

Part VI

Evolutionary population dynamics

Chapter 23

Fundamental theorem replaces Malthusian law

DURING THE preceding parts of the book it has become clear that the fundamental theorem of natural selection does not apply to natural populations in the form proposed by Fisher in 1930. Originally, Fisher's theorem was meant to define natural selection where the intrinsic Malthusian parameter defined fitness so that the maximal and the intrinsic growth rate of the population continued to increase. However, in Chapters 10 to 12 we saw that the fundamental theorem does not apply to natural populations, and this is because the theorem, among other things, is inconsistent with the occurrence of both large-bodied organisms and with the occurrence of highly limited rates of reproduction. Moreover, we saw in Chapter 14 that the intrinsic growth rate is predicted to decline when the environment is stable, a result that is diametrically opposite to the fundamental theorem. More generally, the fundamental theorem holds only in the absence of competitive interactions, a hypothetical case that is fulfilled only at the limit of zero density.

In the same way as Fisher's fundamental theorem of natural selection does not apply as the fundament of natural selection, you might also have noticed that the Malthusian law of exponential increase in a density independent environment generally does not apply as the first law of population dynamics. This is because the Malthusian law is based on the assumption that the intrinsic growth rate is constant. But, this is generally not true. For example, from Fishers fundamental theorem we know that if competitive interactions and density dependence are absent, then the intrinsic growth rate is expected to increase at a rate given by the genetic variance in that growth rate. In other words, the fundamental assumption behind the

classical theory of population dynamics is invalid whenever there is genetic variation in the intrinsic growth rate.

In this chapter I will use Fisher's fundamental theorem to extend the first law of population dynamics so that it also includes the situation with genetic variation in the intrinsic growth rate. This implies that the fundamental theorem will replace the Malthusian law as the cornerstone of the population dynamic theory, and that the classical theory is valid only in the absence of genetic variation.

23.1 Fundamental theorem leads to hyper-exponential increase

Let me in this section describe the population dynamics that follow from the fundamental theorem and the hypothetical case with a density independent environment where competitive interactions are absent. In this environment the fundamental theorem will apply, and this implies that the rate of increase in the intrinsic growth rate (r) is equal to the genetic variance in that growth rate (σ_r^2), i.e., that

$$dr/dt = \sigma_r^2 \quad (23.1)$$

By integrating eqn 23.1 we obtain

$$r_t = r_0 + \sigma_r^2 t \quad (23.2)$$

where r_t and r_0 are the growth rates at time t and time zero. As r_t is the average rate of increase per individual at time t , we have that

$$dN/dt = (r_0 + \sigma_r^2 t)N \quad (23.3)$$

When this expression is solved for the abundance we obtain the law of hyper-exponential increase in the abundance, i.e., we find that

$$N_t = N_0 e^{r_0 t + \sigma_r^2 t^2 / 2} \quad (23.4)$$

This equation indicates that the potential rate of increase in the population abundance may be much higher than it is the case under the classical hypothesis, and it also shows that the new law of hyper-exponential increase reduces to the Malthusian law of exponential increase (i.e., to $N_t = N_0 e^{r t}$) when genetic variation is absent, i.e., when $\sigma_r^2 = 0$. A comparison between the new and the classical law is shown in Fig. 23.1.

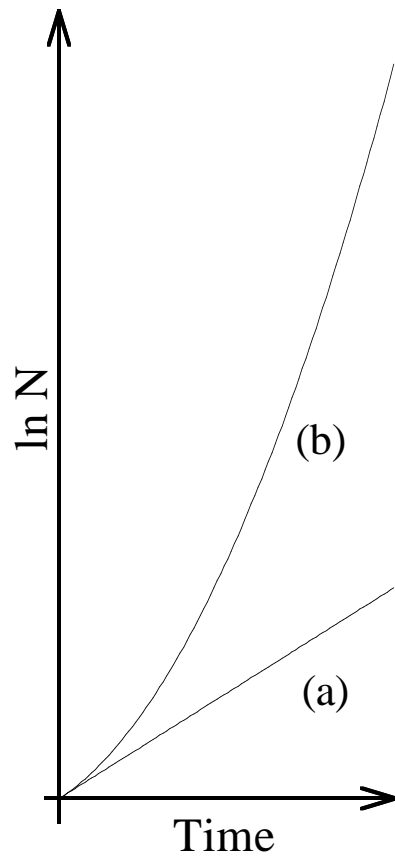


Fig. 23.1 An illustration of exponential (a) and hyper-exponential increase (b).

Chapter 24

Single species cycles

CYCLIC POPULATION DYNAMICS is widespread among the species within the animal kingdom. Who is not familiar with the cyclic outbreak dynamics in small herbivores, like rodents and snowshoe hares, but the dynamics of crustaceans, like *Daphnia*, or insects, like Lepidoptera, also tend to be inherently cyclic. This is unlike the dynamics of the classical theory of population dynamics, which is inherently non-cyclic unless there is some sort of delayed regulation caused by, e.g., over-compensation in age- or stage-structured populations or by interactions with other species.

From the first part of the book we recall that over-compensation in structured populations does not explain the general tendency for cyclic dynamics in natural populations, and that there have been two major hypotheses for the widespread occurrence of cyclic dynamics. On the one hand, it has been argued that the cycles arise from factors intrinsic to populations while on the other hand it has been argued that they arise from interactions between different species, especially between predators and their prey. The former of these two hypotheses is the Chitty hypothesis, which was never confirmed theoretically, while the latter hypothesis is predicted by the Lotka-Volterra predator-prey equations. Hence, as there seems to have been only one plausible hypothesis for cyclic dynamics, it is not surprising that the ecologists of today are returning to the old idea that population cycles in animals as diverse as the snowshoe hare, rodents, and insects are caused by predator-prey interactions in their broadest definition that includes both host-parasitoid and plant-herbivore interactions (e.g., Akçakaya, 1992; Hanski et al., 1993; Hanski and Korpimäki, 1995; Krebs et al., 1995; Berryman, 1996).

This necessity to incorporate predator-prey interactions in order to obtain cyclic dynamics is, though, a limitation imposed by the Malthusian law and the assumption that the maximal growth rate is constant (Ginzburg, 1992). If instead the maximal growth rate is density dependent the dynam-

ics of a single species can be inherently cyclic. This is what I will show in this chapter where I predict cyclic dynamics by exchanging the Malthusian law with the fundamental theorem of natural selection and by incorporating selection by density dependent competitive interactions. Then, the maximal growth rate becomes density dependent, and the dynamics becomes inherently cyclic with periods that resemble the periods in the dynamics of the forest insects we examined in Chapter 3.

The proximate force behind the cyclic dynamics that I deduce in this chapter is an evolutionary and cyclic modulation of the population equilibrium. Due to this modulation the population will cycle because the abundance is always moving toward the population equilibrium, but as this equilibrium is constantly changing the population cannot settle at that equilibrium. It is only at the evolutionary equilibrium that the abundance is stable, and this is because it is only at that particular population equilibrium that there is no selection for a change in the population equilibrium. Dependent of the particular conditions the evolutionary equilibrium may be stable or unstable, but in nearly all cases the dynamics following from a perturbation will cycle around this equilibrium in an either damped, stable, or exploding fashion.

