

Part IV

The evolutionary steady state

Chapter 14

Exponential increase in body mass

COPE (1887) SAW that species in the fossil record continue to increase in size, and this may include up to 90 percent of the mammalian lineages (Maynard Smith and Brown, 1986). Despite this empirical fact main stream evolutionists have continued to reject the idea that evolution is an upward drive. Instead, they have favoured the view that evolution by natural selection is stochastic, historical, and non-directional (e.g., Mayr, 1988; Williams, 1992; Maynard Smith and Szathmáry, 1995). This is probably best illustrated by the recent book of Maynard Smith and Szathmáry (1995:4) in which the authors already in the introduction conclude that “On the theoretical side, there is no reason why evolution by natural selection should lead to an increase in complexity”.

It is also widely accepted that species that increase in size do so only because they arose as small and because evolutionary diffusion will cause the size to increase in at least some species (e.g., Stanley, 1973; Gould, 1988, 1997; McKinney, 1990; Jablonski, 1997). In this and the following chapter I use the framework of Malthusian relativity to show that these traditional propositions on non-directional evolution fail because there *is* a force of selection that causes exponential increase in both the body mass and metabolic rate of mobile organisms. This exponential increase in competitive quality is the evolutionary process occurring in a stable environment when there is no immediate limit to the exploitation efficiency.

The idea of directional evolution is not new, actually we have already seen that the classical theory predicts directional evolution. Fisher’s fundamental theorem of natural selection predicts a continuous increase in the intrinsic Malthusian parameter and this leads to a continuous decline in traits

like body mass and metabolic rate. Today, it seems that the consequences of this straightforward prediction, which obviously does not resemble natural conditions, have been neglected for decades by evolutionists who have defined selection by intrinsic constraints that are evolutionarily unstable.

When we turn to the directional evolution in Malthusian relativity we relax the traditional assumption of evolutionary equilibria. This assumption is problematic because it is based on the generally invalid assumption that the individuals of a given species have a fixed ability to consume resource, i.e., a fixed exploitation efficiency (α) that cannot evolve by natural selection. In this chapter I relax this assumption and let α evolve freed from evolutionary constraints. As it is shown, this implies selection at a steady state that is characterised by exponential increase in both α and body mass. It is shown also that while the body mass increases exponentially the other phenotypic traits will evolve in accordance with the exponents of the body mass allometries. Among other things, this latter result predicts a continuous decline in the intrinsic Malthusian parameter, i.e., it predicts a continuous decline in Fisherian fitness.

The deduction of the steady state also predicts the proportional relation, between lifetime reproduction and body mass, that is used in the classical theory as the intrinsic constraint causing the evolution of large body masses. That is to say, that it turns out that the relation that originally was thought to define natural selection on body mass is the evolutionary result of the ecological constraints that define selection at the evolutionary steady state.

In the analysis of the steady state I will describe selection on the exploitation efficiency before I will deduce the steady state with the exponential increase in body mass. Hereafter, I will show that the across-species allometries, we deduced in Chapter 13, apply also for the steady state. Then, I will deduce the exponent of the within-species allometry between lifetime reproduction and body mass, and use this prediction to confirm that natural populations are situated at the evolutionary steady state. Having done this, I will describe a few relationships between steady state evolution and constraints on the body mass and the exploitation efficiency and, finally, I will conclude that the steady state defines broad scale evolution as a deterministically unfolding process.

14.1 Exponential increase in resource consumption

The first and crucial observation leading to the evolutionary steady state with exponential increase in body mass is that an individual generally does better if it has more resource, or energy, available. That is to say, that

with more resource the individual can produce more offspring and, thus, it can be more fit. This implies that there is selection for an increase in the exploitation efficiency (α). As this parameter has no direct influence on competitive quality selection on α conforms to the classical set-up with Fisherian selection. Then, the fitness profile at the population equilibrium is $\lambda^* = p\alpha E^* e^{-\mu^*} / wB$, and this implies that the selection gradient on $\ln \alpha$ is $\partial x^* / \partial \ln \alpha = 1$. We can then multiply by the genetic variance in $\ln \alpha$ and find that the exploitation efficiency increases exponentially at the following rate

$$d \ln \alpha / dt = \sigma_{\ln \alpha}^2 \quad (14.1)$$

Due to the exponential increase in α the species will have more and more energy available per individual, at least if the resource density remains stable as it is the case at the steady state (shown in Section 14.3). With this increase in the amount of resource per individual the intriguing question is to deduce the allocation of the extra energy among the phenotypic traits.

14.2 Exponential increase in body mass

We now have a situation with exponential increase in the amount of resource consumed by an individual. To analyse the allocation of the extra energy available from this increase, let me first consider selection when the body mass is the only competitive trait. I will then in Chapter 15 extend the analysis to the situation where the metabolic rate per unit body mass acts also as a competitive trait.

Because the rate of reproduction is a very plastic demographic rate and because realised reproduction correlates strongly with fitness we may expect that the extra energy initially will be allocated to an increased rate of reproduction. Then, as the average rate of reproduction increases, the population equilibrium will increase and this will cause an increase in the level of interference competition and, thus, also an increased bias in the access to resource. As this increased bias is in favour of the large-bodied individuals, selection will begin to allocate some fraction of the extra energy from reproduction to body mass. The level of interference will, however, continue to increase as long as the amount of energy selected into body mass is smaller than the amount of energy that continuously is added to reproduction due to the increase in α . At some specific level of interference competition the two rates of allocation will balance and we have the evolutionary steady state that is characterised by exponential increase in both the exploitation efficiency and body mass.

To deduce the evolutionary steady state mathematically we recall that the selection gradient on \ln body mass is given by eqn 10.20. If this gradient

is multiplied by the genetic variance in \ln body mass we find that the rate of evolution is

$$d \ln w / dt = \sigma_{\ln w}^2 [(\psi \gamma_\iota / \gamma) \ln(\rho \alpha / w) - 1] \quad (14.2)$$

with $\rho = pE_m/B$. The evolutionary trajectory described by eqn 14.2 reflects direct selection on body mass, and at the steady state this trajectory is defined also by the evolutionary increase in α together with the steady state relationship between α and body mass within the phylogenetic lineage in time. Although this latter relation between α and body mass is currently unknown to us we can use the unknown function to describe the rate of evolutionary increase in body mass. To do this let us approximate the intra-lineage relation between α and body mass by the power function $\alpha_t \propto w_t^a$, where the exponent a is an unknown constant. From this expression we have that $\ln w_t \propto \ln \alpha_t / a$ and, thus, that

$$d \ln w / dt = a^{-1} d \ln \alpha / dt \quad (14.3)$$

When this expression is combined with eqn 14.1 we find that the rate of evolution in \ln body mass is

$$d \ln w / dt = \sigma_{\ln \alpha}^2 / a \quad (14.4)$$

We now have two independent expressions for the rate of evolution in the natural logarithm of body mass: eqn 14.2 describing the rate of evolution as it is caused by selection on body mass, and eqn 14.4 describing the rate of evolution as it is caused by selection on the exploitation efficiency (α) and the steady state relationship between α and body mass. Where the two rates are balanced against one another we have the evolutionary steady state.

