Chapter Eight

Demographic Bistability and Evolutionary Reversals

In this chapter we show that when the evolutionary state of the community does not uniquely determine the resident demographic attractor, mutation-selection processes may force the resident populations to switch between alternative demographic attractors and cause abrupt changes in the selection pressure acting on the community. As a result, evolutionary cycles can develop even in the extreme case of a community composed of a single resident population characterized by a single adaptive trait. Indeed, periodic switches between alternative demographic equilibria may induce the periodic reversal of the rate of evolutionary change and force the trait to endlessly oscillate. We consider a renewable resource characterized by a single adaptive trait affecting both reproduction and competition for nutrients. The mechanism inducing evolutionary reversals is twofold. First, there exist trait values near which mutants can invade and yet fail to become fixed; although these mutants are eventually eliminated, their transitory growth causes the resident population to switch to an alternative demographic equilibrium. Second, asymmetric competition causes the direction of selection to revert between high and low abundances.

When the conditions for periodic evolutionary reversals are not satisfied, the population evolves toward a steady state of either low or high abundance, depending on the degree of competitive asymmetry and on demographic and environmental parameters. A sharp transition between evolutionary stasis and cycling can occur in response to a smooth parameter change, and this may have implications for our understanding of size-abundance patterns. Most of this chapter is taken from Dercole et al. (2002a).

8.1 INTRODUCTION

The contrasting patterns of evolution in populations with chronically high or low abundances have captured the shared interests of ecologists and geneticists for a long time (Travis, 1990). There has been a considerable amount of verbal and mathematical theory on the subject (reviewed lucidly by Mueller, 1997). In this context, the distinction between the demographic and evolutionary dynamics and the discussion of their coupling (see Chapter 1, Section 1.5 in particular) emphasize that selective pressures exerted on individuals are shaped by population structure and abundance; in return, demographic dynamics are primarily determined by individual adaptive traits that are genetically based and molded by natural selection (Pimentel, 1968; Heino et al., 1998).
Over the last two decades, there has been intensive empirical investigation of the effect of population density on the nature, direction, and strength of selection on life-history traits. Exemplary studies include those by Wilbur (1984) and Travis et al. (1985) on larval anurans, who showed that the role of predatory salamanders as a selective force for rapid growth of tadpoles varies depending on tadpole abundance: at very low densities this force is weak because growth rates are high and encounter rates with predators are low; a greater numerical impact of predators occurs only at higher tadpole densities.

Although much empirical effort has been devoted to understand how crowding influences patterns of selection on life-history traits (Wilbur, 1984; Travis et al., 1985), the backward effect of selection on population abundances, i.e., the other arch of the demographic-evolutionary feedback, remains poorly understood, even theoretically (Metz et al., 1992; Rand et al., 1994; Heino et al., 1998). One important effect is the propensity to generate complex demographic dynamics, including periodic and chaotic oscillations. Much attention has been paid to the question of whether mutation-selection processes could drive adaptive traits from values leading to stable demographic equilibria, to values corresponding to cycles or chaos (see Gatto, 1993; Ferrière and Gatto, 1993, 1995; Doebeli and Koella, 1995; Ferrière and Fox, 1995; Ebenman et al., 1996; see also Chapter 9); contrasting theoretical predictions are awaiting to be tested empirically. A crucial assumption in all models developed around this issue is that any combination of the traits uniquely determines the demographic attractor of the resident populations (De Feo and Ferrière, 2000). However, demographic models can have alternative attractors associated with different patterns of population abundances that can be reached for the very same trait values (demographic bi- or multistability; see Scheffer et al., 2001, for a survey). How the demographic-evolutionary feedback works in these cases is the question we consider in this chapter.

We focus on a very simple single-population, single-trait model characterized by two alternative stable demographic equilibria, one at high and one at low population abundance. At the former, there is selection for trait values that reduce population abundance, while at the latter there is selection for trait values that increase population abundance. Under suitable conditions that we identify by means of the AD approach, these opposing patterns of selection force the population to switch from the high [low] to the low [high] equilibrium abundance, thus causing a so-called evolutionary reversal, namely the sudden change of sign, on the evolutionary timescale, of the trait evolutionary rate of change. A salient result (first noticed by Doebeli and Ruxton, 1997, by relying on alternative stable demographic cycles in spatially structured models) is that there are broad ecological conditions under which periodic evolutionary reversals drive endless trait oscillations (i.e., cyclic Red Queen dynamics, see Section 1.6) of a single adaptive trait.

The chapter is organized as follows. In the next section we give some empirical support to demographic bistability and the biological motivations of our theoretical investigation. Then, in Section 8.3, we describe the model in detail and show that periodic evolutionary reversals indeed occur for suitable parameter settings. This result is reviewed in Section 8.4 through the AD canonical equation, while its discussion is given in the concluding section.
8.2 BIOLOGICAL BACKGROUND

We consider a community composed of a single monomorphic species, namely a renewable resource feeding on constantly available nutrients. The demographic dynamics are determined by a set of fixed ecological (demographic and environmental) parameters, and by life-history parameters that are functions of an adaptive trait. This trait is assumed to be genetically determined and heritable, but it may vary due to mutations of small effects.