The ultimate force that drives the population cycles, including the cycles in the population equilibrium, is an evolutionary and cyclic modulation of the phenotype that in turn is driven by a cyclic form of selection that arises from cyclic and density dependent changes in the number of competitive interactions per individual. The cyclic changes in the phenotype can, among other things, include changes in the body mass, the intrinsic growth rate, and the sex ratio, and these sorts of changes are often observed in the small rodents that have cyclic dynamics.

In order to give a full description of the dynamics following from density dependent competitive interactions I have partitioned this chapter into eight sections and one appendix with three subsections. In the first section I deduce the logistic equation with density dependent selection and I also describe the cyclic dynamics that follow. In Section 24.2 I give a brief description of the dynamics in order to improve the readers intuitive understanding of the system, and in Sections 24.3 and 24.4 I describe the cyclic phenotypes and I examine also the degree to which these phenotypes are observed in natural populations with cyclic dynamics. Then, in Section 23.5, I test the developed model against the dynamics in forest insects, and in the following three sections I deal with respectively a deduction of the Calder hypothesis on the body mass allometry for the population cycle, the implication of the neutral stability of the predicted cycles, and the dynamics that are associated with extreme perturbations, like the introduction of exotic species into new areas.

24.1 Logistic equation with density dependent selection

Until this last part of the book we have dealt either with population dynamics under the assumption that evolutionary changes are absent, or with evolutionary changes under the assumption that population dynamics is absent, i.e., under the assumption that the population is situated at the population equilibrium. In this section I will relax these assumptions and describe population dynamics under the action of selection by density dependent competitive interactions.

To describe this form of dynamics let me focus on the logistic equation that we developed in Chapter 3 for the case with non-overlapping generations. That is, let me use the model

$$N_{t+1} = N_t \lambda_m N_t^{-\gamma} \quad (24.1)$$

When genetic variation is present this equation is no longer valid because selection will alter the maximal growth rate (λ_m) so that it becomes both time and density dependent. The mathematics of this evolutionary modulation is described in the first appendix to this chapter. There, I use selection by density dependent competitive interactions to derive the evolutionary changes in the maximal growth rate, when the abundance is no longer in population equilibrium. As it is shown, this implies that the logistic eqn 24.1 extends to the following two equations

$$\begin{aligned} \lambda_{m,t} &= \lambda_{m,t-1} N_{t-1}^{-\gamma_q} e^{\sigma_{\ln q}^2} \\ N_{t+1} &= N_t \lambda_{m,t} N_t^{-\gamma} \end{aligned} \quad (24.2)$$

where $\gamma_q = \gamma_t \psi \sigma_{\ln q}^2$. These equations are based on the assumption that the phenotypic plasticity in reproduction and survival is environmentally induced only. However, when a population experiences a cyclic selection pressure, as is the case with eqn 24.2, then there is selection for a more flexible phenotype that can be adjusted according to the current selection pressure. This means that cyclic changes in λ_m may reflect not only evolutionary changes, generated by the immediate selection pressure, but also plastic responses, as they have been selected for during larger time spans. When this is the case the parameter $\sigma_{\ln q}^2$ in eqn 24.2 will not only stand for genetic variance, but it will include also a component of phenotypic plasticity.

Before I describe the cyclic dynamics of eqn 24.2, let me briefly consider the two special cases that represent respectively the absence of genetic variance (and a flexible phenotype) and the absence of density regulation. When genetic variance is absent we have that $\gamma_q = 0$ because $\sigma_{\ln q}^2 = 0$

and, thus, the top equation in eqn 24.2 reduces to $\lambda_{m,t} = \lambda_{m,t-1}$. This means that the maximal growth rate is constant so that eqn 24.2 reduces to the logistic equation in the classical theory (eqn 24.1). In other words, the deduced theory reduces to the classical theory when genetic variation is absent.

When instead it is density regulation that is absent we have that $\gamma = 0$, and that $\gamma_q = 0$, because $\gamma_\iota = 0$. In this situation, which is characterised by Fisherian selection, eqn 24.2 reduces to

$$\begin{aligned}\lambda_t &= \lambda_0 e^{\sigma_{\ln q}^2 t} \\ N_t &= N_0 \lambda_0^t e^{\sigma_{\ln q}^2 \sum_{\tau=0}^t \tau}\end{aligned}\tag{24.3}$$

a situation with geometrical increase in the growth rate and hyper-geometrical increase in the abundance. From the earlier parts of the book we recall that this situation is characterised also by a geometrical decline in competitive quality.

In natural situations there are both density regulation and genetic variation, and then the dynamics of the model with density dependent selection is inherently cyclic with an either stable or unstable equilibrium. As it is shown in the first appendix to this chapter, the evolutionarily determined population equilibrium is unstable when $\gamma_q \geq \gamma$, or when $\gamma \geq 2$ and $\gamma_q \leq \gamma - 4$. The latter of these two criteria is associated with dynamics that generally is oscillatory with a period of two generations, and this type of dynamics is driven primarily by over-compensatory density regulation. The former criterion is instead associated with non-over-compensatory dynamics that is cyclic with a highly variable period, and this dynamics is caused primarily by the evolutionary modulation of the phenotype.

In relation to the stability of these latter cycles they are damped when $\gamma_q < \gamma$, stable when $\gamma_q = \gamma$, and repelling or exploding, when $\gamma_q > \gamma$. To examine the conditions that determine this instability recall that $\gamma_q = \gamma_\iota \psi \sigma_{\ln q}^2$ and that $\gamma = \gamma_\alpha + \mu \gamma_\iota$. Therefor, the condition $\gamma_q \geq \gamma$ resembles

$$\gamma_\alpha / \gamma_\iota \leq \psi \sigma_{\ln q}^2 - \mu\tag{24.4}$$

This implies that the dynamics become more stable when the resource regulation (γ_α) or the average cost of interference (μ) are increased. Moreover, the dynamics become more unstable when the density dependence in the level of interference (γ_ι), the genetic variance ($\sigma_{\ln q}^2$), and the intra-population differentiation in interference regulation (ψ) are increased.

