to methodical programming. Pitman Publishing, London, England.

Fisher, R. A. 1958. The genetical theory of natural selection. Dover Books, New York, USA.

Fox, L. R. 1981. Defense and dynamics in plant-herbivore systems. American Zoologist **21**:853-864.

Frank, S. A., and M. Slatkin. 1992. Fisher's Fundamental Theorem of natural selection. Trends in Ecology and Evolution 7:92-95.

Freedman, H. I., and P. Waltman. 1977. Mathematical analysis of some three-species food chain models. Mathematical Biosciences **33**:257-276.

Futuyma, D. J. 1983. Evolutionary interactions among herbivorous insects and plants. Pages 207-231 *in* D. J. Futuyma, and M. Slatkin, editors. Coevolution. Sinauer, Sunderland, Mass., USA.

Futuyma, D. J., and M. Slatkin. 1983a. Introduction. Pages 1-13 *in* D. J. Futuyma, and M. Slatkin, editors. Coevolution. Sinauer, Sunderland, Mass., USA.

Futuyma, D. J., and M. Slatkin. 1983b. Coevolution. Sinauer, Sunderland, Mass., USA.

Gard, T. C. 1982. Top predator persistence in differential equation models of food chains: the effects of omnivory and external forcing of lower trophic levels. Journal of Mathematical Biology **14**:285-299.

Gardner, M. R., and W. R. Ashby. 1970. Connectance of large dynamical (cybernetic) systems: critical values of stability. Nature **228**:784.

Gear, C. W. 1971. Numerical initial-value problems in ordinary differential equations. Prentice-Hall, Englewood Cliffs, New Jersey, USA.

Gillespie, J. 1977. A general model to account for enzyme variation in natural populations. III. Multiple alleles. Evolution **31**:85-90.

Gilpin, M. E. 1975a. Stability of feasible predator-prey systems. Nature **254**:137-139.

Gilpin, M. E. 1975b. Group selection in predator-prey communities. Princeton University Press, Princeton, New Jersey, USA.

Gilpin, M. E. 1979. Spiral chaos in a predator-prey model. American Naturalist **113**:306-308.

Gilpin, M. E., M. P. Carpenter, and M. J. Pomerantz. 1986. The assembly of a laboratory community: multispecies competition in *Drosophila*. Pages 23-40 *in* J. D. Diamond, and T. J. Case, editors. Community ecology. Harper & Row, New York, USA.

Gilpin, M. E., and T. J. Case. 1976. Multiple domains of attraction in competition communities. Nature **261**:40-42.

Ginzburg, L. R. 1979. Why are heterozygotes often superior in fitness? Theoretical Population Biology **15**:264-267.

Ginzburg, L. R., H. R. Akçakaya, and J. Kim. 1988. Evolution of community structure: competition. Journal of Theoretical Biology **133**:513-523.

Gliwicz, Z. M. 1990. Food thresholds and body size in cladocerans. Nature **343**:638-640.

Godfray, H. C. J., and S. P. Blythe. 1990. Complex dynamics in multispecies communities. Philosophical Transactions of the Royal Society, London, Series B **330**:221-233.

Godfray, H. C. J., L. M. Cook, and M. P. Hassell. 1992. Population dynamics, natural selection and chaos. *In* Genes in ecology. Blackwell Scientific, Oxford, England, in press.

Grafen, A. 1991. Modelling in behavioural ecology. Pages 5-31 *in* J. R. Krebs, and N. B. Davies, editors. Behavioural ecology: an evolutionary approach, 3rd edition. Blackwell Scientific, Oxford, England.

Guess, H. A. 1974. Evolution in finite populations with infinitely many types.

Theoretical Population Biology 5:417-430.

Hall, S. J., and D. Raffaelli. 1991. Food-web patterns: lessons from a species-rich web. Journal of Animal Ecology 60:823-842.

Hall, S. J., D. Raffaelli, M. R. Robertson, and D. J. Basford. 1990a. The role of the predatory crab, *Liocarcinus depurator* in a marine food web. Journal of Animal Ecology 59:421-438.

Hall, S. J., D. Rafaelli, and W. R. Turrell. 1990b. Predator caging experiments in marine systems: a reexamination of their value. American Naturalist **136**:657-672.

Hamilton, W. D. 1980. Sex versus non-sex versus parasite. Oikos 35:282-290.

Hamilton, W. D. 1982. Pathogens as causes of genetic diversity in their host organisms. Pages 269-296 *in* R. M. Anderson, and R. M. May, editors. Population biology of infectious disease. Springer-Verlag, Berlin, Germany.

Hamilton, W. D., R. Axelrod, and R. Tanese. 1990. Sexual reproduction as an adaptation to resist parasites. Proceedings of the National Academy of Sciences, USA 87:3566-3573.

