

Epilogue

Chapter 25

Summary

EMBEDDED in most of the traditional models in theoretical evolutionary ecology there is the assumption that we can explain natural patterns by disregarding the effects of interactions among competing individuals. Throughout this book I have tested this classical hypothesis against the contrasting hypothesis that many of the large scale patterns in nature are explained explicitly by the density dependent competitive interactions that exist among the individuals in populations. In this final chapter I will summarise my study and conclude upon the results obtained.

The major part of this book was on evolutionary biology. In relation to this subject the test on the importance of competitive interactions was conducted as a test between the classical theory of evolution, which disregards competitive interactions (reviewed by Roff, 1992; Stearns, 1992; Charnov, 1993; Bulmer, 1994; Charlesworth, 1994), and the theory of Malthusian relativity I developed from selection by density dependent competitive interactions. The test between these two theories of evolution was based on the concept of all-dimensional optima, in abbreviation, ADO (Section 9.2.2). This concept is the hypothesis that the predictions, or optima, of a successful theory of evolution need to be evolutionarily stable in all the phenotypic dimensions included explicitly in the theory. That is to say that when we explain the evolution of certain traits, then we need to make no assumptions with respect to the evolutionary determinants of the other traits.

In this chapter the tests between the proposed and the classical theory of evolution are summarised in the three sections 25.2 to 25.4. In Section 25.2 I deal with the evolution of basic traits like body mass, population abundance, and rate of reproduction, and I also consider the evolution of the body mass allometries. Then in Section 25.3 I focus on the evolutionary steady state that incorporates directionality into the evolutionary process. Having then explained that organisms increase in size, I deal in Section 25.4 with the

evolutionary transitions associated with the transition from a negligible to a relatively large organism. In Section 25.5 I change the topic in order to summarise the population dynamic consequences of selection by density dependent competitive interactions. But first, I deal with the effects of competitive interactions in the traditional framework of theoretical ecology that disregards evolutionary changes.

25.1 Traditional theoretical ecology

The traditional approach to theoretical ecology is based on the population dynamic theory that arose from Malthus' (1798) notion that all living organisms have the potential to increase geometrically in numbers. Malthus inferred that such increase is transient, occurring only up to the limit of the resource where lack of food will prevent further increase. In 1838 this regulation was formulated into the logistic equation by Verhulst to provide a description of the growth curve of a single population. In the early 1920s Lotka and Volterra extended the theory to incorporate interactions among competing species and between predators and their prey. By that time the classical theory had matured to the framework that provides the background for the description of ecology today.

This theory is generally based on the assumption that it is the exploitation of the resource that is essential for a proper description of the patterns in natural communities. In the most simple case, with a single population on a single resource, this idea is present in Lack's hypothesis that the population is resource regulated so that the equilibrium density is the carrying capacity, which is the number of individuals the resource can sustain. This idea is based on the simplifying assumption that the foraging individuals do not encounter one another. In the realistic case, the individuals do encounter one another, the population is both resource and interference regulated, and the equilibrium density is always lower than the carrying capacity.

25.1.1 Food chains

Lack's hypothesis of resource regulation by exploitative competition is contained implicitly in the predator-prey equations developed by Lotka (1925) and Volterra (1926) in order to explain the cyclic dynamics in natural populations. As it was pointed out by Arditi and Ginzburg (1989) the equilibria of these equations fail to explain the proportional relation that exists between the primary production and the biomass at all trophic levels in natural food chains. Instead, the equations predict a proportional response only at some trophic levels, whereas the biomass at other levels is inde-

pendent or even inversely related to the primary production. To avoid this paradox Arditi and Ginzburg introduced ratio-dependent models where the functional response of the predator depends upon the predator-prey ratio instead of being dependent only on the prey density as it is the case in the traditional equations. The rationale behind the ratio-dependent response is that it results from the fact that the time scale of foraging often is faster than the time scale of population dynamics, or that it results from interactions among predators that divide up the resource before they consume it. In Chapter 5 we saw that the proportional response is obtained also if we add the regulatory component of intra-population interference competition to the original Lotka-Volterra equations.

25.1.2 Competitive coexistence

The hypothesis of resource regulation also underlies the traditional studies on the assembly of competing species. This field has been dominated by the Volterra-Gause principle that states that competitive exclusion inevitably takes place among species that occupy similar niches. Since it is virtually impossible to show that two species have truly overlapping niches the Volterra-Gause principle is basically impossible to falsify empirically. This is because a falsification would require that we found two coexisting species with completely overlapping niches. However, as it was shown by Schoener (1976) and as it is illustrated in Chapter 6, it is easy to show theoretically that the Volterra-Gause principle represents only a special case, because it is based on an implicit assumption of pure exploitative competition. When the regulatory effects of intra-specific interference is added to the equations it is no longer a problem to have many species that coexist in a single niche. Furthermore, it turns out that Hutchinson's rule, that two strongly competing species can coexist if their weight ratio is larger than two, follows from the regularities by which inter-specific interference partitions the resource among competing species.