When the cyclic dynamics generated by density dependent selection are stable, i.e., when $\gamma_q = \gamma$, then the period is determined by the γ parameter, and it declines from an infinite number of generations for $\gamma = 0$ to two generations for $\gamma = 4$. On the continuum from $\gamma = 3.5$ to $\gamma = 4$ the cycle

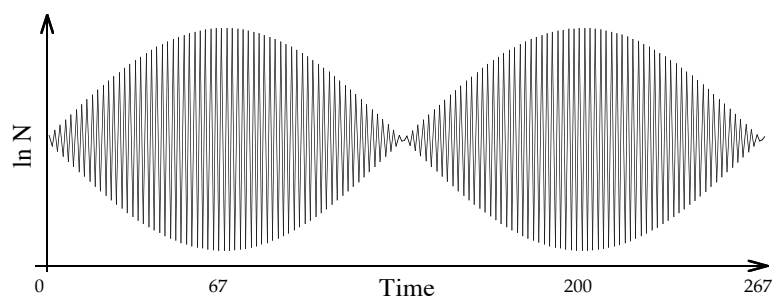


Fig. 24.1 A projection of the logistic equation with selection that shows the occurrence of a cycle in the amplitude of the population cycle; the population cycle has a period of ≈ 2 generations, while the amplitude has a period of ≈ 133 generations.

is dominated increasingly by a cyclic change in the amplitude of the cycle. This latter type of dynamics is illustrated in Fig. 24.1 where the amplitude cycle has a period of approximately 133 generations. As $\gamma \rightarrow 4$ the period of the amplitude cycle continues to increase, from ≈ 10 generations for $\gamma = 3.9$ to an infinite number of generations at the limit $\gamma = 4$. Beyond $\gamma = 4$ the population period is two generations, while the amplitude increases geometrically.

24.2 Population cycle driven by a cyclic population equilibrium

To understand the evolutionary forces underlying the cyclic dynamics consider a downward perturbation of the evolutionary equilibrium, a situation that is illustrated in Fig. 24.2a. Following this perturbation the density regulation is relaxed and, consequently, the reproductive rate will rise and the abundance will increase toward the evolutionary equilibrium.

Associated with the relaxed density regulation there is a decline in the level of interference, and this decline selects for an increase in the intrinsic growth rate at the cost of competitive quality. Thus, when the abundance has reached the evolutionary equilibrium the population will no longer be in population equilibrium at that equilibrium, and this is because the increased growth rate induces an increase in the population equilibrium. Consequently, the population will increase beyond the evolutionary equilibrium heading toward the new population equilibrium. As is illustrated in Fig. 24.2a, the population will never reach this equilibrium, and this is

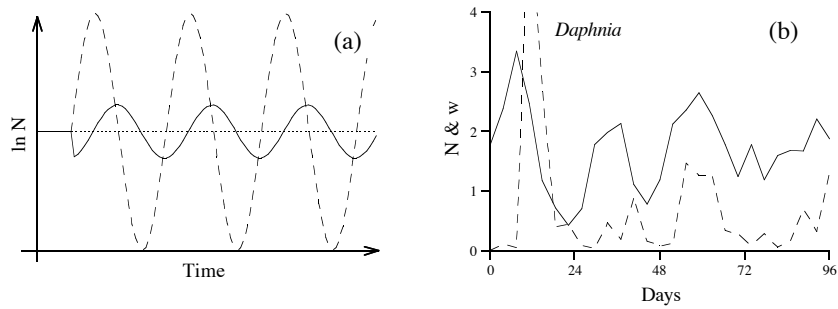


Fig. 24.2 (a) Projection of the logistic equation with selection. The solid curve is the population density, the dashed curve the population equilibrium, and the dotted line the evolutionary equilibrium. (b) The dynamics in the density (N) and body mass (w) of a *Daphnia* population against time. The solid curve is the population density (10^5 *Daphnia* per m^{-3}) and the dashed curve the body mass (μg dry weight). Data from Murdoch and McCauley (1985).

because as soon as the abundance increases beyond the evolutionary equilibrium, then the competitive interactions will select for an increase in competitive quality at the cost of the intrinsic growth rate. Thus, the population equilibrium evolves downward toward the increasing population.

At some intermediate abundance the downward evolving equilibrium and the upward increasing population will intercept, and the population will be in population equilibrium with no change in abundance. At this equilibrium the abundance is at its peak, and selection for competitive quality is thus at its strongest. Hence, the population equilibrium will continue to evolve downward with the result that the abundance will decline in order to keep up with the downward evolving equilibrium.

In Fig. 24.2a the abundance cannot keep up with the equilibrium, and consequently the distance between the abundance and the equilibrium increases until the population intercepts the evolutionary equilibrium with the fastest decline in density that the population encounters during the cycle. Having crossed the evolutionary equilibrium selection reverses, so that energy is allocated from competitive quality to the intrinsic growth rate, and the population equilibrium evolves upward toward the declining population. At some intermediate density the declining population intercepts the upward evolving equilibrium, the rate of change in abundance changes from negative to positive, and the next period begins.

24.3 Cyclic phenotypes

Associated with the population cycle predicted from selection by density dependent competitive interactions, there is a cycle in the phenotype. We have already seen that when the density is above the evolutionary equilibrium, then selection is increasing the competitive quality at the cost of the intrinsic growth rate, while the opposite is the case when the density is below the evolutionary equilibrium.

This cycle in the phenotype resembles the phenotypic cycles found in the small rodents that have cyclic dynamics. Here, it is generally observed that when the densities are low and increasing, then the rodents are small, non-aggressive, and they have a high rate of reproduction. When, instead, the densities are high and declining the rodents are aggressive, 20-30% larger than at low densities, and they have a low rate of reproduction (Krebs, 1978; Boonstra and Krebs, 1979; Stenseth, 1982). Moreover, according to the developed theory we expect that there is strong selection at the peak and bottom densities, and this also coincides with rodent evidence. For example, at the peak density in a rodent cycle Krebs et al. (1973) found that the frequency of the LAPs allele changed from ≈ 0.70 to ≈ 0.40 in less than one generation. These results suggest that selection by density dependent competitive interactions play a role in the generation of cyclic dynamics in small rodents.

You may recall from Chapter 4 that Murdoch and McCauley (1985) observed cyclic dynamics in a *Daphnia* population, and that this cycle occurred even though there were no predators and even though the density of the resource (algae) remained stable. This observation does not fit the hypothesis of a predator-prey driven cycle, but it would fit the current hypothesis if we could detect cyclic changes in the body mass, which are expected to represent competitive quality. From Murdoch and McCauley's Fig. 3 I could calculate the average body mass in the *Daphnia* population, and in Fig. 24.2b I have plotted both the average body mass and the population density against time. From the figure it is apparent that the body mass cycles, and that this cycle is lagging behind the cycle in density, as predicted by the logistic equation with density dependent selection. From eqn 24.14 the predicted relation between the body mass and the population density is

$$\ln w_t - \ln w_{t-1} = \gamma_q \ln N_{t-1} + c \quad (24.5)$$

where c is a constant. This relation is significantly present in the *Daphnia* population ($r = 0.49$, $n = 26$, $\gamma_q = 1.7 \pm 0.5(\text{SE})$, and $c = -0.55 \pm 0.36$), suggesting that selection by density dependent competitive interactions play a role in the cyclic dynamics of *Daphnia* populations.