To deduce some of the characteristics of the evolutionary steady state we may begin with a deduction of the body mass. To obtain the body mass at the steady state set the two rates of evolution given by eqns 14.2 and 14.4 equal to one another and solve for w^{*s} . The obtained w^{*s} can then be inserted into the level of interference as defined by the constraint of the population dynamic equilibrium (eqn 10.18). Hereby we obtain the level of interference at the steady state (ι^{*s}). The obtained ι^{*s} can then be inserted into eqn 10.20 to obtain the selection gradient on body mass at the steady state $[(\lim_{w_i \rightarrow w} \partial x_i^* / \partial \ln w_i)^{*s}]$. By solving these relations we find that the steady state is characterised by

$$\begin{aligned} w_t^{*s} &= \rho \alpha_t e^{-(1 + \sigma_{\ln \alpha}^2 / \sigma_{\ln w}^2 a) \gamma / \gamma_\iota \psi} & (14.5) \\ \iota^{*s} &= (1 + \sigma_{\ln \alpha}^2 / \sigma_{\ln w}^2 a) / \psi \\ (\lim_{w_i \rightarrow w} \partial x_i^* / \partial \ln w_i)^{*s} &= \sigma_{\ln \alpha}^2 / \sigma_{\ln w}^2 a \end{aligned}$$

$$\begin{aligned}(d \ln w / dt)^{*s} &= \sigma_{\ln \alpha}^2 / a \\ (d \ln \alpha / dt)^{*s} &= \sigma_{\ln \alpha}^2\end{aligned}$$

From these equations it is apparent that $\iota^{*s} > \iota^{**} = 1/\psi$, and this means that the level of intra-population interference is higher at the steady state than at the evolutionary equilibrium. When we compare w^{*s} in eqn 14.5 with w^{**} in eqn 10.21 it is apparent that, for a particular exploitation efficiency (α), the body mass at the steady state is smaller than the body mass at the evolutionary equilibrium. Furthermore, from eqn 14.5 we find that the exponential increase in body mass is defined by the exponential increase in the exploitation efficiency in the sense that it is the genetic variance in the exploitation efficiency, and not the genetic variance in body mass, that determines the rate of evolution in body mass. This is because the level of interference will equilibrate so that the selection gradient on body mass is exactly so strong that the body mass absorbs the extra energy that continuously is added from the evolutionary increase in the exploitation efficiency.

Let us now analyse the evolutionary stability of the evolutionary steady state. From the obtained w^{*s} and eqn 14.2 we note that selection on body mass defines the following rates of increase in body mass

$$\begin{aligned}d \ln w / dt &< \sigma_{\ln \alpha}^2 / a \quad \text{for } w > w^{*s} \\ d \ln w / dt &> \sigma_{\ln \alpha}^2 / a \quad \text{for } w < w^{*s}\end{aligned}\tag{14.6}$$

From these equations we have that when $w > w^{*s}$, then selection on body mass causes a smaller increase in body mass than defined by the selection on the exploitation efficiency and the unknown intra-lineage relation between α and w at the steady state. This means that the evolutionary trajectory in body mass will converge toward the trajectory defined by the steady state. The same is true when $w < w^{*s}$ because, then selection on body mass causes a higher increase in the body mass than defined by the steady state trajectory. This implies that the evolutionary trajectory defined by the steady state and an initial value of α will attract all other evolutionary trajectories with the same initial α independently of the initial setting of the body mass. In other words, the evolutionary trajectory of the steady state is the global attractor. In Fig. 14.1a I used eqn 14.5 to plot the evolutionary trajectory of the steady state together with two other trajectories following from differences in the initial body mass.

14.3 Body mass allometries at steady state

We now have a situation where the global attractor is the evolutionary steady state with an exponentially increasing body mass. The intriguing

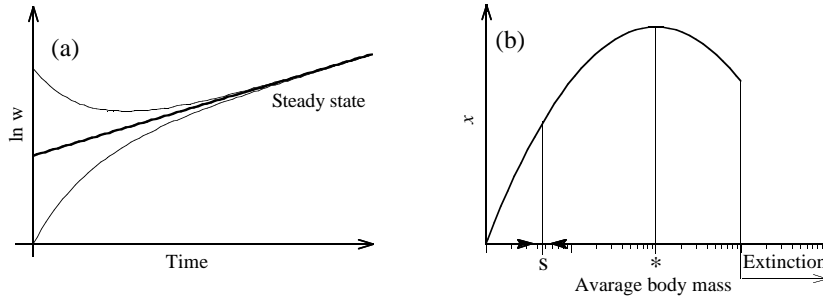


Fig. 14.1 (a) Exponential increase in body mass (w) as defined by selection when $\sigma_{\ln \alpha}^2$ and $\sigma_{\ln w}^2$ are constants. The two different trajectories (thin curves), that are initialised from the same α but two different body masses, converge to the trajectory of the steady state (thick line) for that initial value of α . (b) A selection profile for body mass with the position of the evolutionary equilibrium (*) and the evolutionary steady state (s) for an organism that forages in two dimensions.

questions then are whether the body mass allometries we deduced in Chapter 13 will hold in time for a phylogenetic lineage at steady state, and whether the body mass allometries will hold also across a set of species situated at the evolutionary steady state.

To determine the applicability of the allometric deduction at steady state we recall that the allometric exponents we deduced in Chapter 13 were based on a body mass invariant level of interference. In Chapter 10 we saw that this condition was fulfilled for a body mass in evolutionary equilibrium, but does this assumption also apply to a body mass in evolutionary steady state? From eqn 14.5 we notice that the level of interference at steady state is body mass invariant when the genetic variance in the logarithm to the exploitation efficiency and body mass are independent of respectively the average exploitation efficiency and the average body mass. As this seems to be a reasonable condition we expect that the exponents of the body mass allometries apply also to natural species that are situated at the evolutionary steady state. More exactly, this means that they are valid both across species situated at the evolutionary steady state, and within a phylogenetic lineage evolving along the trajectory of the steady state.

As the deduction of the body mass allometries are valid within a phylogenetic lineage in time we find that when the body mass increases exponentially the other phenotypic traits will evolve in accordance with the exponents of the body mass allometries. Among other things, this implies that the resource density will remain stable, and from the allometric relations $r_m \propto w^{-1/2d}$ and $N^* \propto w^{(1-2d)/2d}$ we find that the Fisherian fitness

defined as r_m and/or N^* will continue to decline. This conclusion is diametrically opposite to the fundamental theorem of natural selection that predicts a continuous increase in the two parameters.

14.3.1 Within-species allometry between reproduction and body mass

The body mass allometries deduced in Chapter 13, and which we have just shown to apply also at the evolutionary steady state, are across-species allometries describing the relationships between the average body mass and the average values of the other traits. At the smaller within-species scale we have a different set of allometries describing the allometric relationships across the individuals within the species. From Chapter 10 on the evolution of body mass, we recall that the within-species allometry between body mass and lifetime reproduction is the essential assumption defining the selection pressure for large body masses in the classical theory. In this section I will show that this classical assumption is explained from the ecological constraints at the steady state, and I will show also that the predicted allometry is confirmed empirically. In order to do this I will examine the selection gradient on body mass at steady state.