We assume that for suitable ecological parameters there can be values of the trait for which the resident resource population is characterized by two alternative stable demographic equilibria. Demographic bistability was first put forward by Holling (1973), Noy-Meir (1975), and May (1977). Subsequently, alternative low- and high-density states have been found in a host of ecological models. Although the first experimental examples that were proposed were criticized strongly (Connell and Sousa, 1983), more recent studies (reviewed in Scheffer et al., 2001) support the view that multiple stable states can characterize natural systems.

Here we consider a simple phenomenological model to generate alternative stable demographic equilibria, akin to the minimal models proposed by Scheffer et al. (2001). One possible interpretation of this model takes into account that mating encounters are more likely in crowded populations. Alternatively, the resource might be harvested by a consumer that exploits a spectrum of other resource species (so-called generalist consumer). The option among various food sources ensures that the consumer demographic and evolutionary dynamics are weakly affected by those of one among many available resources, so that resource-consumer coevolution can be neglected and the abundance of the consumer population considered as constant.

We also assume that the adaptive trait is related to competitive performance, and we call it, for this reason, competitive ability. Thus, variation in individual trait results in asymmetric resident-mutant competition for nutrients. Moreover, individuals that are at competitive advantage are nonetheless expected to suffer some physiological cost: this is why competitive ability is assumed to be costly to some components of reproductive success. A common case involving asymmetric intraspecific competition and physiological costs of higher energy demands occurs when competing individuals differ in size. Often, larger individuals enjoy a competitive advantage because of their superior ability at obtaining limited nutrients (Brooks and Dodson, 1965; Wilson, 1975; Persson, 1985; Calder, 1996), but the opposite can also be true, like in the case of small zooplanktivorous fish outcompeting large ones for food (Persson et al., 1998). However, this dichotomy does not influence our findings, since the only assumption that counts is that a positive variation of the trait is accompanied by an advantage in competition (or growth) and by a counterbalancing disadvantage in growth (or competition).

The body size interpretation of competitive ability may be useful because the relationship between body size and population abundance arguably has attracted great attention. Yet the search for general patterns has not been conclusive (Lawton, 1989; Blackburn and Lawton, 1994; Rosenzweig, 1995). Data from extant populations show that low abundance, under some circumstances, is associated with large body size (Brown, 1995; Gaston and Kunin, 1997), but the pattern is
far from general. For example, Navarette and Menge (1997) found no tendency for small species to occur at higher densities than larger species in the tropical intertidal communities of Panama, in sharp contrast with the pattern in intertidal communities in temperate Chile (Marquet et al., 1990). Thus, though direct measures of competitive performance are difficult to obtain from real communities, there is hope that our theoretical predictions could be tested against the results of experimental studies (like those reported by Lenski and Bennett, 1993, for bacteria) on the evolution of body size.

8.3 ASYMMETRIC COMPETITION AND THE OCCURRENCE OF EVOLUTIONARY REVERSALS

The Resident Community

We start by considering a logistically growing resource population, described by its abundance $n$ and by the competitive ability $x$ of its individuals, where

$$\dot{n} = r(x)n - cn^2.$$ (8.1)

The net growth rate (per capita) $r(x)$ is assumed to decrease exponentially with competitive ability $x$ (i.e., $r(x) = r_0 \exp(-r_1 x)$, with $r_0$ and $r_1$ constant parameters) to express the cost of enhanced competitive performance, while $cn$ measures the extra mortality (or reduced natality) caused by intraspecific competition. Competitive ability $x$ scales between 0 and 1. This scaling can easily be achieved by means of the transformation $x = \log(z/z_{\text{min}}) / \log(z_{\text{max}}/z_{\text{min}})$, where $z$ is the “real” trait value (e.g., body size), and $z_{\text{min}}$ and $z_{\text{max}}$ are minimum and maximum trait values, respectively (Schwinning and Fox, 1995).

Demographic bistability is triggered by discounting the population growth rate in (8.1) by an additional trait-independent demographic factor $H(n)$. As discussed in the previous section, two important examples of such a factor are the reduction of reproduction due to a shortage of mating encounters in sparse population, and the mortality due to the harvesting of a generalist consumer. Both examples can be accounted for by the same discounting function $H(n) = \tau^{-1}n^2/(h^2 + n^2)$ (Dennis, 1989, and references therein; Stephens and Sutherland, 1999), which is called the Holling type III functional response. As the type II functional response $\tau^{-1}n/(h + n)$ introduced in Section 3.3, the discounting function $H(n)$ saturates at $\tau^{-1}$ for high abundances and reaches half of its maximum when $n$ matches the so-called half-saturation constant $h$. However, at low abundances $H(n)$ has a vanishing slope, while the type II functional response has a nonzero initial slope $\tau^{-1}/h$. Thus, the type III response provides a simple way of accounting for spatial heterogeneity in the chance of mating (the probability of mating encounters goes with $n^2$) and for the fact that a generalist consumer tends to harvest on its most available food sources.