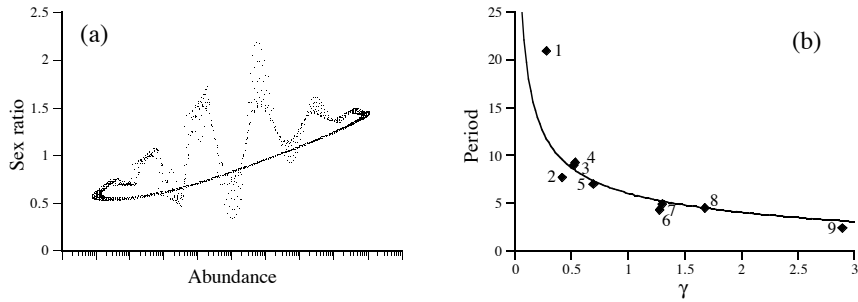


Fig. 24.3 (a) A projection of eqn 24.6 that shows a phase portrait between the sex ratio and the abundance. (b) The period of the population cycle in generations against the γ parameter (assuming $\gamma_q = \gamma$). The curve is defined by eqn 24.2, and the numbered diamonds represent the following species: 1: Spruce budworm. 2: Southern pine beetle. 3: Douglas-fir tussock moth. 4: Larch budmoth. 5: Fall webworm. 6: Nun moth. 7: Pine looper moth. 8: Larch cone fly. 9: Wasp spp.

24.4 The sex ratio cycle

According to the mechanism of selection by density dependent competitive interactions, the cyclic changes in competitive quality include phenotypic traits as diverse as body mass, metabolic rate, antagonistic behaviour, and group size. The sex ratio is also included because the male often is competitively superior to the female. In this section I deal with the incorporation of the sex ratio into the population dynamic equation, a situation that conforms to the transition from an asexual to a sexual species.

The mathematical deduction of the population model for a species with non-overlapping generations, sexual reproduction between males and females, and selection due to density dependent competitive interactions is carried out in the second appendix to this chapter. As it is shown, the incorporation of sexual reproduction leads to the following population equations

$$\begin{aligned}
 \phi_t &= \phi_{t-1} N_{t-1}^{\gamma_\phi} e^{-\phi_t \sigma_{\ln \phi}^2 / (1 - \phi_t)} & (24.6) \\
 \lambda_{m,t} &= \lambda_{m,t-1} N_{t-1}^{-\gamma_q} e^{\sigma_{\ln q}^2} \\
 N_{t+1} &= N_t \lambda_{m,t} (1 - \phi_t) N_t^{-\gamma}
 \end{aligned}$$

This model can generate a variety of dynamics, and in the absence of density dependence, i.e., when $\gamma = \gamma_\phi = \gamma_q = 0$, the model reduces to an asexually reproducing organisms with a hyper-geometrically increasing abundance and a geometrically declining competitive quality. In the realistic situations with density dependence the dynamics is generally cyclic, and

Table 24.1 The parameter estimates of the logistic equation with selection (eqn 24.2, assuming $\gamma_q = \gamma$) for the nine insect species in Table 3.1. N_G is the geometric mean in the data, and r the correlation coefficient of the regression (eqn 24.39) that was used to estimate the parameters.

Species	N_G	P	r	γ	$\sigma_{\ln q}^2$	N^{**}	λ_m^{**}
Tussock moth	4.1	9.0	0.96	0.52	0.77	4.39	2.16
Fall webworm	10.2	7.0	0.82	0.69	1.54	9.83	4.82
Larch budmoth	2.2	9.3	0.96	0.53	0.51	2.62	1.66
Larch cone fly	945	4.5	0.32	1.68	11.5	950	97500
Nun moth	2600	4.1	0.55	1.28	10.0	2630	22900
Pine looper moth	0.66	4.9	0.62	1.30	-0.48	0.69	0.62
Pine beetle	700	7.7	0.94	0.42	2.67	605	14.4
Spruce budworm	1.5	21	0.94	0.28	0.16	1.76	1.17
Wasp spp.	10.2	2.2	-0.57	2.89	6.59	9.78	730

Fig. 24.3a illustrates a stable cycle with a phase portrait between the sex ratio and the population density. This theoretical cycle coincides with the results of the empirical study of Naumov et al. (1969). They found that the percentage of males in small rodents increases when the densities are high, while females predominated during the years with low densities. This resemblance suggests that selection by density dependent competitive interactions plays a role in the cyclic dynamics of small rodents.

24.5 Forest insects

Forest insects, especially Lepidoptera, are known for their very pronounced population cycles, and from Chapter 4 on predator-prey interactions we recall that at least some of these cycles tend to lack a firm coupling to the dynamics of other species. Then, as these insects have non-overlapping generations, like the model in eqn 24.2, it is interesting whether the dynamics of forest insects resemble the dynamics we predict from selection due to intra-specific competitive interactions.

Recall that in Chapter 3 we analysed the data of nine species of forest insects, and that we concluded that their dynamics was not explained by over-compensatory density regulation. As these insects were chosen because they showed cyclic dynamics we can assume that the cycles are stable so that the parameters of eqn 24.2 for those species are easily estimated by the regression in the third appendix to this chapter. For this case, where $\gamma_q = \gamma$, I have listed the estimated parameters in Table 24.1. Before we compare the dynamics between the estimated models and the insect species,

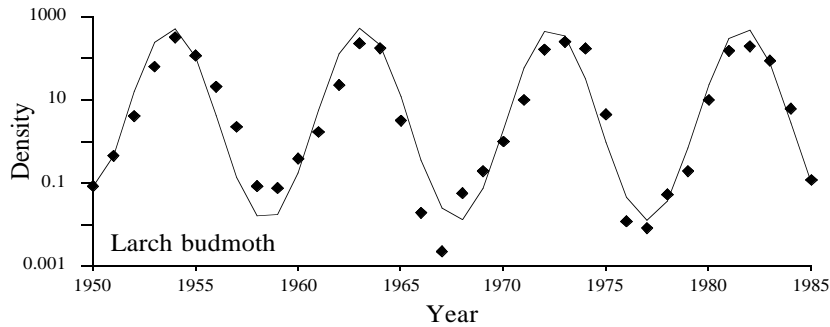


Fig. 24.4 The curve is a projection of eqn 24.2 and the diamonds the yearly densities of the larch budmoth in the Upper Engadine valley from 1950 to 1985. The projection is initialised from the density estimates of 1949, 1950, and 1951. The γ and $\sigma_{\ln q}^2$ parameters of eqn 24.2 is adjusted from those given in Table 24.1 to $\gamma = 0.44$ & $\sigma_{\ln q}^2 = 0.42$ so that the equilibrium is the same and the period resembles the observed period. Data from Baltensweiler and Fischlin (1988).

we may notice that the estimated evolutionary equilibria (N^{**}) resemble the geometric mean of the densities in the time series (N_G), a result that suggests that the assumption of linearity on logarithmic scale is reasonable.

As it has already been mentioned, the period in the dynamics of eqn 24.2 is given by the γ parameter, and in Fig. 24.3b this relationship is shown by the curve that is obtained by numerical simulations. In the same figure the diamonds represent the nine species, where the γ parameter is estimated by the regression in the third appendix and the period is the average period in the data. The resemblance between the theoretically deduced and the observed periods is reasonable, suggesting that selection by density dependent competitive interactions play a role in the cyclic dynamics of forest insects.