To obtain the selection gradient at steady state, from eqn 14.5 we notice that the level of interference and the selection gradient at the steady state are related to the exponent of the body mass allometry for the exploitation efficiency, i.e., related to the exponent a . So far the value of this exponent has been unknown, but as we have just shown that the across-species allometries are valid at the steady state from Chapter 13 we recall that $a = (2d - 1)/2d$, where d is the number of dimensions in which the organism forages. If we insert this a into eqn 14.5 and approximate by setting $\sigma_{\ln w}^2 \approx \sigma_{\ln \alpha}^2$, then we find that the level of interference and the selection gradient at the steady state are

$$i^{*s} = \frac{4d - 1}{2d - 1} \frac{1}{\psi} \quad (14.7)$$

$$\left(\lim_{w_i \rightarrow w} \frac{\partial x_i^*}{\partial \ln w_i} \right)^{*s} = \frac{2d}{2d - 1}$$

From this expression we find that the selection gradient at the steady state is defined by the number of dimensions in which the organism forages. In Fig. 14.1b I used this prediction to plot the position of the steady state on to the selection profile for the body mass defined by eqn 10.22. From the figure it is apparent that the steady state is situated to the left of the evolutionary equilibrium at the position where the slope of the selection

profile is $2d/(2d-1)$. Notice also that as selection increases the body mass the whole selection profile evolves toward the right.

To deduce the within-species allometry between reproduction and body mass let us integrate the selection gradient with respect to the within-population variation in $\ln w$ and obtain

$$\begin{aligned} x_i^* &= \int 2d/(2d-1) \partial \ln w_i \\ &\propto [2d/(2d-1)] \ln w_i \end{aligned} \quad (14.8)$$

Then, as fitness at the population equilibrium is defined as $x_i^* = \ln(p_i R_i)$, we can use eqn 14.8 to find that the within-species allometry between body mass and lifetime reproduction is

$$R_i \propto w_i^{2d/(2d-1)} \quad (14.9)$$

when it is assumed that $p_i \propto w_i^0$. By eqn 7.8 we have that this assumption is likely to hold as long as the energetic differences among the individuals within a population is so small that it affects mainly the rate of reproduction and not the rate of mortality. From Chapter 10 we recall that the within-species allometry of eqn 14.9 resembles the proportional relation between reproduction and body mass that is used as the intrinsic constraint that defines the selection pressure for large body masses in the classical theory. In other words, we can conclude that the classical assumption is explained by the ecological constraints at the evolutionary steady state.

Let us now use the prediction of eqn 14.9 to test whether natural populations are situated near the steady state, with exponential increase in the body mass, or near the evolutionary equilibrium, with a stable body mass. From eqn 14.9 we expect that lifetime reproduction at the steady state is proportional to the positive 4/3rd or 6/5th power of body mass when the organism forages in either 2 or 3 dimensions, i.e., proportional to $R_i \propto w_i^k$ with $k = 1.3$ or $k = 1.2$. In contrast to this we expect from Chapter 10 or Fig. 14.1b that $k = 0$ if the body mass is in evolutionary equilibrium.

From empirical studies it is well-known that the exponent k is positive in most species, and Reiss (1989) and Peters (1983) summarise some estimates of k : The best estimates from fishes are given by Wootton (1979) who used data from 124 studies on 62 species. He estimated an average k of 1.2, as it is predicted by eqn 14.8 if we assume that fishes forage in three spatial dimensions as indicated by Table 13.2. Peterson (1950) estimated a k of 1.03 in spiders, Robertson (1957) a $k \approx 1$ in *Drosophila melanogaster*, and Ridelyand Thompson (1979) estimated k to 0.77 for five species of Asellus (Crustacea; Isopoda). For the house martin I estimated k to 1.4 (data from Bryant, 1988), and for the ant-tended lycaenid butterfly k is approximately

0.9 (data from Elgar and Pierce, 1988). These estimates suggest that natural populations are closer to the evolutionary steady state than they are to the evolutionary equilibrium and, thus, that their body masses tend to increase exponentially.

14.4 Evolutionary constraints

The results that we obtained in the previous sections depend upon the assumption that there are no immediate limit to either the exploitation efficiency or the body mass. These assumptions may hold in a variety of situations. However, in some instances there may be limits that are imposed by the physical constraints of a given biological design. If there is such a constraint to a particular trait, then this limit cannot easily be broken even by artificial selection. This is because the genetic variance in that trait will decline as the trait evolves toward the limit, and this decline arises because it is almost impossible to generate a mutation that can break the barrier imposed by the constraint. In this section I will describe the evolutionary trajectories in the body mass and the level of interference given that this type of constraints operate either on the body mass or on the exploitation efficiency.

In the three subsections below I will examine respectively the evolutionary consequences of respectively a lower constraint on body mass, an upper constraint on body mass, and an upper constraint on the exploitation efficiency. Together with the evolutionary steady state these three situations will define four different levels of interference competition and, as it is apparent from Part V, these different levels of interference will define the selection pressure for many of the phenotypic differences existing between negligibly sized organisms, like prokaryotes and viruses, large-bodied organisms, like the higher eukaryotes, and eusocial organisms, like ants, bees, and termites. These results will indicate that the size of viruses and prokaryotes may coincide with a minimum size that is required for the metabolic and self-replicating processes of those organisms, and that the size of eusocial insects may reflect an upper limit imposed by the ecto-skeleton. If this is the case we have that the body masses of those organisms are defined by their evolutionary constraints, and not by the evolutionary equilibrium or by the evolutionary trajectory of the steady state.

14.4.1 A lower constraint on body mass

If there is a lower limit to the body mass, then the organism will have this minimum size if the individuals can assimilate only the most limited amount of resource. This can, e.g., be the case if the exploitation efficiency

is extremely small, or if the organism due to inter-specific interference competition is excluded from resource rich areas so that it will have to live on marginal resources.

In these situations where the assimilation of resource is extremely limited there is selection for the minimum mass, and this is because the assimilation of resource is so small that the population growth of these organisms cannot generate the amount of intra-population interference required to generate selection for an increase in body mass. In this case, the level of interference will remain approximately zero even though almost all the assimilated energy is allocated to numerical replication. This implies that selection is purely Fisherian and, thus, that the selection gradient on body mass is minus one (from eqn 10.17). From this gradient we expect at first a continuous decline in the body mass, but as the mass is downward constrained there will be no genetic variance upon which selection can operate and, thus, the body mass will remain stable.

From the prediction of Section 14.1, that the exploitation efficiency will increase exponentially, we might at first expect that minimum-sized organisms are evolutionarily unstable because, eventually, the exploitation efficiency will increase to a limit where selection by interference competition will begin to favour a larger body mass. However, in Section 14.4.3 we will find that this is not necessarily the case if the resource density is sufficiently low. In the Chapters 17, 20, and 21 I will consider this situation in further detail in order to show that a downward constrained body mass may be the essential component that can explain that prokaryotes and viruses have no soma, that they do not senesce, that they are haploid, and that they have asexual reproduction.

14.4.2 An upper constraint on body mass

If there is an upper limit to the body mass, then the organism will have this maximum body mass if the individuals pass beyond some upper threshold in their ability to assimilate resource.