With this choice of $H(n)$, the resident model of the community, therefore becomes

$$\dot{n} = n \left( r(x) - cn - \frac{\tau^{-1}n}{h^2 + n^2} \right).$$ (8.2)
Notice that if body size is a measure of competitive ability and $H(n)$ is consumption rate, it would be more realistic to assume a trait-dependent discounting function, since prey body size typically influences the functional response of the consumer. However, this would give rise to an analytically intractable model even if the final result would be qualitatively the same. In any case, model (8.2) applies when competitive ability does not influence predation or when body size has only a weak influence on the predator functional response.

Further notice that there are two causes of density dependence in (8.2), namely two terms in the population per-capita growth rate (the term in parenthesis) affected by $n$: a negative density dependence due to intraspecific competition ($-cn$ decreases with $n$), and a positive density dependence due to the additional discounting factor $(-\tau^{-1}n/(h^2 + n^2))$ increases with $n$.

Finally, it is also worth noticing that there is no apparent advantage for the population to evolve toward higher competitive abilities, since this would result only in reduced reproduction rates. However, as we will soon see, a more competitive mutant population can be at advantage and replace a less competitive resident population, thus resulting in an overall disadvantage for the population. This clearly points out once more that mutation-selection processes do not imply any sort of benefit or optimization at community level.

### Demographic Bistability

As shown in Figure 8.1, there is a lower threshold on competitive ability ($x_l$) below which the resident model (8.2) has a single stable equilibrium $\hat{n}_h(x)$ at high abundance, and an upper threshold ($x_h$) above which model (8.2) has a single stable equilibrium $\hat{n}_l(x)$ at low abundance. For $x$ values between $x_l$ and $x_h$, there are two alternative stable equilibria ($\hat{n}_h(x)$ and $\hat{n}_l(x)$) corresponding to high and low abundance, respectively, separated by an unstable equilibrium at intermediate abundance. Thus, the high-density equilibrium $\hat{n}_h(x)$ is defined only for $x < x_h$, while the low-density equilibrium $\hat{n}_l(x)$ only for $x > x_l$. These two subsets of the one-dimensional trait space therefore identify the so-called evolution sets associated with the possible demographic attractors of the resident community.

The transition from three to one demographic equilibria, which occurs when $x$ is at the threshold value $x_l$ [$x_h$], corresponds to a saddle-node bifurcation (see Appendix A), through which the low- [high-] density stable equilibrium and the unstable equilibrium collide and disappear. In any trait-parameter plane (see, e.g., the $(x,c)$ plane in Figure 8.2), the two saddle-node bifurcation curves determine the thresholds $x_l$ and $x_h$ for each value of $c$ within an appropriate range. These two curves meet at a cusp point (see Appendix A), which identifies the $c$ value beyond which no demographic bistability can occur. By writing the standard conditions for saddle-node bifurcations, we find

$$x_l = \frac{1}{r_1} \ln \left( \frac{\hat{n}_l(x_l)}{r_0} \left( c + \frac{\tau^{-1}}{h^2 + \hat{n}_l^2(x_l)} \right) \right),$$  
$$x_h = \frac{1}{r_1} \ln \left( \frac{\hat{n}_h(x_h)}{r_0} \left( c + \frac{\tau^{-1}}{h^2 + \hat{n}_h^2(x_h)} \right) \right),$$

(8.3a, 8.3b)
Figure 8.1  Demographic bistability. The equilibria of the resident model (8.2) are given by the intersection of the trait-dependent logistic growth rate \( r(x)n - cn^2 \) (the family of parabola) and the discounting function \( H(n) \). For \( x \) between the lower threshold \( x_l \) and the upper threshold \( x_h \) (see dashed parabola), the resident population has three demographic equilibria: two stable equilibria (filled circles), \( \bar{n}_l(x) \) at low abundance and \( \bar{n}_h(x) \) at high abundance; and an unstable equilibrium (empty circle). For \( x \) at the two critical values \( x_l \) and \( x_h \), one of the stable equilibria collides with the unstable equilibrium (see half-filled circles). Parameter values: \( r_0 = 1, r_1 = 1, c = 0.1, h = 0.75 \).