Harrison, G. W. 1979. Global stability of food chains. American Naturalist **114**:455-457.

Harvey, P. H., and M. D. Pagel. 1991. The comparative method in evolutionary biology. Oxford University Press, Oxford, England.

Hassell, M. P., and R. M. Anderson. 1989. Predator-prey and host-pathogen interactions. Pages 147-196 *in* J. M. Cherret, editor. Ecological concepts: the contribution of ecology to an understanding of the natural world. Blackwell Scientific, Oxford, England.

Hassell, M. P., J. H. Lawton, and R. M. May. 1976. Patterns of dynamical behaviour in single species populations. Journal of Animal Ecology **45**:471-486.

Hastings, A., and T. Powell. 1991. Chaos in a three-species food chain. Ecology 72:896-903.

REFERENCES

Heckel, D. G., and J. Roughgarden. 1980. A species near its equilibrium in a fluctuating environment can evolve a lower intrinsic rate of increase. Proceedings of the National Academy of Sciences, USA 77:7497-7500.

Hespenheide, H. A. 1973. Ecological inferences from morphological data. Annual Review of Ecology and Systematics 4:213-229.

Hofbauer, J. 1988. Saturated equilibria, permanence, and stability for ecological systems. Pages 625-642 *in* T. G. Hallam, L. G. Gross, and S. A. Levin, editors. Mathematical ecology. World Scientific, Singapore.

Hofbauer, J., V. Hutson, and W. Jansen. 1987. Coexistence for systems governed by difference equations of Lotka-Volterra type. Journal of Mathematical Biology 25:553-570.

Hofbauer, J., and K. Sigmund. 1988. The theory of evolution and dynamical systems. Cambridge University Press, Cambridge, England.

Hofbauer, J., and K. Sigmund. 1989. On the stabilizing effect of predators and competitors on ecological communities. Journal of Mathematical Biology 27:537-548.

Hoffman, A. 1991. Testing the Red Queen hypothesis. Journal of Evolutionary Biology 4:1-7.

Hoffman, A., and J. A. Kitchell. 1984. Evolution in a pelagic planktic system: a palaeobiologic test of models of multispecies evolution. Palaeobiology 10:9-33.

Hogeweg, P. 1989. MIRROR beyond MIRROR, puddles of LIFE. Pages 297-316 *in* C. G. Langton, editor. Artificial Life. Addison-Wesley, Redwood City, California, USA.

Holling, C. S. 1961. Principles of insect predation. Annual Review of Entomology 6:163-182.

Hutchinson, G. E. 1959. Homage to Santa Rosalia or why are there so many kinds of animals? American Naturalist 93:145-159.

Hutson, V., and R. Law. 1981. Evolution of recombination in populations experiencing frequency-dependent selection with time delay.

Proceedings of the Royal Society, London, Series B 213:345-359.

Hutson, V., and R. Law. 1985. Permanent coexistence in general models of three interacting species. Journal of Mathematical Biology 21:285-298.

Jansen, W. 1987. A permanence theorem for replicator and Lotka-Volterra systems. Journal of Mathematical Biology 25:411-422.

Janzen, D. H. 1980. When is it coevolution? Evolution 34:611-612.

Jayakar, S. D. 1984. Coevolution at two trophic levels. Pages 247-253 *in* K. Wöhrmann, and V. Loeschcke, editors. Population biology and evolution. Springer-Verlag, Berlin, Germany.

Jayakar, S. D., and L. A. Zonta. 1990. Coevolution at two trophic levels. Pages 349-366 *in* K. Wöhrmann, and S. K. Jain, editors. Population biology: ecological and evolutionary viewpoints. Springer-Verlag, Berlin, Germany.

Jeffrey, A. 1989. Mathematics for engineers and scientists. Van Nostrand Reinhold International, London, England.

Jeffries, M. J., and J. H. Lawton. 1984a. Enemy free space and the structure of ecological communities. Biological Journal of the Linnean Society 23:269-286.

Jeffries, M. J., and J. H. Lawton. 1984b. Predator-prey ratios in communities of freshwater invertebrates: the role of enemy free space. Freshwater Biology 15:105-112.

Jenkins, B., and R. L. Kitching. 1990. The ecology of water-filled treeholes in Australian rainforests: food web reassembly as a measure of community recovery after disturbance. Australian Journal of Ecology 15:199-206.

Juliano, S. A., and J. H. Lawton. 1990. Extrinsic vs. intrinsic food shortage and the strength of feeding links: effects of density and food availability on feeding rate of *Hyphydrus ovatus*. Oecologia 83:535-540.

Karlin, S. 1981. Some natural viability systems for a multiallelic locus: a theoretical study. Genetics 97:457-473.