In this case, with an upper limit to the body mass, the evolutionary trajectory can be described by the evolutionary steady state when the genetic variance in $\ln w$ declines with an increase in body mass. For example, the upper limit may be defined by the following relation

$$\sigma_{\ln w}^2 = \sigma_{\ln w,0}^2 e^{-hw} \quad (14.10)$$

where $\sigma_{\ln w,0}^2$ is the unconstrained level of genetic variance in $\ln w$, and h is a positive constant.

The situation of eqn 14.10 is shown in Fig. 14.2a where the body mass and the level of interference is plotted against time. Here, the body mass

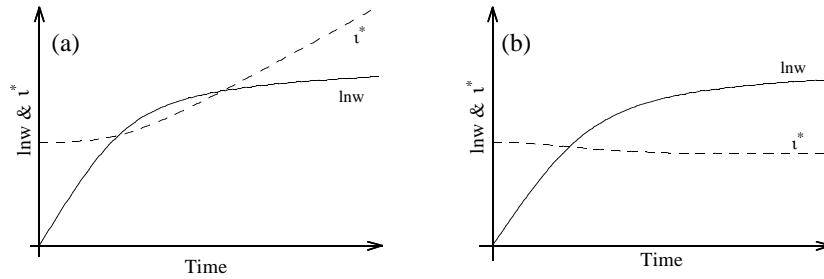


Fig. 14.2 Two evolutionary trajectories in body mass (w) and intra-population interference (t^*). (a) When the body mass is upward constrained by eqn 14.10. (b) When the exploitation efficiency is upward constrained by eqn 14.11.

increases exponentially at first, and then this increase stabilises as an increase in the level of interference appears. This increase in interference is in contrast to both the unconstrained steady state and to the evolutionary equilibrium where the level of interference is constant. With an upward constrained body mass the level of interference increases because at some point the constrained body mass can no longer absorb the free energy that is available from the evolutionary increase in the exploitation efficiency. Hereafter, selection is allocating the extra energy to numerical replication so that the population density and the level of interference increases. This result depends upon the assumption that the exploitation efficiency can evolve beyond the point that is associated with the transition in the allocation of the assimilated resource. As illustrated below, this may not always be the case if the resource density is too low. In Chapter 22 I will consider the situation with an upward constrained body mass in further detail, and this is done in order to show that it may be the essential component promoting the evolutionary transition to the eusocial colonies known from ants, termites, and bees.

14.4.3 An upper constraint on the exploitation efficiency

It is not only the body mass that can be upward constrained, it might also be the case for the exploitation efficiency. If there is such an upper limit to the exploitation efficiency, then the organism is expected to evolve to this limit at which the body mass will cease to increase.

To analyse this situation consider the case where the exploitation efficiency increases in a stable environment. Then, at some point it is likely that it becomes increasingly harder to improve the exploitation efficiency,

and this is because there is expected to be an upper limit to the rate at which the resource can be harvested by a given type of design. In such instances we find that the amount of genetic variation in $\ln \alpha$ will decline with α , e.g., as it is indicated by the relation

$$\sigma_{\ln \alpha}^2 = \sigma_{\ln \alpha, 0}^2 e^{-ha} \quad (14.11)$$

where $\sigma_{\ln \alpha, 0}^2$ is the unconstrained level of variation in $\ln \alpha$ and h is a positive constant.

The situation of eqn 14.11 is shown in Fig. 14.2b where the body mass and the level of interference are plotted against time. Here, the body mass increases exponentially before it stabilises, but in contrast to the constrained body mass the constrained exploitation efficiency causes a decline in the level of interference. From eqn 14.5 we see that this is because as $\sigma_{\ln \alpha}^2 \rightarrow 0$, then the level of interference approaches the level at the evolutionary equilibrium. In relation to this result we recall that the evolutionary equilibrium is defined by a non-evolving α , and by eqn 14.1 α does not evolve when $\sigma_{\ln \alpha}^2 = 0$.

14.5 Evolution as a deterministically unfolding process

We have now a situation where there is a direction to the evolutionary process, and although the direction may not continue indefinitely (Section 14.4), and although the assumption of a constant environment may not strictly apply in most situations, the underlying forces of selection seem to be so general that we may conclude that broad scale evolution is a deterministically unfolding process where living organisms have an inherent tendency to increase in mass and competitive quality.

The inherent tendency to increase in body mass is well documented from the fossil record where it is known as Cope's law (e.g., Cope, 1887; Depéret, 1909; Stanley, 1973; McKinney, 1990). According to Kurtén (1953) this paleontologic rule of evolution "is second in repute only to 'Dollo's law' of . . . irreversibility." In order to explain the increase in body mass many advantages of being big have been proposed (see Newell, 1949; Rensch, 1960; Peters, 1983; McKinney, 1990), and they include that larger individuals are superior in interference competition (e.g., Newell, 1949; Brown and Maurer, 1986; Maynard Smith and Brown, 1986). However, as shown in Chapter 10, it is not the component of competitive superiority that in itself can explain the increase in body mass, and this is because the average body mass will stabilise if α is constant. Instead, it is the combination of density dependent interference competition and the continuous increase in α that generate the evolution of exponential increase in body mass.

In this chapter we have focused on the evolutionary increase in body mass, but selection by competitive interactions at the steady state implies that it is competitive quality in general, and not only the body mass, that increases over time. Thus, among other things, we expect a continuous increase in the metabolic rate and in the complexity of the behavioural interactions that are used to control conspecifics. As the competitive quality increases we also expect that the overall complexity of the organisms will increase. For example, when the size of the organism increases beyond a certain level we may expect that multi-cellular organisms evolve because a multi-cellular design is more flexible than a single cell design. Also, to maintain a high metabolic rate within a relatively large organism it is a necessity that an intra-individual transportation systems is developed in order to elevate the exchange of chemical compounds above the rate of pure diffusion. Likewise, to perform complex behaviour an information processing system, as the neural-network, must develop. In Chapters 17 to 22 we will also see that the transitions in the level of interference, that we have described, e.g., in Section 14.4, will explain the transition from a haplodiploid and negligibly sized asexual organisms that do not senesce to a large-bodied organism with traits like senescence, soma, males, sexual reproduction, a diploid or a haplodiploid genome, and explain the additional transition to eusocial communities.

In conclusion, let me summarise the predicted evolutionary unfolding from self-replicating molecules to the complex organisms of today. At the origin of life the energetic level of the self-replicating molecules must have been so low that their density and their level of intra-population interference virtually were zero. At that time natural selection resembled Fisherian selection generating a continuous increase in the intrinsic Malthusian parameter through an increase in α and through evolutionary modifications in the allocation of the assimilated resource. As the evolutionary process proceeded through Fisherian selection the population density and the level of interference continued to increase. At a specific time in the history of life the level of interference would have risen to the level that is specified by the evolutionary equilibrium. As interference rose beyond this level the selection pressure changed from Fisherian to that of Malthusian relativity, and this change caused an evolutionary reallocation of the assimilated resource so that antagonistic traits could evolve together with the energy consuming competitive traits. As selection continued to increase α the level of interference would eventually equilibrate at the evolutionary steady state implying a steady increase in the various traits of competitive quality and their associated physiological complexity.