Figure 8.2  Bifurcation diagram of the resident model (8.2). Two saddle-node bifurcation curves meet at the cusp point \( C \). Three equilibria of model (8.2) (two stable, one unstable) are present in the cusp (shaded) region, while a single stable equilibrium is present outside the cusp region. Parameter values as in Figure 8.1.
where

\[ \bar{n}_i(x_i) = \left( \frac{\tau^{-1} - 2ch^2 - \sqrt{\tau^{-1}(\tau^{-1} - 8ch^2)}}{2c} \right)^{1/2}, \quad (8.4a) \]

\[ \bar{n}_h(x_h) = \left( \frac{\tau^{-1} - 2ch^2 + \sqrt{\tau^{-1}(\tau^{-1} - 8ch^2)}}{2c} \right)^{1/2}. \quad (8.4b) \]

The cusp point is given by

\[ x = \frac{1}{r_1} \ln \left( \frac{8r_0\tau h}{3\sqrt{3}} \right), \quad (8.5a) \]

\[ c = \frac{1}{8\tau h^2}. \quad (8.5b) \]

**Resident-Mutant Interactions**

We now specify the demographic dynamics of interacting resident and mutant populations, characterized by traits \( x \) and \( x' \) and abundances \( n \) and \( n' \), respectively, by the following resident-mutant model:

\[ \dot{n} = n \left( r(x) - cn - \gamma(x, x')n' - \frac{\tau^{-1}(n + n')}{h^2 + (n + n')^2} \right), \quad (8.6a) \]

\[ \dot{n'} = n' \left( r(x') - \gamma(x', x)n - cn' - \frac{\tau^{-1}(n + n')}{h^2 + (n + n')^2} \right). \quad (8.6b) \]

We assume that there is no discrimination between resident and mutant populations with regard to discounting (e.g., individual traits do not affect mating encounters or consumption), so that the discounting function in (8.6a) is given by

\[ \frac{n}{n + n'} \frac{\tau^{-1}(n + n')^2}{h^2 + (n + n')^2} = \frac{\tau^{-1}n(n + n')}{h^2 + (n + n')^2} \]

(similarly in (8.6b), where \( n \) and \( n' \) are exchanged).

By contrast, the logistic growth rate (per capita) must incorporate the effect of intraspecific competition between two similar traits. This is achieved by the trait-dependent competition coefficient \( \gamma(x, x') \), which is taken to depend only on the difference \( x' - x \) and is equal to \( c \) at \( x' = x \). It should increase as the difference \( x' - x \) increases, expressing a stronger deleterious effect on the \( x \)-population growth of better \( x' \)-competitors. The positive slope

\[ c_1 = \left. \frac{\partial}{\partial(x' - x)} \gamma(x, x') \right|_{x' = x} \]

provides a measure of the strength of the asymmetry, and is called **competitive asymmetry** in the following.

In the numerical analysis, we use

\[ \gamma(x, x') = 2c \left( 1 - \frac{1}{1 + \exp(\gamma_1(x' - x))} \right), \]

which has all the properties mentioned above \( (c_1 = c\gamma_1/2). \)
Periodic Evolutionary Reversals

As we saw in Chapter 3, all possible outcomes of the resident-mutant competition can be classified by means of a bifurcation analysis of the resident-mutant model (8.6) in the trait space \((x, x')\). Under the assumption that mutations have small effects, it is legitimate to restrict the analysis to the vicinity of the diagonal \(x' = x\), that is, to the region of the trait space where mutant individuals differ only slightly from residents.

The result is shown in Figure 8.3, which unravels seven regions above the diagonal that have at least one point in common with it. For \(x' < x\) the bifurcation diagram is not shown, because it is given by a symmetric copy with respect to the diagonal. The seven corresponding demographic state portraits are also shown in the figure, and must be read in the space \((n, n')\), if corresponding to a point \((x, x')\) above the diagonal, and in the space \((n', n)\), if \(x' < x\) and the symmetric point \((x', x)\) lies in one of the regions 1–7.

In region 1, the resident population has only one stable equilibrium, namely the high-density equilibrium \(n_h(x)\). Small mutations characterized by slightly larger trait values invade and replace the resident type (side panel 1). The evolutionary random walk takes on a small step toward higher competitive abilities, and this results in a slightly decreased equilibrium abundance (see Figure 8.1). The same outcome is observed in regions 2–5 (see corresponding side panels). In all these regions, a mutant with a slightly larger trait value can invade and eliminate the resident type. Thus, starting from any ancestral state of high abundance for which \(x\) is less than \(x_h\), evolution proceeds through the gradual increase of individual competitive ability, causing the concurrent, slow, decrease of population abundance.

A new phenomenon is observed in region 6, where the resident trait is still slightly less than \(x_h\) while the mutant trait is now slightly greater than \(x_h\). In this case, the mutant first invades, but the resident “strikes back” (side panel 6): after its initial increase, the mutant reaches a peak abundance, then it starts declining and eventually goes extinct. This unexpected temporary invasion arises from the existence, for the resident population, of two alternative demographic equilibria that differ in their vulnerability to invasion by the mutant. Initially the resident population stands on its high-density equilibrium, which appears to be invasible. As the mutant population grows, the resident population cannot sustain its high density any longer and starts to approach its low-density state. While doing so, it creates a competitive environment that becomes noninvasible by the mutant. Now the latter is doomed, and as it goes extinct the population is sent back to its original evolutionary state; but in the meantime the demographic state has changed: the resident population experienced a sudden transition from the state of high abundance to the state of low abundance (switch of the resident demographic attractor; see also Mylius and Diekmann, 2001).