Karlin, S., and M. W. Feldman. 1981. A theoretical and numerical assessment of genetic variability. Genetics **97**:475-493.

Kauffman, S. A. 1991. Antichaos and adaptation. Scientific American **265**:64-70.

Kauffman, S. A., and S. Johnsen. 1991. Coevolution to the edge of chaos: coupled fitness landscapes, poised states, and the coevolutionary avalanches. Journal of Theoretical Biology **149**:467-505.

Keith, T. P. 1983. Frequency distributions of esterase-S alleles in two populations of *Drosophila pseudoobscura.* Genetics **105**:135-155.

Kingman, J. F. C. 1988. Typical polymorphisms maintained by selection at a single locus. Pages 113-125 *in* J. Gani, editor. A celebration of applied probability. (Journal of Applied Probability special volume **25A**). Applied Probability Trust, Sheffield, England.

Kitchell, J. A., C. H. Boggs, J. F. Kitchell, and J. A. Rice. 1981. Prey selection by naticid gastropods: experimental tests and application to the fossil record. Palaeobiology **7**:533-552.

Kitching, R. L. 1987. Spatial and temporal variation in food webs in water-filled treeholes. Oikos **48**:280-288.

Kneidel, K. A. 1983. Fugitive species and priority during colonization in carrion-breeding Diptera communities. Ecological Entomology **8**:163-169.

Knowlton, N., and G. A. Parker. 1979. An evolutionarily stable strategy approach to indiscriminate spite. Nature **279**:419-420.

Lack, D. 1973. The number of species of hummingbirds in the West Indies. Evolution **27**:326-337.

Langton, C. G., editor. 1989a. Artificial life. Santa Fe Institute studies in the sciences of complexity **6**. Addison-Wesley, Redwood City, California, USA.

Langton, C. G. 1989b. Artificial life. Pages 1-47 *in* C. G. Langton, editor. Artificial life. Addison-Wesley, Redwood City, California, USA.

Langton, C. G. 1991. Life at the edge of chaos. Pages 41-92 *in* C. G.

Langton, C. Taylor, J. D. Farmer, and S. Rasmussen, editors. Artificial life II. Addison-Wesley, Redwood City, California, USA.

Langton, C. G., C. Taylor, J. D. Farmer, and S. Rasmussen, editors. 1991. Artificial life II. Santa Fe Institute studies in the sciences of complexity **10**. Addison-Wesley, Redwood City, California, USA.

Law, R. 1991. Fishing in evolutionary waters. New Scientist **129**:35-37.

Law, R., and J. C. Blackford. 1992. Self-assembling food webs: a global analysis of coexistence of species in Lotka-Volterra communities. Ecology **73**:567-578.

Law, R., and R. D. Morton. 1992. Alternative permanent states of ecological communities. Ecology, submitted.

Lawlor, L. R. 1978. A comment on randomly constructed model ecosystems. American Naturalist **112**:445-447.

Lawlor, L. R. 1980. Structure and stability in natural and randomly constructed competitive communities. American Naturalist **116**:394-408.

Lawlor, L. R., and J. Maynard Smith. 1976. The coevolution and stability of competing species. American Naturalist **110**:79-99.

Lawton, J. H. 1989. Food webs. Pages 43-78 *in* J. M. Cherret, editor. Ecological concepts: the contribution of ecology to an understanding of the natural world. Blackwell Scientific, Oxford, England.

Lawton, J. H., and P. H. Warren. 1988. Static and dynamic explanations for patterns in food webs. Trends in Ecology and Evolution **3**:242-245.

Lessells, C. M. 1991. The evolution of life histories. Pages 32-65 *in* J. R. Krebs, and N. B. Davies, editors. Behavioural ecology: an evolutionary approach, 3rd edition. Blackwell Scientific, Oxford, England.

Levin, S. A. 1978. On the evolution of ecological parameters. Pages 2-27 *in* P. F. Brussard, editor. Ecological genetics: the interface. Springer-Verlag, Berlin, Germany.

Levin, S. A., L. A. Segel, and F. R. Adler. 1990. Diffuse coevolution in plant-herbivore communities. Theoretical Population Biology **37**:171-191.

Levins, R. 1975. Evolution in communities near equilibrium. Pages 16-50 *in* M. L. Cody, and J. M. Diamond, editors. Ecology and evolution of communities. Harvard University Press, Cambridge, Mass., USA.

Lewontin, R. C. 1969. The meaning of stability. Pages 13-24 *in* G. M. Woodwell, and H. H. Smith, editors. Diversity and stability in ecological systems. Brookhaven National Laboratory, Upton, New York, USA.

Lewontin, R. C. 1974. The genetic basis of evolutionary change. Columbia University Press, London, England.