Chapter 15

Exponential increase in metabolic rate

THE ABILITY to metabolise energy into speed and power can be a crucial component for the outcome of a competitive interaction. This means that a high metabolic rate can evolve by density dependent competitive interactions because it can enhance the ability by which the individual can allocate energy to competitive interactions. Due to this type of selection the metabolic rate is expected to increase exponentially in the same way as it was deduced for the body mass in the previous chapter. In this sense it is not only the body mass, but also the metabolic rate, which absorbs the exponentially increasing amount of energy that the average individual has available from the exponential increase in the exploitation efficiency.

It is not surprising that Cope's law was established for body mass and not for the metabolic rate. Unlike body mass it is almost impossible to estimate the metabolic rate from fossil data. We all know that the dinosaurs were very big, but we still do not really know if they were homoio- or poikilotherms. Due to the problems in estimating the metabolic rate from fossils it is difficult to examine whether the prediction of a continuously increasing metabolic rate holds for fossil data. This is nevertheless what I intend to do in this chapter where I construct a model by which we can estimate the rate of increase in the metabolic rate from the rate of increase in body mass. This model can be applied to organisms that have undergone unconstrained evolution in the sense that they have been situated at the evolutionary steady state. As it is shown, when this is the case, then the exponent of the body mass allometry for the rate of increase in body mass is given by the rate of change in the metabolic rate per unit body mass.

One of the best documented candidates for unconstrained evolution is

the fossil horse, where the body mass has increased more or less exponentially for the last 57 million years (MacFadden, 1986). Evidently this lineage has not yet reached the upper limit to body mass, and it is also likely that the exploitation efficiency has evolved without constraints, because the plants eaten by the horse are easy to gather. Furthermore, as the fossil data on this taxon are almost perfect, it is likely that we can get a solid estimate of the rate of change in the metabolic rate. Hereby, it will be possible to estimate both the metabolic rate and the lifespan of the horse that lived 57 million years ago.

In the two sections below I will first describe the theoretical coupling between the evolutionary increase in body mass and metabolic rate, and then I will analyse the data on fossil horses.

15.1 Scaling time with metabolism

The comparisons we have performed in the previous chapters between empirical patterns and theoretical predictions have all been of the kind where we compared instantaneous patterns having no duration in time. For example, when in Chapter 14 we tested whether the body masses of natural species were increasing exponentially we did not look at the evolutionary trajectory in time, instead we examined the selection profile on body mass. In this chapter I will take the alternative approach and test the prediction of an exponentially increasing metabolic rate through an examination of the evolutionary trajectory in the body mass of fossil horses. This cannot be done by a simple projection of the equations that we described in the previous chapter, and this is because we need to consider the relationship between the time scale of the evolutionary process and the astronomical time scale on which empirical measurements are carried out.

As evolutionary changes caused by natural selection occur with a built-in delay of a single generation we have that the scaling of the evolutionary process to astronomical time is changing with evolutionary changes in lifespan. Then, as the lifespan is inversely related to the metabolic rate per unit body mass (eqn 7.26) we find that the evolutionary changes in the metabolic rate will alter the rate of the evolutionary increase in body mass. In the previous chapter we saw that if the body mass is the only competitive trait, then we expect that the intercepts of the body mass allometries are constant and that the evolutionary changes in lifespan and metabolic rate are defined by the evolutionary changes in body mass and the allometric relationships we deduced in Chapter 13. These allometries imply that while the body mass is increasing exponentially the lifespan is increasing exponentially too, while the metabolic rate is decreasing exponentially. In this relatively simple case the time scaling of the evolutionary trajectory in body mass involves only

the allometric relation between lifespan and body mass.

In the more general case where the metabolic rate is also a competitive trait that evolves due to selection by competitive interactions we find that the time scaling of the evolutionary trajectory in body mass becomes more complex, and this is because the intercepts of the body mass allometries for lifespan and metabolic rate are evolving also. For example, if selection on the metabolic rate is so strong that the rate increases exponentially, then the lifespan will decline exponentially and this implies that the evolutionary increase in body mass is accelerating at a faster rate when it is observed on an astronomical time scale. In other words, when the evolutionary trajectory in body mass is observed on an astronomical time scale, we can use the shape of the growth curve to determine whether the lifespan and the metabolic rate is increasing or decreasing exponentially. This is the idea behind the analysis that I will perform in this chapter.

To describe the relationship between the evolutionary trajectory in body mass and the evolutionary trajectories in lifespan and metabolic rate let, on a per generation time scale, the rate of exponential change in the metabolic rate be the rate of increase in body mass (s) times a constant (v). Then

$$\begin{aligned} dw/dt &= sw \\ dB/dt &= vsB \end{aligned} \quad (15.1)$$

and when solved

$$\begin{aligned} w_t &= w_0 e^{st} \\ B_t &= B_0 e^{vst} \end{aligned} \quad (15.2)$$

where w_0 and B_0 are the body mass and metabolic rate at time $t = 0$. Now, solve the growth equation for body mass with respect to time, obtain $t = \ln(w_t/w_0)/s$, and insert this expression into the growth equation for the metabolic rate. Then

$$B_t = (B_0/w_0^v)w_t^v \quad (15.3)$$

From eqn 7.26 we have that the physiological relationship between lifespan and the metabolic rate is $T = \omega/B$, and if this B is exchanged with B in eqn 15.3 we find that

$$T_t = \tau w_t^{-v} \quad (15.4)$$

where $\tau = \omega w_0^v/B_0$. As the growth equations in eqn 15.1 are given on a per generation time scale we need to scale these equations with respect to T_t if we want to predict the evolutionary trajectory on an astronomical time scale. For example, if the growth equation for body mass ($dw/dt = sw$) is scaled with respect the lifespan in eqn 15.4, then we find that the allometric relation for the growth curve in body mass depends upon v relating the

growth rate in the metabolic rate to the growth rate in body mass. That is, we find that

$$dw/dt = \dot{s}w^{1+v} \quad (15.5)$$

with $\dot{s} = s/\tau$. Notice here that this result depends upon the assumption that the senescence parameter ω , that is incorporated in τ , is constant.

If we consider first the case where it is only the body mass that represents competitive quality, whereas the metabolic rate does not, then we expect that the free energy available from the exponential increase in the exploitation efficiency is selected into the body mass while the other traits evolve in concordance with the exponents of the body mass allometries (Chapters 13 and 14). In this case the intercepts of the allometries are constant, and from the allometric deduction in Chapter 13 we have that the lifespan in eqn 15.4 is $T_t = \tau w_t^{1/2d}$, where d is the number of spatial dimensions in which the organism forages. This means that the evolutionary trajectory in the body mass of an organism foraging in two dimensions is described by the allometric relation $dw/dt \propto w^{3/4}$, and that the trajectory for an organism foraging in three dimensions is described by $dw/dt \propto w^{5/6}$. More generally we do not know the allometric scaling of eqn 15.5, but this scaling is easily estimated from evolutionary trajectories in body mass, and this is what we will do for fossil horses in the next section.

15.2 Metabolic rate and lifespan of horses 57 million years ago

Probably the most well-known example of Cope's law is the fossil horses that have increased in size more or less exponentially for millions of years. This increase is well documented especially by MacFadden (1986) who gives estimates of both the body mass and the rate of changes in body mass for a period that reach back 57 million years. In Fig. 15.1a I used his data to plot the rate of evolutionary increase in body mass against body mass on a double logarithmic scale. From the figure we see that the exponent of this relationship is 1.5, and this implies that $v = 0.5$. In other words, while the body mass of the horse has increased exponentially it seems that the metabolic rate per unit mass has increased exponentially at half the rate of the increase in mass and that this latter increase has caused a comparable decline in lifespan. In Fig. 15.1b I show the evolutionary trajectory in the body mass of the fossil horses together with a trajectory of the fitted model.