Let me now focus on the larch budmoth that lacks a firm predator-prey interaction although it has the best documented cycle among forest insects (Berryman, 1996). The data on one population of this species are shown by the diamonds in Fig. 24.4, where the curve represents a projection of the model in eqn 24.2. Again, the resemblance between theory and data is reasonable, suggesting that selection by density dependent competitive interactions play a role in the cyclic dynamics of the larch budmoth.

24.6 Population cycle allometry

The essential time lag that generates the cyclic dynamics of eqn 24.2 is one generation, and this is because evolution by natural selection is operating with a built-in delay of one generation. In eqn 24.2 this time lag is implicit

in the sense that the model is developed for organisms with non-overlapping generations. This implies that the period of eqn 24.2 is given in generations and, thus, for a given γ the period in astronomical time is proportional to the lifespan (T).

From the allometric deduction in Chapter 13, we have that $T \propto w^{1/2d}$, where w is the body mass and d is the number of dimensions in which the organism forages. Hence, the period of the population cycle is expected to have a similar scaling, and this means that it is expected to be proportional to the positive 1/4 power of body mass, at least for the terrestrial organisms that forage in two spatial dimensions. On empirical grounds this scaling is known as the Calder hypothesis, and it is shown in Fig. 24.5a where it is confirmed for terrestrial homiotherms (Calder, 1983, 1984; Peters, 1983; Peterson et al., 1984; Krukoni and Shaffer, 1991).

24.7 Implications of neutral stability

The cycles generated by selection due to density dependent competitive interactions are neutrally stable in the sense that their amplitude is given by initial conditions even though the period is fixed and given by the particular value of γ . The alternative to a neutrally stable cycle is a limit cycle where both the amplitude and the period is fixed and given by parameter values. In this latter case it is the whole cycle of a given population that is fixed being the global attractor toward which all initial perturbations of the population equilibrium converges.

It is relatively easy to determine whether the population cycles of natural species are neutrally stable, or limit, cycles. If the cycles are limit cycles we expect only a small and relatively similar degree of variation in both the period and the amplitude of the cycle. If, on the other hand, the cycles are neutrally stable, as it is expected by eqn 24.2, then, for a given species the amplitude is expected to be much more variable than the period. This prediction coincides with Batzli's (1981) conclusion stating that for small mammals in any given place the period of the cycle is more regular than its amplitude, and the same is true for the cycle of the Canadian lynx (Moran 1953; Bulmer, 1974).

Also, if the cycle is neutrally stable, then the amplitude is determined by the magnitude of the environmental perturbations. This implies that the amplitude will increase on a cline from a stable to a fluctuating environment. One such cline is from temperate areas toward the polar regions where an increased frequency and severity of unfavourable climatic conditions occur. It is thus not surprising that population cycles generally vanish toward the south while they become progressively more pronounced with progressively larger amplitudes toward Arctic regions (Howell, 1923; Hansson and Henttonen, 1985; Hansson, 1987; Akçakaya, 1992).

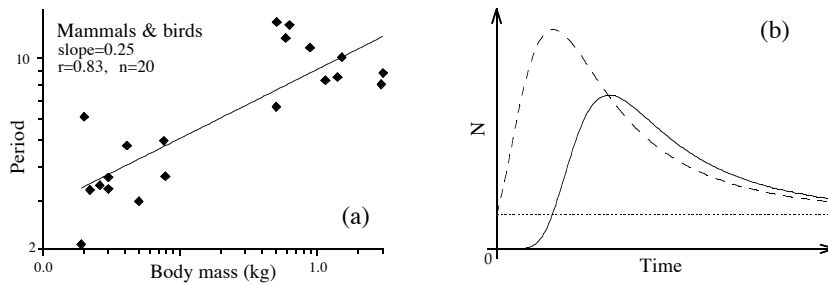


Fig. 24.5 (a) The period of population cycles against body mass for terrestrial homiotherms on double logarithmic scale. Data from Peterson et al. (1984), obtained through Krukonis and Shaffer (1991). One outlier removed. (b) A projection of eqn 24.2 to illustrate the dynamics of an introduced species with strongly damped dynamics ($\gamma = 0.07$ & $\gamma_a = 0.01\gamma$). At time zero the species is introduced at a density that is 10^{-7} times smaller than the density at the evolutionary equilibrium. The solid curve is the population density, the dashed curve the population equilibrium, and the dotted line the evolutionary equilibrium.

24.8 Extreme perturbations

As the amplitude of the population cycle depends on the magnitude of the environmental perturbation it follows that a special type of dynamics can arise from extreme perturbations of relatively stable equilibria. To illustrate this, consider a species that invades or is introduced into a new area from which it previously has been absent. If such invasions are successful there is often an extreme perturbation with an extraordinarily low population density. This implies that interference competition is almost absent and that there is strong selection for an increase in the intrinsic growth rate. In Fig. 24.5b I have simulated such an introduction of a species with strongly damped dynamics. From the figure it is apparent that, following the introduction, there is a lack phase with only a marginal increase before the evolutionary increase in the intrinsic growth rate causes the population to explode to extreme densities. These densities are associated with high levels of interference where antagonistic behaviour selects energy from the demographic traits to competitive quality, and this causes the population to decline slowly to the normal and stable density given by the evolutionary equilibrium. This type of dynamics with a single, or a few, over-shoots are often observed when humans release exotic species into new areas (e.g., Elton 1927; Adam et al., 1993).

In the extreme case, the dynamics may be so unstable that a severe

environmental perturbation might “kick” a species into an orbit that will lead of extinction. If such cases occur, the extinction event will follow after an extreme peak density. I can recall one such extinction; the passenger pigeon in America. Indeed the densities of this species were extreme prior to the extinction: “a single town in Michigan marketed 15,840,000 birds in two years, while another town sold 11,880,000 in forty days” Elton (1927:105). As the passenger pigeon went extinct during the settlements in America it might be that it experienced a major change in the habitat, and that this change “kicked” this species into an orbit of extinction.

Not only might such extinctions be caused directly by a large environmental perturbation, but maybe even more likely, they might be the result of an environmentally induced transition from a damped to a repelling or exploding cycle. This could, e.g., be the case if an environmental alternation induces changes in the parameters that determine the stability of the population cycle. As it is indicated by eqn 24.4, such an environmental transition to a repelling cycle may occur if the mode of density regulation is shifted toward exploitative competition, or if the biased access to resource at a given density is increased.

Even if the cycle is repelling the environment may be sufficiently heterogeneous to ensure that at least a few individuals will survive during the lows of the population cycle. In such cases a species with a repelling cycle will be characterised by many local extinctions after which it will spread from “epidemic centers” during the increasing phase of its cycle. This pattern of expiration and colonisation is observed for many of the forest insects with cyclic dynamics (see Berryman, 1988; Watt et al., 1990).