Lewontin, R. C., L. Ginzburg, and S. Tulijapurkar. 1978. Heterosis as an explanation for large amounts of genic polymorphism. Genetics 88:149-170.

Lindgren, K. 1991. Evolutionary phenomena in simple dynamics. Pages 295-312 *in* C. G. Langton, C. Taylor, J. D. Farmer, and S. Rasmussen, editors. Artificial life II. Addison-Wesley, Redwood City, California, USA.

Łomnicki, A. 1988. Population ecology of individuals. Princeton University Press, Princeton, New Jersey, USA.

Łomnicki, A. 1989. Avoiding chaos. Trends in Ecology and Evolution 4:239.

Macdonald, N. 1979. Simple aspects of food web complexity. Journal of Theoretical Biology 80:577-588.

Mani, G. S. 1989. Avoiding chaos. Trends in Ecology and Evolution 4:239-240.

Marks, R. W., and H. G. Spencer. 1991. The maintenance of single-locus polymorphism. II. The evolution of fitnesses and allele frequencies. American Naturalist 138:1354-1371.

Marrow, P., and C. Cannings. 1992. Evolutionary instability in predator-prey systems. Journal of Theoretical Biology, in press.

Marrow, P., R. Law, and C. Cannings. 1992. The coevolution of predator-prey interactions: ESSs and Red Queen dynamics. Proceedings of the Royal

Society, London, Series B, in press.

Matsuda, H., and T. Namba. 1991. Food web graph of a coevolutionarily stable community. Ecology **72**:267-276.

May, R. M. 1972. Will a large complex system be stable? Nature **238**:413-414.

May, R. M. 1973. Stability and complexity in model ecosystems. Princeton University Press, Princeton, New Jersey, USA.

May, R. M. 1974. Biological populations with nonoverlapping generations: stable points, stable cycles and chaos. Science **186**:645-647.

May, R. M. 1976. Simple mathematical models with very complicated dynamics. Nature **261**:459-467.

May, R. M. 1981a. Models for two interacting populations. Pages 78-104 *in* R. M. May, editor. Theoretical ecology, 2nd edition. Blackwell Scientific, Oxford, England.

May, R. M., editor. 1981b. Theoretical ecology. 2nd edition. Blackwell Scientific, Oxford, England.

May, R. M., and R. M. Anderson. 1983a. Epidemiology and genetics in the coevolution of parasites and hosts. Proceedings of the Royal Society, London, Series B **219**:281-313.

May, R. M., and R. M. Anderson. 1983b. Parasite-host coevolution. Pages 186-206 *in* D. J. Futuyma, and M. Slatkin, editors. Coevolution. Sinauer Associates, Sunderland, Mass., USA.

May, R. M., and G. F. Oster. 1976. Bifurcations and dynamical complexity in simple ecological models. American Naturalist **110**:573-599.

Maynard Smith, J. 1968. Mathematical ideas in biology. Cambridge University Press, Cambridge, England.

Maynard Smith, J. 1969. The status of neo-Darwinism. Pages 82-89 *in* C. H. Waddington, editor. Towards a theoretical biology. Volume 2. Edinburgh University Press, Edinburgh, Scotland.

Maynard Smith, J. 1976a. A comment on the Red Queen. American

Naturalist **110**:325-330.

Maynard Smith, J. 1976b. What determines the rate of evolution? American Naturalist **110**:331-338.

Maynard Smith, J. 1982. Evolution and the theory of games. Cambridge University Press, Cambridge, England.

Maynard Smith, J., and R. L. W. Brown. 1986. Competition and body size. Theoretical Population Biology **30**:166-179.

Maynard Smith, J., and G. R. Price. 1973. The logic of animal conflict. Nature **246**:15-18.

Mayr, E. 1988. Toward a new philosophy of biology. Princeton University Press, Princeton, New Jersey, USA.

McBrien, H., R. Haraman, and A. Crowder. 1983. A case of insect grazing affecting plant succession. Ecology **64**:1035-1039.

McCune, B., and T. F. H. Allen. 1985. Will similar forests develop on similar sites? Canadian Journal of Botany **63**:367-376.

Metz, J. A. J. 1992. Evolution from chaos to stability. MS, in preparation.

Metz, J. A. J., and H. C. J. Godfray. 1992. The evolution of demographic traits in chaotically fluctuating populations. MS, in preparation.

Metz, J. A. J., R. M. Nisbet, and S. A. H. Geritz. 1992. How should we define 'fitness' for general ecological scenarios? Trends in Ecology and Evolution **7**:198-202.

Michod, R. E. 1979. Evolution of life histories in response to age-specific mortality factors. American Naturalist **113**:531-550.

Minitab, Inc. 1989. Minitab reference manual, release 7. Minitab, Inc., State College, Penn., USA.