From eqn 15.3 it is possible to estimate the proportional increase that has occurred in the metabolic rate during the period $t=0$ to $t=t$, and this is done as $B_t/B_0 = (w_t/w_0)^v$. Due to the body mass allometry that we deduced in Chapter 13 for the metabolic rate, i.e., due to the relation $B_t = \beta_t w_t^{-1/2d}$, it is though more intuitively useful to estimate the proportional

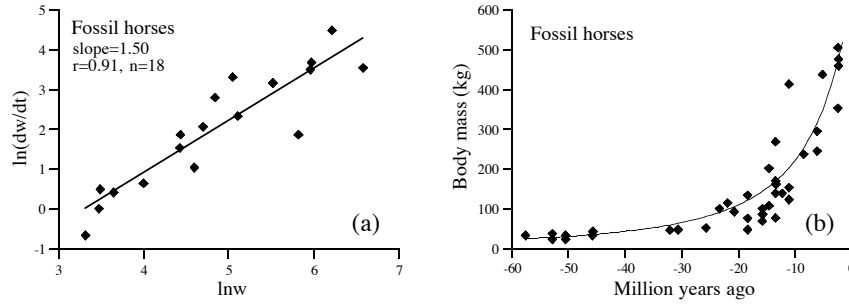


Fig. 15.1 (a) The rate of evolutionary increase in body mass (dw/dt) against body mass (w) on a double logarithmic scale for fossil horses. The diamonds are data from MacFadden (1986), and the line the linear regression. (b) The evolutionary trajectory for the body mass of fossil horses (diamonds), and a projection of eqn 15.5 (curve) with $v = 0.5$.

increase in the intercept of this allometry, i.e., estimate β_t/β_0 . In order to estimate this ratio, insert $B_t = \beta_t w_t^{-1/2d}$ and $B_0 = \beta_0 w_0^{-1/2d}$ into $B_t/B_0 = (w_t/w_0)^v$, rearrange, and obtain

$$\beta_t/\beta_0 = (w_t/w_0)^{v+1/2d} \quad (15.6)$$

From MacFadden we have that the horse weighed ≈ 25 kg 57 million years ago, and today it weighs ≈ 500 kg. Then, as horses forage in two dimensions we have that $d = 2$, and this implies that eqn 15.6 gives us the estimate $\beta_t/\beta_0 = 10$. That is to say that, when we correct for the allometric relationship between the metabolic rate and body mass, then the metabolic rate of the horse is ≈ 10 times larger today than it was 57 million years ago. In comparison, it can be mentioned that the metabolic rate of homoiotherms is ≈ 30 times larger than the metabolic rate of poikilotherms (Peters, 1983).

Due to the inverse relationship between the metabolic rate and lifespan the proportional decline in the intercept of the allometric relation between lifespan and body mass can be estimated as

$$\tau_t/\tau_0 = \beta_0/\beta_t \quad (15.7)$$

For a fixed body mass this implies that the lifespan has been reduced by 90% over the 57 million years. Thus, as today a 500 kg horse lives for ≈ 20 years (Nowak, 1991) we estimate that a hypothetical similarly sized horse that lived 57 million years ago would have had a lifespan of ≈ 200 years. If, instead, we incorporate the evolutionary changes that have occurred in body mass we find that $T_0 = T_t(w_t/w_0)^v$ and, thus, we estimate a lifespan of approximately 90 years for the 25 kg horse that lived 57 million years ago.

Chapter 16

Dwarfing and extinction

FROM THE FOSSIL record we know that the conditions on Earth are not so stable that all organisms tend to increase in size at all times. Instead, at any time there seems to be at least some organisms that dwarf, i.e., decline in size, and at particular events dwarfing even tends to predominate over Cope's rule of size increase. Associated with the events of widespread dwarfing there are normally many extinctions that tend to eliminate predominantly the larger species (Martin and Klein 1984; Donovan, 1989; McKinney, 1990). This type of crisis has occurred on many occasions during the history of the biota on Earth, but it is especially the five major mass extinctions that are well-known. These occurred at the end of Ordovician (≈ 440 million years ago (ma)), Devonian (≈ 360 ma), Permian (≈ 245 ma), Triassic (≈ 210 ma) and Cretaceous (≈ 65 ma), and they were big in the sense that between 70 and 95 percent of the species became extinct on each event (Jablonski, 1995). In this chapter I study the evolutionary processes that can explain the association between dwarfing and widespread extinction that eliminate predominantly the larger species.

A species may dwarf if its individuals have progressively less resource available, because then the rate of reproduction will decline causing a decline in the population equilibrium, the level of intra-population interference, and the biased access to resource. Due to this latter decline selection may allocate energy from body mass to numerical replication. This means that a species may dwarf in a stable environment if a larger species invades and by interference competition excludes the first species from the main habitat so that it will have to live in habitats of lower quality. In the same way, widespread dwarfing can occur if the primary production or the availability of resources decline. Furthermore, if the decline in primary production occurs faster than the phenotype can evolve, then, at a certain stage, the individuals can no longer find sufficient resource for self-replication and the

species becomes extinct. This type of extinction will affect predominantly the larger species, and this is because the rate of evolution is inversely related to the lifespan so that a small species having a short lifespan may be able to keep up with the environmental changes while a larger species with a longer lifespan may not.

So far there have been many proposals for the type of disturbances that might induce mass extinction, and these include meteoric impact, ice-ages, and increased human activity (see Martin and Klein, 1984; Donovan, 1989). There has, however, not yet been a general theory describing the biological processes that can explain why it was the large dinosaurs and not the small mammals that became extinct at the end of the Cretaceous, and why widespread dwarfing tends to co-occur with events of mass extinction. It is such a theory that I develop in this chapter where the mechanism that is involved is selection at steady state during periods with a decline in the primary production.

Apart from the patterns of extinction and dwarfing, the steady state with a declining primary production also generates a disturbance in the regularities behind the body mass allometries. Due to this disturbance it seems that the life-history patterns among organisms during periods of crisis are different from the life-history patterns that we know from the body mass allometries. Also, the steady state with a declining production provides us with a prediction of what is going to happen when the source that provides the energy for the primary production vanishes. In this case we find that, if the physical conditions remain suitable for life, then the body masses of all persisting species are expected to decline until they reach the molecular level. In other words, the evolutionary process seems to be reversible with the actual direction being defined by environmental conditions.

In the four sections below I will first consider the general process of dwarfing, then the allometric disorder during environmental crises, the evolutionary consequences of a continuous decline in the primary production, and finally, why it was the dinosaurs and not the mammals that became extinct during the perturbation at the end of the Cretaceous.

16.1 Dwarfing

From Chapter 14 we have that the steady state in a stable environment will stabilise at a level of interference where the exponentially increasing amount of energy available from the evolutionary increase in the exploitation efficiency is selected into body mass while lifetime reproduction remains constant. However, when the environment is unstable because the primary production is declining, an average individual has less energy available for reproduction, and this implies that the steady state will stabilise at a lower

level of interference where selection allocates less energy from reproduction to body mass, if energy is not allocated in the opposite direction.