25.2 Evolution of basic traits

Basic traits are traits that all organisms have, and these traits can be traced back to the self-replicating molecules at the origin of life. Among other things, basic traits include self-replication (reproduction), the population abundance, the size (body mass), and the energy metabolised by an individual. The evolutionary modulation of the quantitative values of these traits can generally be seen as the evolution of the balance by which the energy available per individual is allocated between numerical replication and traits like body mass and metabolic rate. In the following three subsec-

tions I describe this balance in respectively the dimensions of body mass, population abundance, and rate of reproduction. Then, in the fourth subsection I consider the body mass allometries that describe the across-species relationships between the different traits.

25.2.1 Body mass

According to the classical explanation of Roff (1981) a large body mass evolves from the within-species proportionality that often exists between reproduction and body mass. As shown in Chapter 10, this hypothesis is falsified by evidence because it is based on an assumption of constant relative fitnesses: Constant relative fitnesses imply that the fitness profile (i.e., the relative fitness of the i 'th variant in a population as a function of the mass of that variant) is similar to the selection profile (i.e., the relative fitness of the average variant as a function of the mass of that variant). This implies that if the classical hypothesis holds, then the selection pressure on body mass is given by the across-species relation between the intrinsic growth rate and body mass. Across natural species with large body masses the intrinsic growth rate is proportional to the $-1/4$ th power of body mass (Fenchel, 1974). Thus, the classical framework predicts the evolution of negligible body masses, and this is paradoxical because this prediction is estimated from the occurrence of organisms with large body masses. Due to this paradox the relative fitnesses are relative and not constant, as it is assumed in the classical theory.

From this result it is evident that the two major assumptions behind the classical theory on the evolution of body mass need some modifications before we can construct a model that is consistent with the patterns that exist both within and across species. First of all, the proportional relation between reproduction and body mass is inappropriate as an assumption, because the relation has evolved by natural selection, and thus it does not represent an evolutionary constraint. If instead, the proportional relation is exchanged with an inverse relation, then the relation between reproduction and body mass will reflect the evolutionary constraint defined by the physical constraint that the energy allocated to reproduction can be used only once. Then, by turning to the hypothesis of evolution by density dependent competitive interactions the second assumption of constant relative fitnesses is also avoided. As shown in Chapter 10, in this framework large body masses can evolve by the density dependence in the number of competitive interactions and the relation that large-bodied individuals can dominate small-bodied individuals during competitive encounters.

The body masses evolving by density dependent competitive interactions behave in resemblance to general observations. For example, they are inversely related to the rate of mortality, as it is observed in guppies (Reznick

et al., 1996). And they are positively related to the production in the resource, which is in agreement with the observations made by McNab (1971) and Geist (1986) in relation to Bergmann's rule. This rule was originally meant to cause thermal homeostasis, but now it is seen to reflect the duration of the productivity pulse in the resource. The predicted body masses also behave in resemblance to the island rule (Foster, 1964), which describes that large animals generally are smaller on islands than on mainlands, while small animals tend to be larger.

25.2.2 Population limitation

The classical approach with Fisherian selection and exploitative competition generally fails to explain the evolution of a population equilibrium that is limited so that the resource is not over-exploited. This is because Fisher's fundamental theorem of natural selection predicts that the equilibrium continues to increase while the resource becomes progressively more over-exploited.

This straightforward prediction is not in resemblance to empirical evidence where terrestrial herbivores often eat less than 10% of the edible plant biomass. To avoid this paradox Hairston et al. (1960) developed, and Hairston and Hairston (1993) elaborated, the influential argument that it is the inter-specific predator-prey interactions that maintain nature in a state of balance, where over-exploitation does not occur. Here, the essential argument is that the predators will eat the herbivores and with fewer herbivores the herb is no longer over-exploited. However, this argument holds only in the absence of evolutionary changes. With Fisherian selection the density of at least one species in the food chain is expected to increase in an uncontrolled manner. It is thus very understandable that Wynne-Edwards (1962, 1986, 1993) continues to argue that group selection is a necessity in order to explain the balance of nature, i.e., in order to explain the existence of balanced population densities.

Group selection is, though, not a necessity. As shown in Chapter 11, this is because balanced population equilibria are predicted by the type of individual selection that arises from density dependent competitive interactions. These equilibria are balanced in the sense that the equilibrium densities are the densities where the density dependent bias in the within-population access to resource is balanced against the intrinsic trade-off between the demographic traits and competitive quality. This theoretically deduced balance includes the well established empirical relations that the densities at all trophic levels are proportional to the primary production, that poikilotherm vertebrates are ≈ 30 times more abundant than homoiotherm vertebrates, that the population density is proportional to the $-3/4$ th power of body mass, and that the exploitation of the resource is body mass

invariant.