24.9 Appendix

24.9.1 Population equation with selection

In this appendix I develop and analyse a population dynamic equation for a species with non-overlapping generations and selection due to density dependent competitive interactions. This is done in three steps. First, I describe the evolutionary changes in the maximal growth rate in order to develop the population equation. Second, I show that the evolutionary equilibrium is the equilibrium of the population equation, and third I analyse the stability of the equilibrium and the dynamic behaviour of the equation.

Evolutionary changes in the growth rate

Let me use the logistic equation eqn 24.1 that we developed in Chapter 3 for a species with non-overlapping generations, and let us assume that the

exploitation efficiency (α) is stable so that the evolutionarily determined population equilibrium resembles the evolutionary equilibrium. For this equilibrium we have previously shown that

$$\begin{aligned}\lambda &= \lambda_m^{**} N^{**-\gamma} = 1 & (24.7) \\ N^{**} &= \sqrt[\gamma]{\lambda_m^{**}} \\ N^{**} &= e^{1/\gamma\iota\psi} \\ \lambda_m^{**} &= e^{\gamma/\gamma\iota\psi}\end{aligned}$$

To predict the evolutionary change in λ_m let

$$\lambda_m = \rho/q \quad (24.8)$$

where ρ is a positive constant and q is the energetic and competitive quality of an average individual. Then the discrete growth rate of the population in the t th generation is

$$\lambda_t = \rho N_t^{-\gamma}/q_t \quad (24.9)$$

while it for the i th variant is

$$\begin{aligned}\lambda_{i,t} &= \rho N_t^{-\gamma_i}/q_{t,i} & (24.10) \\ &= \lambda_t (\rho N_t^{-\gamma_i}/q_{t,i}) / (\rho N_t^{-\gamma}/q_t) \\ &= \lambda_t (q_t/q_{i,t}) N_t^{\gamma\iota\psi(\ln q_{i,t} - \ln q_t)}\end{aligned}$$

with $\gamma_i = \gamma_\alpha + \mu_i\gamma_\iota$ and $\Delta\mu_i = \psi(\ln q - \ln q_i)$. This equation can be rearranged to

$$\lambda_{i,t} = \lambda_t e^{(\gamma_\iota\psi \ln N_t - 1)(\ln q_{i,t} - \ln q_t)} \quad (24.11)$$

If we differentiate this equation with respect to $\ln q_{i,t}$ and let $q_{i,t} \rightarrow q_t$ we obtain the per generation selection gradient on the average of $\ln q$, i.e.

$$\lim_{q_{i,t} \rightarrow q_t} \partial\lambda_{i,t}/\partial \ln q_{i,t} = \lambda_t (\gamma_\iota\psi \ln N_t - 1) \quad (24.12)$$

When this selection gradient is combined with Robertson (1968) the per generation change in $\ln q$ is

$$\begin{aligned}\Delta \ln q_t &= \frac{\sigma_{\ln q}^2}{\lambda_t} \lim_{q_{i,t} \rightarrow q_t} \frac{\partial\lambda_{i,t}}{\partial \ln q_{i,t}} & (24.13) \\ &= \sigma_{\ln q}^2 (\gamma_\iota\psi \ln N_t - 1)\end{aligned}$$

Then, from eqn 24.13 and $\ln q_t = \ln q_{t-1} + \Delta \ln q_{t-1}$ the average quality at time t is

$$q_t = q_{t-1} N_{t-1}^{\gamma_\iota\psi\sigma_{\ln q}^2} e^{-\sigma_{\ln q}^2} \quad (24.14)$$

and from eqns 24.8 and 24.14, the maximal growth rate in generation t is

$$\begin{aligned}\lambda_{m,t} &= \rho N_{t-1}^{-\gamma_i \psi \sigma_{\ln q}^2} e^{\sigma_{\ln q}^2} / q_{t-1} \\ &= \lambda_{m,t-1} N_{t-1}^{-\gamma_q} e^{\sigma_{\ln q}^2}\end{aligned}\quad (24.15)$$

with $\gamma_q = \gamma_i \psi \sigma_{\ln q}^2$. Then, from eqns 24.1 and 24.15 the population dynamic equation with density dependent selection is

$$\begin{aligned}\lambda_{m,t} &= \lambda_{m,t-1} N_{t-1}^{-\gamma_q} e^{\sigma_{\ln q}^2} \\ N_{t+1} &= N_t \lambda_{m,t} N_t^{-\gamma}\end{aligned}\quad (24.16)$$

This equation has three parameters (γ , γ_q , & $\sigma_{\ln q}^2$) and two initial conditions (N_t & $\lambda_{m,t}$).

The evolutionary equilibrium

If the evolutionary equilibrium eqn 24.7 is the equilibrium of the population equation eqn 24.16, then it must satisfy the conditions $\lambda_{m,t+1} = \lambda_{m,t}$ and $N_{t+1} = N_t$ for all t . From eqn 24.16 the condition $N_{t+1} = N_t$ is satisfied when

$$\lambda_{m,t} N_t^{-\gamma} = 1 \quad (24.17)$$

If we insert λ_m^{**} and N^{**} from eqn 24.7 into eqn 24.17 we have

$$e^{\gamma/\gamma_i \psi} e^{-\gamma/\gamma_i \psi} = 1 \quad (24.18)$$

which reduces to $1 = 1$. Hence, for the evolutionary equilibrium the condition $N_{t+1} = N_t$ is satisfied for all t when the condition $\lambda_{m,t+1} = \lambda_{m,t}$ is satisfied also. From eqn 24.16 we see that the condition $\lambda_{m,t+1} = \lambda_{m,t}$ is satisfied when

$$N_t^{-\gamma_q} e^{\sigma_{\ln q}^2} = 1 \quad (24.19)$$

If we insert N^{**} from eqn 24.7 into eqn 24.19 we have

$$e^{-\gamma_q/\gamma_i \psi} e^{\sigma_{\ln q}^2} = 1 \quad (24.20)$$

which for $\gamma_q = \gamma_i \psi \sigma_{\ln q}^2$ is equivalent to

$$e^{-\gamma_i \psi \sigma_{\ln q}^2 / \psi \gamma_i} e^{\sigma_{\ln q}^2} = 1 \quad (24.21)$$

which reduces to $1 = 1$. Hence, the condition $\lambda_{m,t+1} = \lambda_{m,t}$ is satisfied and the evolutionarily determined population equilibrium (eqn 24.7) is the equilibrium of the population dynamic model eqn 24.16.