To deduce this mathematically let us follow the procedure in Chapter 14 and make the additional assumption that the primary production (r_e) declines exponentially due to some major astronomic, geological, or climatical perturbation. Let this decline be

$$d \ln r_e / dt = -\xi \quad (16.1)$$

where ξ is a positive constant. As the decline in production is induced by abiotic factors it occurs in astronomical time and, thus, to connect the process of selection in the consumer organism to this decline we need to specify the evolutionary process in astronomical time also. The rate of evolution in body mass is then given as the rate defined by eqn 14.2, divided by the lifespan, i.e., as

$$d \ln w / dt = \sigma_{\ln w}^2 [(\psi \gamma_l / \gamma) \ln(\rho \alpha r_e / w) - 1] / T \quad (16.2)$$

where $\rho = p / \gamma_e B$.

The trajectory described by eqn 16.2 reflects direct selection on body mass, and at the steady state this trajectory is defined also by the relation in time between the body mass and the evolutionary increase in α and the environmental decline in r_e . Let us approximate these relations by the two power functions $\alpha_t \propto w_t^a$ and $r_{e,t} \propto w_t^e$, where the exponents a and e are unknown. Then, $\alpha_t r_{e,t} \propto w_t^{a+e}$ and, thus, $w_t \propto (\alpha_t r_{e,t})^{1/(a+e)}$. From this expression we find that $\ln w_t \propto (\ln \alpha_t + \ln r_{e,t}) / (a + e)$ and, thus, that

$$\frac{d \ln w}{dt} = \left(\frac{d \ln \alpha}{dt} + \frac{d \ln r_e}{dt} \right) \frac{1}{a + e} \quad (16.3)$$

From eqn 14.1 it is apparent that $d \ln \alpha / dt = \sigma_{\ln \alpha}^2 / T$, and from eqn 16.1 that $d \ln r_e / dt = -\xi$. When these two expressions are inserted into eqn 16.3 we find that

$$\frac{d \ln w}{dt} = \frac{\sigma_{\ln \alpha}^2 - \xi T}{T(a + e)} \quad (16.4)$$

We now have the two independent expressions (eqns 16.2 and 16.4) that define the rate of evolution in body mass at steady state. By setting the two rates equal to one another, and by following the procedure for eqn 14.5, we find that the steady state is characterised by

$$\begin{aligned} w_t^{*s} &= \rho \alpha_t r_{e,t} e^{-[1 + (\sigma_{\ln \alpha}^2 - \xi T_t) / \sigma_{\ln w}^2 (a + e)] \gamma / \gamma_l \psi} \\ \iota_t^{*s} &= [1 + (\sigma_{\ln \alpha}^2 - \xi T_t) / \sigma_{\ln w}^2 (a + e)] / \psi \\ \left(\lim_{w_i \rightarrow w} \partial x_i^* / \partial \ln w_i \right)_t^{*s} &= (\sigma_{\ln \alpha}^2 - \xi T_t) / \sigma_{\ln w}^2 (a + e) \end{aligned}$$

$$\begin{aligned}
(d \ln w / dt)_t^{*s} &= (\sigma_{\ln \alpha}^2 / T_t - \xi) / (a + e) \\
(d \ln \alpha / dt)_t^{*s} &= \sigma_{\ln \alpha}^2 / T_t \\
(d \ln r_e / dt)^{*s} &= -\xi
\end{aligned}
\tag{16.5}$$

If we compare these equations with the steady state in a stable environment (eqn 14.5) it is apparent that both the level of interference and the selection gradient are smaller when the resource is declining than when it is stable, and that the body mass is larger for given values of r_e and α . We also notice that, when lifespan is positively related to body mass, then the rate of evolution in body mass is inversely related to body mass. For example, if the relation between lifespan and body mass is $T = \tau w^c$, with $\tau > 0$ and $c > 0$, then the organisms that are smaller than $\sqrt[c]{\sigma_{\ln \alpha}^2 / \tau \xi}$ will increase in size, while the organisms that are larger will dwarf.

Dwarfing is often observed in the fossil record. For example, in the last interglacial isolated red deer became reduced to one-sixth of their body weight in less than six thousand years (Lister, 1989). Moreover, there is an indirect way to test whether dwarfing in the fossil record has occurred by the action of selection due to density dependent competitive interactions. This is because selection by competitive interactions associates body mass increase with a high level of intra-population interference competition while it associates dwarfing with a low level of interference competition. This implies that there is a differentiated selection pressure on the size of the morphological traits that are used as social weaponry: When the organism increases in size there is a high level of interference competition and it will pay to allocate a relatively large amount of energy to social weaponry, but this energy is more or less wasted when the organism is dwarfing because, then there is only a low level of interference competition. In resemblance with this pattern we have Guthrie's (1984:262) conclusion from the fossil record: "Related to this dwarfing was a decrease in size of antlers, tusks, horns, and other social weaponry."

16.2 Allometric disorder

From Chapter 13 we recall that the deduction of the exponents of the body mass allometries is based on the occurrence of a body mass invariant level of interference competition. Moreover, we have previously shown that this condition was fulfilled both at the evolutionary equilibrium and at the evolutionary steady state in a stable environment. However, when the primary production is declining we find that this assumption no longer is fulfilled. This is because eqn 16.5 predicts that the level of interference is negatively related to lifespan, and because lifespan is expected to be positively related to body mass. Thus, we expect that the level of interference is negatively re-

lated to body mass. So in conclusion, we do not expect that the body mass exponents we deduced in Chapter 13 will apply to systems with a declining primary production. Instead, in this situation there seems to be no simple allometric solution to the life-history patterns among mobile organisms.

This disorder may be temperately only. To see this we note that even during an environmental crisis it seems to be reasonable to assume that lifespan is related positively to the body mass as $T_t = \tau w_t^c$ with $c > 0$. Then, from eqn 16.5, we find that the body mass will increase when $\xi < \sigma_{\ln \alpha}^2/T$, and this will cause an increase in lifespan and, consequently, we find that $\sigma_{\ln \alpha}^2/T \rightarrow \xi$. In comparison, when $\xi > \sigma_{\ln \alpha}^2/T$ we have that the body mass will decline and, thus, we find again that $\sigma_{\ln \alpha}^2/T \rightarrow \xi$. Then, as $\sigma_{\ln \alpha}^2/T$ will converge to ξ , by eqn 16.5, we find that the steady state will converge toward

$$\begin{aligned}
 w_t^{*s} \rightarrow w^{**} &= \rho \alpha_t r_{e,t} e^{-\gamma/\gamma_t \psi} & (16.6) \\
 \iota_t^{*s} \rightarrow \iota^{**} &= 1/\psi \\
 \left(\lim_{w_i \rightarrow w} \partial x_i^* / \partial \ln w_i \right)_t^{*s} &\rightarrow \left(\lim_{w_i \rightarrow w} \partial x_i^* / \partial \ln w_i \right)^{**} = 0 \\
 (d \ln w / dt)_t^{*s} \rightarrow (d \ln w / dt)^{**} &= 0 \\
 (d \ln \alpha / dt)_t^{*s} &\rightarrow \xi \\
 (d \ln r_e / dt)^{*s} &= -\xi
 \end{aligned}$$

This implies that we may expect that the body mass will stabilise at an equilibrium value that is maintained because the evolutionary increase in α is balanced against the exponential decline in r_e so that the product $\alpha_t r_{e,t}$ and the amount of resource consumed per individual, remains constant. For this steady state we note the body mass is independent of the initial body mass being defined only by the initial values of α and r_e . Furthermore, the selection gradient on body mass is zero and the level of interference resembles the level at the evolutionary equilibrium. Therefore, the level of interference is body mass invariant and, consequently, the well-known body mass allometries are reestablished.