Mirmirani, M., and G. Oster. 1978. Competition, kin selection and evolutionary stable strategies. Theoretical Population Biology **13**:304-339.

Mithen, S. J., and J. H. Lawton. 1986. Food web models that generate constant predator-prey ratios. Oecologia **69**:542-550.

REFERENCES

Moore, J. C., D. E. Walter, and H. W. Hunt. 1989. Habitat compartmentation and environmental correlates of food chain length. Science **243**:238-239.

Moran, V. C., and T. R. E. Southwood. 1982. The guild composition of arthropod communities on trees. Journal of Animal Ecology **51**:289-306.

Morin, P. J. 1984. Odonate guild composition: experiments with colonization history and fish predation. Ecology **65**:1866-1873.

Mueller, L. D., and F. J. Ayala. 1981. Dynamics of single-species population growth: stability or chaos. Ecology **62**:1148-1154.

Murray, J. D. 1989. Mathematical biology. Springer-Verlag, Berlin, Germany.

Nee, S. 1989. Antagonistic co-evolution and the evolution of genotypic randomisation. Journal of Theoretical Biology **140**:499-518.

Nee, S. 1990. Community construction. Trends in Ecology and Evolution **5**:337-339.

Newman, C. M., and J. E. Cohen. 1986. A stochastic theory of community food webs. IV. Theory of food chain lengths in large webs. Proceedings of the Royal Society, London, Series B **228**:355-377.

Nicholson, A. J. 1957. The self adjustment of populations to change. Cold Spring Harbour Symposia in Quantitative Biology **22**:153-173.

Nisbet, R. M., S. Blythe, B. Gurney, H. Metz, and K. Stokes. 1989. Avoiding chaos. Trends in Ecology and Evolution **4**:238-239.

Nitecki, M. H., editor. 1983. Coevolution. University of Chicago Press, Chicago, Illinois, USA.

Numerical Algorithms Group. 1990. NAG Fortran library mark 14 manual. NAG Ltd., Oxford, England.

Nunney, L. 1980. The stability of complex model ecosystems. American Naturalist **115**:639-649.

Osman, R. W. 1977. The establishment and development of a marine epifaunal community. Ecological Monographs **47**:37-63.

Packard, N. H. 1989. Intrinsic adaptation in a simple model for evolution. Pages 141-155 *in* C. G. Langton, editor. Artificial life. Addison-Wesley, Redwood City, California, USA.

Paine, R. T. 1980. Food webs: linkage, interaction strength and community infrastructure. Journal of Animal Ecology 49:667-685.

Paine, R. T. 1988. On food webs: road maps of interactions or grist for theoretical development? Ecology 69:1648-1654.

Paine, R. T. 1992. Food-web analysis through field measurement of per capita interaction strength. Nature 355:73-75.

Parker, G. A. 1983. Arms races in evolution - an ESS to the opponent-independent costs game. Journal of Theoretical Biology 101:619-648.

Parker, G. A. 1985. Population consequences of evolutionarily stable strategies. Pages 33-58 *in* R. M. Sibly, and R. H. Smith, editors. Behavioural ecology: ecological consequences of adaptive behaviour. Blackwell Scientific, Oxford, England.

Parker, G. A., and N. Knowlton. 1980. The evolution of territory size - some ESS models. Journal of Theoretical Biology 84:445-476.

Parker, G. A., and J. Maynard Smith. 1990. Optimality theory in evolutionary biology. Nature 348:27-33.

Peschel, M., and W. Mende. 1986. The predator-prey model: do we live in a Volterra world? Akademie-Verlag, Berlin, GDR.

Peters, R. H. 1983. The ecological implications of body size. Cambridge University Press, Cambridge, England.

Pimentel, D. 1961. Animal population regulation by the genetic feed-back mechanism. American Naturalist 95:65-79.

Pimm, S. L. 1982. Food webs. Chapman & Hall, London.

Pimm, S. L. 1984. The complexity and stability of ecosystems. Nature 307:321-326.

Pimm, S. L. 1991. The balance of nature? Ecological issues in the conservation of species and communities. Chicago University Press, Chicago, Illinois, USA.

Pimm, S. L., and R. L. Kitching. 1987. The determinants of food chain length. Oikos 50:302-307.

Pimm, S. L., and J. H. Lawton. 1977. The number of trophic levels in ecological communities. Nature 268:329-331.

Pimm, S. L., and J. H. Lawton. 1978. On feeding on more than one trophic level. Nature 275:542-544.

Pimm, S. L., and J. H. Lawton. 1980. Are food webs divided into compartments? Journal of Animal Ecology 49:879-898.

Pimm, S. L., J. H. Lawton, and J. E. Cohen. 1991. Food web patterns and their consequences. Nature 350:669-674.