Stability and dynamic behaviour

In this subsection I analyse the stability of the evolutionary equilibrium, and the dynamics following from a perturbation of that equilibrium. To do this let $r = \ln \lambda_m$ and $n = \ln N$. Then, take the natural logarithm to eqn 24.16 and obtain $r_t = G(r_{t-1}, n_{t-1})$ and $n_{t+1} = F(r_t, n_t)$ where the two functions G and F are defined as

$$\begin{aligned} G &= r_{t-1} - \gamma_q n_{t-1} + \sigma_{\ln q}^2 \\ F &= r_t + (1 - \gamma)n_t \end{aligned} \quad (24.22)$$

If we now follow the procedure in Bulmer (1994) the stability of the evolutionary equilibrium is given by the eigenvalues of the Jacobian matrix

$$\begin{bmatrix} \partial G/\partial r & \partial G/\partial n \\ \partial F/\partial r & \partial F/\partial n \end{bmatrix} \quad (24.23)$$

where the equilibrium is unstable when the absolute value of the dominant eigenvalue is larger than or equal to one. For the two-dimensional matrix eqn 24.23 the eigenvalues are

$$(T \pm \sqrt{T^2 - 4D})/2 \quad (24.24)$$

where D is the determinant and T the trace of that matrix. To determine this D and T we have that $D = (\partial G/\partial r)(\partial F/\partial n) - (\partial F/\partial r)(\partial G/\partial n)$, that $T = \partial G/\partial r + \partial F/\partial n$, and that $\partial G/\partial r = 1$, $\partial G/\partial n = -\gamma_q$, $\partial F/\partial r = 1$, and $\partial F/\partial n = 1 - \gamma$ for eqn 24.22 for all r and n including the equilibrium. Hence, we find that

$$\begin{aligned} D &= 1 - \gamma + \gamma_q \\ T &= 2 - \gamma \end{aligned} \quad (24.25)$$

so that the eigenvalues are

$$(2 - \gamma \pm \sqrt{\gamma^2 - 4\gamma_q})/2 \quad (24.26)$$

for eqn 24.16 on logarithmic scale. This means that the eigenvalues are real when $\gamma^2 \geq 4\gamma_q$ and complex when $\gamma^2 < 4\gamma_q$. Then, for the situation $\gamma^2 \geq 4\gamma_q$ with real eigenvalues we find that the equilibrium is unstable when $\gamma > 4$ or when $\gamma_q \leq 2\gamma - 4$ and $2 \leq \gamma \leq 4$ while it is otherwise stable. For the situation $\gamma^2 < 4\gamma_q$ with complex eigenvalues the absolute value of the eigenvalues is $\sqrt{1 - \gamma + \gamma_q}$ so that the evolutionary equilibrium is unstable when $\gamma \leq \gamma_q$.

When genetic variation is absent, i.e., when $\sigma_{\ln q}^2 = 0$, the instability criterion associated with the real eigenvalues merges into the instability

criterion of the logistic equation without selection, i.e., it merges into the instability criterion of the equation we analysed in Chapter 3. This implies that the instability criterion $\gamma_q \leq 2\gamma - 4$ reduces to $\gamma \geq 2$ because $\gamma_q = 0$ at the limit where genetic variation is absent. In this sense the instability connected with real eigenvalues is generated by over-compensatory density regulation. This is in contrast to the instability criterion associated with the complex eigenvalues, where the instability arises from the evolutionary modulation of the growth rate. This latter type of instability is impossible when genetic variation is absent, and this is because the absence of genetic variation imposes the constraint $\gamma_q = 0$ so that the inequality $\gamma \leq \gamma_q$ is false because γ is positive for natural situations.

Let us now turn to the dynamics that follow from a perturbation of the evolutionary equilibrium of eqn 24.16. For the situation where genetic variation is absent, i.e., when $\gamma_q = 0$, the dynamics are described in Chapter 3, and this is because eqn 24.16 reduces to eqn 3.15 at the limit with no genetic variation. When instead genetic variation is present the long-term dynamics, i.e., for $t \rightarrow \infty$, is given by the eigenvalues of the Jacobian matrix eqn 24.23. If these eigenvalues are real and their absolute values are smaller than one, then the perturbation will decline geometrically toward the equilibrium, while it will increase geometrically if the absolute value of the dominant eigenvalue is larger than one. Hence, for eqn 24.16 the perturbation will increase geometrically when $\gamma > 4$ or when $\gamma_q \leq 2\gamma - 4$ and $2 \leq \gamma \leq 4$, while the dynamics are damped otherwise. Moreover, if the sign of the dominant eigenvalue is negative the long-term dynamics is oscillatory with a period of two generations, while it is monotonic if the value is positive. Hence, the long-term dynamics of eqn 24.16 are oscillatory when $\gamma > 2$ while it is monotonic for $\gamma < 2$. Numerical simulations though do show that the short-term dynamics following from a perturbation of the equilibrium often is oscillatory even when $\gamma < 2$.

If instead the eigenvalues are complex they will induce a cycle with a highly variable period. To describe this cycle, let a complex eigenvalue be given by the polar coordinates in the Argand diagram, i.e., let x be its absolute value and θ its argument. Then the period of the cycle is $P = 2\pi/\theta$ while the amplitude is proportional both to the initial perturbation and to x . This amplitude is stable if $x = 1$, it declines geometrically if $x < 1$, and it increases geometrically if $x > 1$. That is, $x < 1$ corresponds to a damped cycle, $x = 1$ to a stable, and $x > 1$ to a repelling cycle. For eqn 24.16 we find that

$$\begin{aligned} x &= \sqrt{1 - \gamma + \gamma_q} \\ P &= 2\pi / \arctan \left| \frac{\sqrt{4\gamma_q - \gamma^2}}{2 - \gamma} \right| \end{aligned} \quad (24.27)$$

This implies that the cycle caused by the evolutionary modulation of the growth rate is damped when $\gamma < \gamma_q$, stable when $\gamma = \gamma_q$, and repelling when $\gamma > \gamma_q$. Also, when the cycle is stable the period has a minimum of 4 generations at $\gamma = 2$, while the period increases monotonically to infinity as γ goes toward either 0 or 4. For $\gamma < 0$ the system is not biologically defined, and at the limit of, and beyond, $\gamma = 4$ the eigenvalues are real with the dominant eigenvalue being smaller than -1 so that an initial perturbation increases geometrically and oscillatorily without limits.

Now, let the period of the population cycle be defined as the time between two neighbouring events, where the population abundance crosses the equilibrium in the same direction. Then numerical simulations show that the population period has a close resemblance to the period defined by eqn 24.27 when $\gamma_q \approx \gamma < 2$. When instead $\gamma_q \approx \gamma \geq 2$ and $\gamma_q \approx \gamma \rightarrow 4$ the population period declines monotonically from 4 to 2 generations, while the increasing period given by eqn 24.27 has a close resemblance to a period that turns up in the amplitude of the population cycle. The period of the population cycle is shown in Fig. 24.3b together with data from forest insects. An example of the period in the amplitude is shown in Fig. 24.1.

24.9.2 Population equation with selection on the sex ratio

In the population model eqn 24.16 it is not taken into account that a species might reproduce sexually. In such instances we may also want to model the evolutionary changes in the sex ratio, and this is because the sex ratio is expected to be modulated also by selection due to density dependent competitive interactions.