The same picture holds for the dual case, starting from an ancestral state of low abundance and intermediate or high competitive ability \((x\) larger than \(x_1)\). Here mutation-selection processes drive the slow decrease of the trait and the concomitant slight increase of population abundance. When competitive ability comes close to the low threshold \(x_1\), any invasion attempt by mutants smaller than \(x_1\) triggers
the switch of the resident demographic equilibrium, from $\bar{n}_l(x)$ to $\bar{n}_h(x)$.

Altogether this analysis shows that the evolutionary dynamics never come to a halt. The competitive ability characterizing the population oscillates between a minimum ($x_l$) and a maximum ($x_h$) value (cyclic Red Queen dynamics). The abundance of the population switches between the low- and the high-density equilibria every time the adaptive process reaches either of these threshold trait values.
Invasion Does Not Imply Fixation

The analysis performed above points out a case in which the invasion of the mutant population does not imply its “fixation” in the community, namely its permanence with resident status. By contrast, in Chapter 3 we have seen that an invading mutant population generically substitutes the similar resident population, or coexists with it in the vicinity of evolutionary equilibria. No other possibilities are available, under the assumption that both $x$ and $x'$ correspond to evolutionary states in the evolution set associated with the current resident demographic attractor. However, this is not in conflict with the resident-strikes-back scenario because in that case the resident population is settled at its high- [low-] density demographic equilibrium and $x$ is slightly smaller [greater] than $x_h$ [$x_l$], while $x'$ is slightly greater [smaller] than $x_h$ [$x_l$]. In other words, when the resident strikes back, only the resident trait corresponds to an evolutionary state in the evolution set associated with the current resident demographic attractor. This implies that the resident substitution cannot occur, since the equilibrium of the resident-mutant model (8.6) at which the substitution transient should end does not exist (see Figure 8.3, panel 6 in space $(n, n_0)$ [2 in space $(n', n)$]).

Finally, notice that when mutational effects are limited, the resident-strikes-back scenario is not the generic cause of the resident attractor switch. In fact, the boundary ($x_h$ or $x_l$) of the evolution set associated with the resident demographic equilibrium $(\bar{n}_h(x) \text{ or } \bar{n}_l(x))$ corresponds to a saddle-node bifurcation of the resident model (8.2), so that when $x$ is close to such a boundary, the resident demographic equilibrium is close to the unstable equilibrium of model (8.2) and, hence, to the boundary of its basin of attraction. Small demographic fluctuations of the resident population abundance, not necessarily involving mutations, can therefore result in a demographic state $(\bar{n})$ in the basin of attraction of the other demographic equilibrium, which would then be reached on the demographic timescale.

8.4 SLOW-FAST APPROXIMATION OF THE AD CANONICAL EQUATION

One can achieve the same conclusions obtained in the previous section by using a slow-fast approximation of the AD canonical equation, which reads

\[
\dot{x} = k n s(n, x),
\]

\[
\epsilon \dot{n} = n \left( r(x) - cn - \frac{\tau^{-1} n}{h^2 + n^2} \right),
\]

where $\epsilon$ is a small timescaling factor separating the demographic and evolutionary timescales, $k$ is a constant mutational rate (proportional to the frequency and variance of mutations), and $s(n, x)$ is the so-called selection derivative, i.e., the slope of the mutant fitness landscape (see (8.6b)) in the vicinity of the resident trait

\[
s(n, x) = \frac{\partial}{\partial x} \left( r(x') - \gamma(x', x)n - cn' - \frac{\tau^{-1}(n + n')}{h^2 + (n + n')^2} \right) \bigg|_{n' = 0 \atop x' = x} = -r_0 r_1 \exp(-r_1 x) + \frac{c r_1}{2} n.
\]
The dynamics of model (8.7) involve a fast component, that of the resident population abundance $n$ governed by the first equation, and a slow component, that of the competitive ability $x$ described by the second equation. The analysis of such a slow-fast system can be performed through a timescale separation method popularized in ecology by May (1977) (see also Rinaldi and Scheffer, 2000, for a recent survey, and Matsuda and Abrams, 1994b; Khinbin and Kondrashov, 1997, for applications in the context of evolutionary dynamics). The analysis requires two steps. First, the two stable equilibria $n_h(x)$ and $n_l(x)$ of the fast component are determined for each frozen value of the slow variable $x$. This yields the thin curves shown in the first column of Figure 8.4. Then the sign of $\dot{x}$ at each point $(x, n_h(x))$ and $(x, n_l(x))$ is determined so as to predict the direction of evolutionary change. This amounts merely to finding the isocline $s(n, x) = 0$ in the space $(n, x)$, which is defined by

$$n = \frac{2r_0r_1}{c_1} \exp(-r_1 x).$$

Figure 8.4, where the boundary of each gray region is the isocline $s(n, x) = 0$, displays the three possible evolutionary outcomes. In Figure 8.4A, starting from point 0, we observe a first, fast, demographic transient $(0 \to 1)$, followed by a slow evolutionary transient $(1 \to 2)$, entraining a slow demographic change yet leaving the population with low abundance. At point 2, a fast demographic transient abruptly brings the population to high abundance $(2 \to 3)$, and from point 3 a final slow evolutionary transient takes place, driving the population toward an evolutionary equilibrium at point 4, where low competitive ability is associated with high population abundance. At this point, selection may turn disruptive, causing evolutionary branching, but this phenomenon is not investigated here. Figure 8.4B shows a similar pattern whereby the adaptive process drives the population toward a state of permanent low abundance and promotes high competitive ability.