Polis, G. A. 1991. Complex trophic interaction in deserts: an empirical critique of food-web theory. American Naturalist 138:123-155.

Post, W. M., and S. L. Pimm. 1983. Community assembly and food web stability. Mathematical Biosciences 64:169-192.

Raffaelli, D., and H. Milne. 1987. An experimental investigation of the effects of shorebird and flatfish predation on estuarine invertebrates. Estuarine, Coastal & Shelf Science 24:1-13.

Rand, D. A., and H. Wilson. 1991. Chaotic stochasticity: a ubiquitous source of unpredictability in epidemics. Proceedings of the Royal Society, London, Series B 246:179-184.

Ray, T. S. 1991. An approach to the synthesis of life. Pages 371-408 *in* C. G. Langton, C. Taylor, J. D. Farmer, and S. Rasmussen, editors. Artificial life II. Addison-Wesley, Redwood City, California, USA.

Reed, J., and N. C. Stenseth. 1984. On evolutionarily stable strategies. Journal of Theoretical Biology 108:491-508.

Reznick, D., and J. A. Endler. 1982. The impact of predation on life history evolution in Trinidadian guppies (*Poecilia reticulata*). Evolution 36:160-177.

Roberts, A. 1974. The stability of a feasible random ecosystem. Nature 251:607-608.

Roberts, A., and K. Tregonning. 1980. The robustness of natural systems.

Nature **288**:265-266.

Robinson, J. V., and J. E. Dickerson. 1984. Testing the invulnerability of laboratory island communities to invasion. Oecologia **61**:169-174.

Robinson, J. V., and J. E. Dickerson. 1987. Does invasion sequence affect community structure? Ecology **68**:587-595.

Robinson, J. V., and M. A. Edgemon. 1988. An experimental evaluation of the effect of invasion history on community structure. Ecology **69**:1410-1417.

Robinson, J. V., and W. D. Valentine. 1979. The concepts of elasticity, invulnerability, and invadability. Journal of Theoretical Biology **81**:91-104.

Rosenzweig, M. L. 1973. Evolution of the predator isocline. Evolution **27**:84-94.

Rosenzweig, M. L., J. S. Brown, and T. L. Vincent. 1987. Red Queens and ESS: the coevolution of evolutionary rates. Evolutionary Ecology **1**:59-94.

Rosenzweig, M. L., and R. H. MacArthur. 1963. Graphical representation and stability conditions of predator-prey interactions. American Naturalist **97**:209-233.

Rosenzweig, M. L., and W. M. Schaffer. 1978. Homage to the Red Queen II: coevolutionary response to enrichment of exploitation ecosystems. Theoretical Population Biology **14**:158-163.

Rosenzweig, M. L., and J. A. Taylor. 1980. Speciation and diversity in Ordovician invertebrates: filling niches quickly and carefully. Oikos **35**:236-243.

Roughgarden, J. 1976. Resource partitioning among competing species-a coevolutionary approach. Theoretical Population Biology **9**:388-424.

Roughgarden, J. 1979. Theory of population genetics and evolutionary ecology: an introduction. Collier Macmillan, London, England.

Roughgarden, J. 1983. The theory of coevolution. Pages 33-64 *in* D. J.

Futuyma, and M. Slatkin, editors. Coevolution. Sinauer, Sunderland, Mass., USA.

Roughgarden, J. 1989. The structure and assembly of communities. Pages 203-226 *in* J. Roughgarden, R. M. May, and S. A. Levin, editors. Perspectives in ecological theory. Princeton University Press, Princeton, New Jersey, USA.

Rummel, J. D., and J. Roughgarden. 1983. Some differences between invasion structured and coevolution-structured competitive communities: a preliminary theoretical analysis. Oikos **41**:477-486.

Rummel, J. D., and J. Roughgarden. 1985. A theory of faunal buildup for competition communities. Evolution **39**:1009-1033.

Schaffer, W. M. 1984. Stretching and folding in lynx fur returns: evidence for a strange attractor in nature? American Naturalist **124**:798-820.

Schaffer, W. M. 1985. Order and chaos in ecological systems. Ecology **66**:93-106.

Schaffer, W. M., and M. Kot. 1985. Nearly one dimensional dynamics in an epidemic. Journal of Theoretical Biology **112**:403-427.

Schaffer, W. M., and M. L. Rosenzweig. 1978. Homage to the Red Queen I: coevolution of predators and their victims. Theoretical Population Biology **14**:135-157.

Schoenly, K., and J. E. Cohen. 1991. Temporal variation in food web structure: 16 empirical cases. Ecological Monographs **61**:267-298.

Shigesada, N., K. Kawasaki, and E. Teramoto. 1988. Communities with interference competition: direct and indirect effects of predation on their structure. Pages 659-681 *in* T. G. Hallam, L. R. Gross, and S. A. Levin, editors. Mathematical ecology. World Scientific, Singapore.