If we assume a stable α and non-overlapping generations, then the evolutionary equilibrium of a sexual mobile organism is

$$\begin{aligned} \lambda &= \lambda_m^{**}(1 - \phi^{**})N^{**-\gamma} = 1 & (24.28) \\ N^{**} &= \sqrt[\gamma]{\lambda_m^{**}(1 - \phi^{**})} \\ N^{**} &= e^{1/\gamma \cdot \psi} \\ \lambda_m^{**} &= e^{\gamma/\gamma \cdot \psi} / (1 - \phi^{**}) \\ \phi^{**} &= 1/2 \end{aligned}$$

where λ_m^{**} represents maximal net reproduction per female and ϕ^{**} is the proportion of males. From eqn 24.28 we find that the projection of the population density for a single time step is

$$N_{t+1} = N_t \lambda_{m,t} (1 - \phi_t) N_t^{-\gamma} \quad (24.29)$$

To predict the population trajectory from this equation we also need to predict the evolutionary trajectory in both maximal reproduction and the

proportion of males. To predict these trajectories let $\lambda_m = \rho/q$ so that the discrete growth rate of an average individual is

$$\lambda_t = \rho(1 - \phi_t)N_t^{-\gamma}/q_t \quad (24.30)$$

We can then follow the procedure for eqns 24.10 to 24.15 and find that maximal reproduction at time t is given by eqn 24.15. If we now assume independence between q and the proportion of males (ϕ) we can follow the same procedure to determine ϕ at time t . When we do this we find, in resemblance with eqn 24.10, that the discrete growth rate of the i th variant is

$$\begin{aligned} \lambda_{i,t} &= \rho(1 - \phi_{t,i})N_t^{-\gamma_i}/q_t & (24.31) \\ &= \lambda_t[\rho(1 - \phi_{t,i})N_t^{-\gamma_i}/q_t]/[\rho(1 - \phi_t)N_t^{-\gamma}/q_t] \\ &= \lambda_t[(1 - \phi_{t,i})/(1 - \phi_t)]N_t^{\gamma_i\psi(\ln \phi_{i,t} - \ln \phi_t)} \end{aligned}$$

with $\gamma_i = \gamma_\alpha + \mu_i\gamma_\iota$ and $\Delta\mu_i = \psi(\ln \phi - \ln \phi_i)$. If we differentiate this equation with respect to $\ln \phi_{i,t}$ and let $\phi_{i,t} \rightarrow \phi_t$ we obtain the per generation selection gradient on the population average of $\ln \phi$

$$\lim_{\phi_{i,t} \rightarrow \phi_t} \partial \lambda_{i,t} / \partial \ln \phi_{i,t} = \lambda_t[\gamma_\iota \psi \ln N_t - \phi_t / (1 - \phi_t)] \quad (24.32)$$

and thus the per generation change in $\ln \phi$

$$\begin{aligned} \Delta \ln \phi_t &= \frac{\sigma_{\ln \phi}^2}{\lambda_t} \lim_{\phi_{i,t} \rightarrow \phi_t} \frac{\partial \lambda_{i,t}}{\partial \ln \phi_{i,t}} & (24.33) \\ &= \sigma_{\ln \phi}^2[\gamma_\iota \psi \ln N_t - \phi_t / (1 - \phi_t)] \end{aligned}$$

Then, from eqn 24.33 and $\ln \phi_t = \ln \phi_{t-1} + \Delta \ln \phi_{t-1}$ the proportion of males at time t is

$$\phi_t = \phi_{t-1} N_{t-1}^{\gamma_\phi} e^{-\phi_t \sigma_{\ln \phi}^2 / (1 - \phi_t)} \quad (24.34)$$

with $\gamma_\phi = \gamma_\iota \psi \sigma_{\ln \phi}^2$. The population equation for a sexually reproducing mobile organisms is then given by the eqns 24.15, 24.29, and 24.34, which is summarised by the following population equation

$$\begin{aligned} \phi_t &= \phi_{t-1} N_{t-1}^{\gamma_\phi} e^{-\phi_t \sigma_{\ln \phi}^2 / (1 - \phi_t)} & (24.35) \\ \lambda_{m,t} &= \lambda_{m,t-1} N_{t-1}^{-\gamma_q} e^{\sigma_{\ln q}^2} \\ N_{t+1} &= N_t \lambda_{m,t} (1 - \phi_t) N_t^{-\gamma} \end{aligned}$$

This equation has five parameters ($\gamma, \gamma_\phi, \gamma_q, \sigma_{\ln \phi}^2$, & $\sigma_{\ln q}^2$) and three initial conditions (N_t, ϕ_t & $\lambda_{m,t}$).

24.9.3 Parameter estimation

Given the assumption of a stable cycle, i.e., given $\gamma_q = \gamma$, in this appendix I describe how to estimate the parameters of the population model eqn 24.2. By eqn 24.2 we have assumed that the effects of density regulation vanishes at the density $N = 1$. This is generally not the case when densities are scaled arbitrarily, and therefore we need an extra constant (c) so that $\lambda_t = \lambda_{m,t}cN^{-\gamma}$. Then, to estimate $\lambda_{m,t}$ and c from time series of densities we need an independent estimate of either $\lambda_{m,t}$ or c . As such estimates are generally not available let me simplify and exchange $\lambda_{m,t}$ in eqn 24.2 with $\lambda_{c,t} = \lambda_{m,t}c$. For this definition of density regulation it can be shown that the term $e^{\sigma_{\ln q}^2}$ in eqn 24.2 is exchanged with e^δ when $\delta = \gamma_q \ln c/\gamma$. Then, from the assumptions $\gamma_q = \gamma$ and $\lambda_t = \lambda_{c,t}N_t^{-\gamma}$ the population model of eqn 24.2 is equivalent to

$$\begin{aligned}\lambda_{c,t} &= \lambda_{c,t-1}N_{t-1}^{-\gamma}e^\delta \\ N_{t+1} &= N_t\lambda_{c,t}N_t^{-\gamma}\end{aligned}\quad (24.36)$$

To estimate the two parameters γ and δ , from the bottom equation of eqn 24.36, we have

$$\lambda_{c,t} = N_{t+1}N_t^{\gamma-1}\quad (24.37)$$

If we then insert $\lambda_{c,t-1}$ and $\lambda_{c,t}$ as given by eqn 24.37 into the top equation of eqn 24.36 we obtain

$$N_{t+1}N_t^{\gamma-1} = N_tN_{t-1}^{\gamma-1-\gamma}e^\delta\quad (24.38)$$

This equation can be rearranged so that we can estimate γ and δ by the linear regression

$$\ln N_{t+1} + \ln N_{t-1} = (2 - \gamma) \ln N_t + \delta\quad (24.39)$$

From $\lambda_c^{**} = \lambda_c^{**}N^{**-\gamma}e^\delta$ (eqn 24.36) the density at the equilibrium is $N^{**} = e^{\delta/\gamma}$, which combined with $N^{**} = N^{**}\lambda_c^{**}N^{**-\gamma}$ (eqn 24.36) gives us the estimate $\lambda_c^{**} = e^\delta$.