In contrast, the adaptive process never comes to a halt in the case shown in Figure 8.4C (which corresponds to the parameter setting of Figure 8.3). After a first, fast demographic transient $(0 \to 1)$, and a slow evolutionary transient $(1 \to 5)$, the system is trapped forever on a slow-fast limit cycle $(5 \to 2 \to 3 \to 4 \to 5)$.

One can see by comparing Figures 8.4A, B, and C that the necessary and sufficient condition for the existence of such an evolutionary cycle is that the selection isocline $s(n, x) = 0$ separates the two stable branches of resident demographic equilibria. This is a general condition for the existence of slow-fast limit cycles, known as separation principle (Muratori and Rinaldi, 1991). In the present case, elementary algebra yields the following conditions:

$$n_l(x_l) < \frac{2r_0r_1}{c_1} \exp(-r_1 x_l) < \frac{r_0h^2}{c_1h^2(x_l)} \exp(-r_1 x_l), \quad (8.8a)$$

$$\frac{r_0h^2}{c_1h^2(x_h)} \exp(-r_1 x_h) < \frac{2r_0r_1}{c_1} \exp(-r_1 x_h) < n_h(x_h) \quad (8.8b)$$

(where $x_l, x_h, n_l(x_l)$, and $n_h(x_h)$ are given in (8.3) and (8.4)), which respectively correspond to the fact that in Figure 8.4C the isocline $s(n, x) = 0$ passes between points 2 and 3 at $x = x_l$ and between points 4 and 5 at $x = x_h$. 

Figure 8.4 Evolutionary dynamics in the space of competitive ability \( x \) and resident population abundance \( n \) (first column) and corresponding time evolution of \( x \) and \( n \) (second column). In the first column, thin curves indicate the set of demographic equilibrium abundances as a function of \( x \) (solid [dotted] portions: stable [unstable] equilibria); shaded region: \( s(n,x) < 0 \); thick curve: exemplary trajectory (single arrows: slow (evolutionary) dynamics, double arrows: fast (demographic) dynamics). (A) Evolution toward low competitive ability and permanent high abundance (\( \gamma_1 = 2.4 \)). (B) Evolution toward high competitive ability and permanent low abundance (\( \gamma_1 = 32 \)). (C) Periodic evolutionary reversals (\( \gamma_1 = 8.0 \)). Other parameter values as in Figure 8.1 and \( k = 10^{-4} \).
The occurrence of periodic evolutionary reversals depends on six ecological parameters: the maximum growth rate (per capita) $r_0$, the physiological cost of enhanced competitive performance $r_1$, the intraspecific competition coefficient $c$, the competitive asymmetry $c_1$, and the discounting parameters $\tau$ and $h$. Evolutionary reversals can develop only when the resident population has two alternative demographic equilibria, which imposes the condition

$$c < \frac{1}{8\tau h^2}$$

(see (8.5b) and Figure 8.2). Thus, demographic bistability requires that the competition coefficient is lower than a threshold set by the discounting parameters; this constraint becomes weaker as the discounting pressure increases (smaller $\tau$ and/or smaller $h$).

Conditions (8.8) and (8.9) are analytically known bifurcation conditions of model (8.7), and are graphically represented in Figure 8.5 with respect to parameters $c$, $c_1$, $\tau$, and $h$. In bistable resident populations, the occurrence of periodic evolutionary reversals is determined by the strength of competitive asymmetry ($c_1$), which has to lie within a range of intermediate values such that the selective pressure on the adaptive trait reverts at low and high abundances. Figures 8.5A and B show that this range shrinks under harsher conditions expressed by a larger competition coefficient $c$, whereas for fixed $c$, it expands if discounting is enhanced (smaller $\tau$ and/or smaller $h$). Altogether, a consistent pattern is that evolutionary reversals are more likely to occur in species characterized by significant competitive asymmetry, and facing strong discounting pressures.

When conditions for periodic evolutionary reversals are not satisfied, permanent low and high abundance represent alternative by-products of mutation-selection processes operating on competitive ability. Although there is a narrow parameter range for which permanent high abundance evolves concomitantly with intermediate competitive ability ($x_l < x < x_h$, see Figure 8.5C), there is a clear tendency for high abundance to evolve most often along with small trait values, whereas permanent low abundance can be associated with the evolution of large as well as intermediate trait values. This may help to understand why the association of scarcity and large body size in groups of closely related species remains difficult to establish empirically.