Shigesada, N., K. Kawasaki, and E. Teramoto. 1989. Direct and indirect effects of invasions of predators on a multiple-species community. Theoretical Population Biology **36**:311-338.

Simmons, G. F. 1974. Differential equations: with applications and historical notes. Tata-McGraw Hill, New Dehli, India.

Slatkin, M., and J. Maynard Smith. 1979. Models of coevolution. Quarterly Review of Biology 54:233-263.

Slobodkin, L. B. 1961. Growth and regulation of animal populations. Holt, Rinehart and Winston, New York, USA.

Slobodkin, L. B. 1974. Prudent predation does not require group selection. American Naturalist 108:665-678.

Sokal, R. R., and F. J. Rohlf. 1981. Biometry. W. H. Freeman, New York, USA.

Spencer, H. G., and R. W. Marks. 1988. The maintenance of single-locus polymorphism. I. Numerical studies of a viability selection model. Genetics 120:605-613.

Spencer, H. G., and R. W. Marks. 1992. The maintenance of single-locus polymorphism. IV. Mutations from existing alleles. Genetics, in press.

Stanley, S. M., B. van Valkenburg, and R. S. Steneck. 1983. Coevolution and the fossil record. Pages 328-349 *in* D. J. Futuyma, and M. Slatkin, editors. Coevolution. Sinauer, Sunderland, Mass., USA.

Stearns, S. C. 1992. The evolution of life histories. Oxford University Press, Oxford, England.

Stenseth, N. C. 1983. A coevolutionary theory for communities and food web configurations. Oikos 41:487-495.

Stenseth, N. C. 1985. The structure of food webs predicted from optimal food selection models: an alternative to Pimm's stability hypothesis. Oikos 44:361-364.

Stenseth, N. C. 1986. Darwinian evolution in ecosystems: a survey of some ideas and difficulties together with some possible solutions. Pages 105-145 *in* J. L. Castri, and A. Karlquist, editors. Complexity, language and life: mathematical approaches. Springer-Verlag, Berlin, Germany.

Stenseth, N. C., and J. Maynard Smith. 1984. Coevolution in ecosystems: Red Queen evolution or stasis? Evolution 38:870-880.

Stokes, T. K., W. S. C. Gurney, R. M. Nisbet, and S. P. Blythe. 1988. Parameter evolution in a laboratory insect population. Theoretical Population Biology 34:248-265.

Strong, D. R., J. H. Lawton, and T. R. E. Southwood. 1984. Insects on plants. Blackwell Scientific, Oxford, England.

Sugihara, G. 1984. Graph theory, homology and food webs. Proceedings of Symposia in Applied Mathematics 30:83-101.

Sutherland, J. P. 1974. Multiple stable points in natural communities. American Naturalist 108:859-873.

Sutherland, J. P., and R. H. Karlson. 1977. Development and stability of the fouling community at Beaufort, NC. Ecological Monographs 47:425-446.

Svirezhev, Y. M., and D. O. Logofet. 1983. Stability of biological communities. Mir, Moscow, USSR.

Szathmáry, E., I. Scheuring, C. Hegedüs, G. Németh, I. Molnár, and G. Vida. 1990. The engagement of the Red Queen and King Midas in the Phylogenerator model. Coenoses 5:130-141.

Takada, T., and J. Kigami. 1991. The dynamical attainability of ESS in evolutionary games. Journal of Mathematical Biology 29:513-529.

Talbot, F. H., B. C. Russell, and G. R. V. Anderson. 1978. Coral reef fish communities: unstable, high-diversity systems? Ecological Monographs 48:425-446.

Taylor, C. E., D. R. Jefferson, S. R. Turner, and S. R. Goldman. 1989. RAM: artificial life for the exploration of complex biological systems. Pages 275-295 *in* C. G. Langton, editor. Artificial life. Addison-Wesley, Redwood City, California, USA.

Taylor, P. J. 1985. Construction and turnover of multispecies communities: a critique of approaches to ecological complexity. PhD thesis, Harvard University, Cambridge, Mass., USA.

Taylor, P. J. 1988. The construction and turnover of complex community models having generalized Lotka-Volterra dynamics. Journal of Theoretical Biology **135**:569-588.

Taylor, P. J. 1989. Developmental versus morphological approaches to modelling ecological complexity. Oikos **55**:434-436.

Taylor, R. J. 1984. Predation. Chapman & Hall, London, England.

Thomas, W. R., M. J. Pomerantz, and M. E. Gilpin. 1980. Chaos, asymmetric growth and group selection for dynamical stability. Ecology **61**:1312-1320.