16.3 Deterministic back-folding of biological systems

The predictions given by eqns 16.5 and 16.6 are expected to apply only during perturbations that are so short that there are no constraints on the exploitation efficiency. On longer perspectives, the exponential increase in the exploitation efficiency is likely to cease, and this is because of constraints on the magnitude of α in environments with extremely limited resources.

In such instances we expect that the decline in the genetic variance in $\ln \alpha$, which here is described by eqn 14.11, is functionally related to the primary production as indicated by the relation

$$\sigma_{\ln \alpha}^2 = \sigma_{\ln \alpha, 0}^2 e^{-h\alpha/r_e} \quad (16.7)$$

According to this expression we have that $\sigma_{\ln \alpha} \rightarrow 0$ when $r_e \rightarrow 0$, and this implies that the ultimate steady state is characterised as

$$\begin{aligned} w_t^{*s} &= \rho \alpha_t r_{e,t} e^{-[1 - \xi T_t / \sigma_{\ln w}^2 (a+e)] \gamma / \gamma_t \psi} \\ \iota_t^{*s} &= [1 - \xi T_t / \sigma_{\ln w}^2 (a+e)] / \psi \\ \left(\lim_{w_i \rightarrow w} \partial x_i^* / \partial \ln w_i \right)_t^{*s} &= -\xi T_t / \sigma_{\ln w}^2 (a+e) \\ (d \ln w / dt)_t^{*s} &= -\xi / (a+e) \\ (d \ln \alpha / dt)_t^{*s} &= 0 \\ (d \ln r_e / dt)_t^{*s} &= -\xi \end{aligned} \quad (16.8)$$

From this expression we find that the level of interference will eventually be both body mass and time dependent and, thus, the well-known exponents to the body mass allometries will be invalid too. By eqn 16.8 we also expect that the body masses of all species will eventually decline if the primary production continues to do so.

The equations we have developed in this chapter consider only the body mass component of competitive quality, but their conclusions also apply to most of the other energy requiring traits that distinguish the complex organisms of today from simple self-replicating entities. This means that a continuous decline in the influx of energy to the biological system is expected to cause a deterministic back-folding, where complex organisms generally evolve toward the origin of life. This process is opposite to the evolutionary and deterministic unfolding that occurs in a stable environment with a sufficiently high influx of energy, and this result suggests that the evolutionary process is reversible, with the actual direction being defined by environmental conditions.

16.4 Why did mammals persist when dinosaurs became extinct?

When an organism dwarfs, selection allocates energy from body mass to numerical reproduction in the sense that an average individual can produce progressively more offspring from the same amount of resource. This implies that dwarfing will promote the persistence of a species, and this is because it can prevent a severe decline in the rate of reproduction when the

primary production continues to decline. But, if the decline in the primary production occurs too fast, then the allocation of energy from body mass to reproduction will be so slow that dwarfing cannot prevent that the reproductive rate will decline below the limit leading to extinction. Moreover, as evolution by natural selection is delayed with one generation, it is especially the larger species with the longer lifespans that are most severely affected by a decline in the primary production and, thus, it is predominantly these organisms that will go extinct.

In order to describe the different effects that an environmental perturbation will have on species that differ in body mass, let us recall from Chapter 14 that the per generation selection gradient on \ln body mass is $4/3$, or $6/5$, at the evolutionary steady state of organisms foraging in respectively two or three spatial dimensions, that it is zero at the evolutionary equilibrium, and that it is minus one at the limit of extinction. As it is shown below, this implies that the degree to which a species is affected by a decline in the primary production can be described by the magnitude of a downward change in the selection gradient from $4/3$ or $6/5$: where a selection gradient of $4/3$ or $6/5$ defines a healthy population in a stable environment, where progressively smaller gradients define progressively more perturbed populations, and where a gradient of approximately minus one defines a population that is so disturbed that it is about to become extinct.

In order to describe the different effects that an environmental perturbation will have on the selection gradient of species with different body masses we need a few simplifying assumptions, and this is because the steady state during an environmental crisis is not so clearly defined as the steady state in a stable environment. As indicated by eqns 16.5, 16.6, and 16.8 there are at least three different types of steady state to choose among, and let us choose the steady state defined by eqn 16.5, because this is the state we expect immediately posterior to the transition from a stable environment to a situation with an exponentially declining primary production. Just prior to this transition the environment is stable, the body mass allometries are valid, and by the prediction of eqn 14.7 there is reason to believe that $\sigma_{\ln \alpha}^2 \approx \sigma_{\ln w}^2$ for many species. If these conditions hold, then, for an organism foraging in two dimensions we have that $a = 3/4$, $e = 0$, and that $T = \tau w^{1/4}$. Thus, the selection gradient in eqn 16.5 is

$$\lim_{w_i \rightarrow w} \partial x_i^* / \partial \ln w_i = 4/3 - \dot{\xi}(w^{*s})^{1/4} \quad (16.9)$$

on a per generation time scale where $\dot{\xi} = 4\xi\tau/3\sigma_{\ln w}^2$ is a positive constant. From this expression we note that the selection gradient is negatively related to both the rate of decline in primary production (ξ in $\dot{\xi}$) and to the average body mass (w^{*s}). As dwarfing occurs when the selection gradient is negative, we find from eqn 16.9 that it occurs only among the species

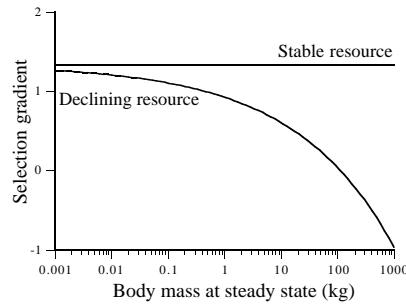


Fig. 16.1 The selection gradient for \ln body mass against the average body mass at the steady state for a stable and an exponentially declining primary production (resource). The rate of decline is so high that it causes the extinction of the animals larger than one ton.

that are larger than $w^{*s} > (4/3\dot{\xi})^4$ and, as a selection gradient of minus one represents the limit of extinction, we find that the species that are larger than $w^{*s} > (7/3\dot{\xi})^4$ become extinct. In Fig. 16.1 I have illustrated the situation where it is the species heavier than ≈ 110 kg that dwarf, and it is the species heavier than one ton that become extinct. This predicted association between dwarfing and extinction that eliminate predominantly the larger species is well-known from the fossil record (e.g., Martin and Klein, 1984; Barnosky, 1989; McKinney, 1990; Guthrie, 1984; King and Saunders, 1984). It is thus not surprising that it was the dinosaurs and not the mammals that became extinct during the perturbation at the end of the Cretaceous.