The ecological parameters may vary in response to environmental change. It turns out that even small and smooth changes in parameters may have a dramatic impact on the evolutionary dynamics of the population. Here we focus our discussion on the transition between periodic evolutionary reversals and permanent low abundance. A transition of this kind caused by a slight environmental deterioration should imply a dramatic rise of the extinction risk. Evolutionary cycling may suddenly disappear and be replaced with a state of permanent low abundance when selection at low density ceases to be directional (toward the critical trait value $x_l$ at which evolutionary reversal occurs) and becomes stabilizing instead (transition from Figure 8.4C to B). By inspection of Figure 8.5, this can happen as a result of (i) slightly more competition (larger competition coefficient $c$), (ii) a small increase in competitive asymmetry ($c_1$), (iii) slightly less discounting (small increase of $\tau$ or $h$).
Figure 8.5 Bifurcation diagram of model (8.7) with respect to parameters $c$ (intraspecific competition coefficient), $c_1$ (competitive asymmetry), and $\tau$ and $h$ (discounting parameters). (A) Effect of $c$, $c_1$, and $h$. The volume bounded by the displayed surface contains parameter combinations that give rise to periodic evolutionary reversals. Permanent low abundance evolves above the surface. Permanent high abundance evolves below the surface. Demographic bistability occurs only for values of $c$ and $h$ lying outside the shaded region in the horizontal plane. (B) Effect of $\tau$ on the region (inside curves) of the $(c, c_1)$ plane corresponding to periodic evolutionary reversals. (C) Effect of $c$ and $c_1$ on the transition between periodic evolutionary reversals and either permanent low abundance with high competitive ability or permanent high abundance with low competitive ability. The shaded region indicates parameter combinations for which permanent low and high abundance evolve along with intermediate trait values ($x_l < x < x_h$). In (B) and (C), the bold curve bounds the $(c, c_1)$ region where periodic evolutionary reversals develop, and corresponds to the cross section indicated in (A). Fixed parameters as in Figure 8.1.


8.5 DISCUSSION AND CONCLUSIONS

How density can influence and be influenced by evolutionary processes has concerned biologists ever since Darwin suggested that abundant species were more likely than rare species to be the sources of evolutionary novelties. Nonetheless, despite considerable attention to the matter, evolutionary biologists still hold widely varying views on the consequences of population density on evolution (Orians, 1997) and on the role of evolution in determining population abundance and dynamics (Holt, 1997). The theoretical study reported in this chapter has investigated the interaction between population density and life-history evolution by focusing on an individual trait related to competitive performance that is potentially under different selection pressures depending on the population abundance. The model allows for multiple demographic equilibria, which entails that the population may rest on a state of low abundance or on a state of high abundance under the very same conditions.

Evolutionary Reversals and Population Dynamics

In ecological systems characterized by alternative equilibria, the demographic equilibrium on which the population settles depends on ecological history, and recurrent jumps between equilibria have been traditionally explained by means of environmental or ecological factors (see, e.g., Southwood and Comins, 1976; Hanski, 1985; Crawley, 1992). In contrast, our analysis shows that the periodic alternation between low-density and high-density demographic equilibria can develop at an evolutionary timescale as a result of a purely endogenous mechanism: periodic reversals of the selection pressure on an adaptive trait.

The simple, deterministic model considered here produces perfectly regular evolutionary cycles in trait value and population abundance. Random variability, however, is inherent to all populations. In a stochastic environment, the regularity of such slow-fast cycles is likely to break down (Rinaldi and Scheffer, 2000), in lieu of which more irregular alternations of phases of low and high abundance should be expected. Documenting such fluctuations in population abundance requires exceptional data sets collected at a timescale seldom accessible to ecologists. Perhaps the best example of such data is provided by fossil deposits of pelagic fish, from which several millennia of demographic dynamics have been reconstructed with time resolution as fine as a decade (see, e.g., Figure 1.8 in Section 1.9).

In the Pacific sardine *Sardinops caerulea* (Soutar and Isaacs, 1974; Baumgartner et al., 1992), population data show that the species has persisted at very low density over more than 55% of the time, through phases of irregular durations, from 10 to 200 years. Alternations between low and high abundance occurred rapidly and more or less in unison across the whole species range. Interestingly, a competitor, and possibly predator species, the Northern anchovy *Engraulis mordax*, has been fluctuating more smoothly without reaching extreme population densities, suggesting that direct environmental factors may not be solely responsible for the dynamics of the sardine. Similar patterns have been documented in *Sardinops sagax* over the whole Holocene period, with bouts of very low abundance spanning up to 500 years.
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(De Vries and Pearcy, 1982); and in Sardinops melanistica at the timescale of the last four centuries (Tsuboi, 1984; Kondô, 1986). Tens and even hundreds of consecutive generations at either high or very low abundance may have given ample time for contrasting selective pressures to operate on traits related to competitive performance, and cause the alternations of high and low abundance observed in the data.

The combination of multiple demographic equilibria and evolutionary reversals between them offers an alternative explanation, previously suggested in a verbal model by Cury (1988), to purely ecological models of such long-term fluctuations between high and low density in fish communities (Ferrière and Cazelles, 1999). It would therefore be interesting to reanalyze the fossil fish scale data to investigate the occurrence of concomitant changes in fish body size (or other adaptive traits related to competitive abilities), which could be indicative of density fluctuations driven by evolutionary reversals.