Thompson, D. J. 1975. Towards a predator-prey model incorporating age structure: the effects of predator and prey size on the predation of *Daphnia magna* by *Ischnura elegans*. Journal of Animal Ecology **44**:907-916.

Thompson, J. N. 1986. Constraints on arms races in coevolution. Trends in Ecology and Evolution **1**:105-107.

Tregonning, K., and A. Roberts. 1979. Complex systems which evolve towards homeostasis. Nature **281**:563-564.

Turchin, P., and A. D. Taylor. 1992. Complex dynamics in ecological time series. Ecology **73**:289-305.

Turelli, M. 1984. Heritable genetic variation via mutation-selection balance: Larch's Zeta meets the abdominal bristle. Theoretical Population Biology **25**:138-193.

Turelli, M., and L. R. Ginzburg. 1983. Should individual fitness increase with heterozygosity? Genetics **104**:191-209.

Turelli, M., and D. Petry. 1980. Density-dependent selection in a random environment: an evolutionary process that can maintain stable population dynamics. Proceedings of the National Academy of Sciences, USA **77**:7501-7505.

Uniras Ltd. 1989. Uniras reference guide, version 6. Uniras Ltd., Slough, England.

Van Valen, L. 1973. A new evolutionary law. Evolutionary Theory **1**:1-30.

Vasco, D. A., A. D. Nazarea, and R. H. Richardson. 1987. Dynamics and stability in coevolutionary ecological systems. I. Community stability and coevolutionarily stable states. Theoretical Population Biology **31**:273-303.

Vermeij, G. J. 1982. Unsuccessful predation and evolution. American Naturalist **120**:701-720.

Vermeij, G. J. 1983. Intimate associations and coevolution in the sea. Pages 311-327 *in* D. J. Futuyma, and M. Slatkin, editors. Coevolution. Sinauer, Sunderland, Mass., USA.

Vermeij, G. J. 1987. Evolution and escalation: an ecological history of life. Princeton University Press, Princeton, New Jersey, USA.

Vermeij, G. J., and A. P. Covitch. 1978. Coevolution of freshwater gastropods and their predators. American Naturalist **112**:833-843.

Vézina, A. F. 1985. Empirical relationships between predator and prey size among terrestrial vertebrate predators. Oecologia **67**:555-565.

Vickers, G. T., and C. Cannings. 1988. Patterns of ESSs I. Journal of Theoretical Biology **132**:387-408.

Vida, G., E. Szathmáry, G. Németh, G. Hegedüs, P. Juhász-Nagy, and I. Molnár. 1990. Towards modelling community evolution: the Phylogenerator. Pages 409-422 *in* J. Maynard Smith, and G. Vida, editors. Organizational constraints on the dynamics of evolution. Manchester University Press, Manchester, England.

Wang, Y. H., and A. P. Gutierrez. 1980. An assessment of the use of stability analyses in population ecology. Journal of Animal Ecology **49**:435-452.

Warren, P. H. 1988. The structure and dynamics of a freshwater benthic food web. DPhil thesis, University of York, York, England.

Warren, P. H. 1989. Spatial and temporal variation in the structure of a freshwater food web. Oikos **55**:299-311.

Warren, P. H., and J. H. Lawton. 1987. Invertebrate predator-prey body size relationships: an explanation for upper triangular food webs and patterns in food web structure? Oecologia **74**:231-235.

Werner, E. E., and J. F. Gilliam. 1984. The ontogenetic niche and species interactions in size-structured populations. Annual Review of Ecology and Systematics **15**:393-425.

West, K., Cohen, A., and M. Baron. 1991. Morphology and behaviour of crabs and gastropods from Lake Tanganyika, Africa: implications for lacustrine predator-prey coevolution. Evolution **45**:589-607.

Wiens, J. A. 1984. On understanding a non-equilibrium world: myth and reality in community patterns and processes. Pages 439-457 *in* D. R. Strong, Jr., D. Simberloff, L. G. Abele, and A. B. Thistle, editors. Ecological communities: conceptual issues and the evidence. Princeton University Press, Princeton, New Jersey, USA.

Wilson, D. S. 1983. The group selection controversy: history and current status. Annual Review of Ecology and Systematics **14**:159-187.

Winemiller, K. O. 1990a. Must connectance decrease with species richness? American Naturalist **134**:960-968.

Winemiller, K. O. 1990b. Spatial and temporal variation in tropical fish trophic networks. Ecological Monographs **60**:331-367.

Yodzis, P. 1981. The structure of assembled communities. Journal of Theoretical Biology. **92**:103-117.

Yodzis, P. 1984a. Energy flow and the vertical structure of real ecosystems. Oecologia **65**:86-88.

Yodzis, P. 1984b. The structure of assembled communities II. Journal of Theoretical Biology **107**:115-126.