Mechanism Causing Evolutionary Reversals

The biological mechanism causing evolutionary reversals involves two ingredients. First, there must exist trait values near which mutant traits can invade and yet fail to go to fixation, while their transitory presence causes the resident population to switch between two demographic attractors. This phenomenon brings new evidence that mutant invasion does not imply mutant fixation, as often assumed in evolutionary models (see the discussion on the fitness landscapes approach in Section 2.7). Except for Dercole et al. (2002a), on which this chapter is based, the few examples known to contradict the “invasion implies fixation” principle had been constructed by resorting to mutations of unlikely large effect (Doebeli, 1998; Diekmann et al., 1999; De Feo and Ferrière, 2000; Mylius and Diekmann, 2001; see also Case, 1995, and Abrams and Shen, 1989, in the context of species invasion).

The second key ingredient for evolutionary reversals is that the selective pressure operates in opposite directions on the same trait values, depending on whether the population density is high or low. Why this contrasting effect of selection arises in our model is easily understood: at high population density, a mutant is engaged in many competitive contests; thus, it has much to gain by investing more into competitive efficiency (through an increased trait value) at the expense of reducing its reproductive rate (provided that the trade-off between competition and reproduction is not too steep). In contrast, at low density encounters are few, and there is little to be gained from improved competitive ability; thus, one can expect advantageous mutants to be characterized by a larger intrinsic reproductive rate, achieved with reduced trait values.

Doebeli and Ruxton (1997) showed that cyclic evolution involving sharp transitions between multiple resident demographic attractors can occur in spatially structured communities, and Khbunik and Kondashov (1997) found similar Red Queen dynamics of multispecies coevolution. Our study demonstrates that spatial heterogeneity and coevolutionary scenarios are not necessary to explain the reversal of selective pressures between different demographic attractors and the endless variations in adaptive traits; purely local intraspecific interactions are sufficient.
Matsuda and Abrams (1994a) also considered the evolution of body size under asymmetric competition, but the uniqueness of the demographic resident equilibrium at any trait value prevented the mechanism causing evolutionary reversals from operating in their model. As a consequence, they could only observe the evolutionary runaway to large body size and low population density, a process that could lead to population extinction (see Section 1.8). In contrast, if the conditions for evolutionary reversals are met in our model, the evolution toward high competitive abilities terminates at a trait value where the population abundance quickly and dramatically drops, whereas the selective pressure reverts and “rescues” the population from extinction by promoting the reduction of competitive ability and the increase of population abundance as a by-product.

Concluding Remarks

Any ecological scenario that makes the number of demographic attractors dependent upon an adaptive trait sets the stage for attractor switches driven by the evolutionary dynamics of the trait. This has been clearly recognized and exploited by Matsuda and Abrams (1994b), who showed that the evolution of antipredator ability may result in self-extinction of a prey population. Here we have used the same principle to demonstrate that the occurrence of evolutionary reversals and consequent evolutionary cycling is a likely property of ecological systems that possess alternative demographic equilibria (see also Doebeli and Ruxton, 1997; Khibnik and Kondrashov, 1997). We stress that this property is not bound to the assumption that multiple demographic equilibria are caused by a special ecological mechanism. A discounting function of the form of Holling type III response was chosen here to make the analysis mathematically tractable. Qualitatively similar results would be obtained with a Holling type II-like discounting function; the low-abundance stable equilibrium would simply be replaced with the zero equilibrium, thus making the evolutionary extinction (actually a case of evolutionary suicide, see Sections 1.8 and 3.6) of the population almost unavoidable (Gyllenberg and Parvinen, 2001).

Interestingly, some compelling evidence for evolutionary reversals of social traits has been gathered recently (Velicer et al., 1998; Hibbett et al., 2000). Sociality can induce an Allee effect (i.e., a positive density dependence in the population per-capita growth rate; Allee, 1931) that may be responsible for a discounting factor of the type considered here (Courchamp et al., 1999). Thus, adaptive switches between multiple demographic equilibria may point to a purely endogenous mechanism responsible for the repeated evolutionary rise and fall of social behavior.

Our study delineates two ways in which selection may depend on resident population density. In the first and classical case, each value of a trait uniquely determines the population density. If the density varies monotonically (e.g., decreases) with the trait value, the direction of adaptation may change with density as a mere consequence of directional selection toward an intermediate trait value: at a lower trait value, hence higher density, selection would favor an increase of the trait; at a higher trait value, hence lower density, selection would promote the decrease of the trait. In contrast, when multiple demographic equilibria are feasible, the direction and strength of selection may differ at the same trait value, depending upon
the demographic state (e.g., high versus low density) on which the population is actually resting. Real systems possessing multiple demographic equilibria should therefore be useful to set up laboratory experiments in which the effect of density on selection is strictly isolated.