These balanced equilibria behave distinctively different from the equilibria in the classical theory of population dynamics. Population limitation in the classical theory is based on the concept that a limiting factor is any factor that when changed causes a change in either reproduction, survival, and/or density regulation. Among other things, this implies that an environmentally induced change in reproduction and/or survival is converted directly into a change in the population equilibrium. For example, if we begin to remove individuals at a constant rate from the population the equilibrium density will decline. This is not the case under the hypothesis of density dependent competitive interactions where, as a first approximation, the evolutionarily determined population equilibrium is invariant with respect to environmentally induced changes in reproduction and/or survival. This means that if we begin to remove individuals at a constant rate from the population, then the equilibrium density will remain the same. The reason for this is that, after the evolutionary equilibration has occurred, the energy taken from the population by the removal of individuals is taken from the body mass and the metabolic rate instead of being taken from the equilibrium density, as held in classical theory.

25.2.3 Reproduction

The classical theory on the evolution of the reproductive rate is based on Lack's clutch size, which is the idea that the optimal rate of reproduction is the rate where most offspring survive. According to this hypothesis the reproductive rate is a derived trait that evolves from a more fundamental trade-off that exists between reproduction and offspring, or parent, survival. This hypothesis has been confirmed on a local scale where demographic models are fitted to the empirical evidence within species.

In Chapter 12 it was shown that Lack's clutch size fails as a theory on the evolution of a limited rate of reproduction. This is because the fundamental theorem of natural selection predicts a continuous increase in the intrinsic growth rate, and because the evident solution to this problem is a continuous increase in the rate of reproduction. More specifically, the continuous increase in reproduction occurs because the trade-offs between reproduction and survival are part of the phenotype so that selection operates not only on the rate of reproduction, but also upon the trade-offs. When this is the case, it follows from the classical framework that the absolute values of the trade-offs continue to decline generating a continuous increase in the reproductive rate.

This classical prediction of unlimited reproduction is in contrast to the prediction from the hypothesis of selection by density dependent competitive interactions. In this latter situation a limited rate of reproduction will evolve

because fitness no longer is equivalent to the intrinsic growth rate. Instead, when the level of interference competition is high, a large variant with low intrinsic reproduction may easily out-reproduce a small variant with high intrinsic reproduction, and this is because the large variant has access to more resource than the small variant. If instead, the level of interference is low, then the two variants have access to approximately the same amount of resource and it is the small variant with the highest intrinsic growth rate that will out-reproduce the large variant.

In general, selection by density dependent competitive interactions implies that reproduction is balanced in accordance with the ecological constraints that determine the within-species bias in the access to resource. This balance implies that poikilotherm vertebrates reproduce at a higher rate than homoiotherm vertebrates, that the intrinsic rate of reproduction is positively related to the primary production, that it is negatively related to the size of the resource quanta for which the individuals compete, and that it is balanced against the extrinsic level of mortality. These predictions are generally confirmed by empirical evidence.

When a limited growth rate has evolved by density dependent competitive interactions it follows that the selection procedure underlying Lack's clutch size is consistent with the new prediction. This consistency is intuitively sound because, irrespective of the evolutionary optimum to the intrinsic growth rate, we always expect that selection will optimise reproduction against mortality. Only in relation to the original proposal of Lack, that it is the reproductive rate that evolves from the trade-off between reproduction and survival, the causality is changed around so that it is the absolute value of the trade-off that evolves from the optimal growth rate given by ecological constraints. Also, the new prediction is evolutionarily stable while Lack's prediction is evolutionarily unstable.

25.2.4 Body mass allometries

During this century the major life-histories across natural species have been empirically established as allometric relations describing the various traits as power functions of body mass. These relations are now reviewed in books by Calder (1984), Peters (1983) and Reiss (1989), and it is generally agreed that the rounded exponents of the allometric relations are $3/4$ for the metabolic rate, $1/4$ for lifespan, $1/4$ for the level of social behaviour, $-1/4$ for the intrinsic growth rate, $-3/4$ for the population density, 1 for the home-range area, 0 for the resource consumed by a population, and 0 for maximal lifetime reproduction. While a number of explanations have been proposed for these relations it is generally agreed that no single one is convincing.

However, in Chapter 13 I showed that the empirically estimated exponents are explained by the ecological constraints associated with a foraging process that is optimised by natural selection. The essential constraints are the number of competitive encounters per individual and foraging self-inhibition, i.e., the degree to which the exploitation of an individual inhibits the foraging of that individual. The regulation of the foraging efficiency by these two processes are counteractive so that there is an intermediate optimum from which it is possible to deduce the allometric exponents. According to this deduction the 1/4th and 3/4th exponents apply to organisms foraging in two dimensions, whereas the expected exponents are 1/6 and 5/6 among organisms that forage in three dimensions. The two-dimensional exponents are confirmed by terrestrial organisms while the three-dimensional exponents generally apply to pelagic organisms.

25.3 Evolutionary steady state

These results suggest that selection by density dependent competitive interactions is essential, but they do not suggest that evolution is directional. This conclusion depends on the assumption that the per individual exploitation efficiency is fixed, an assumption that does not hold because an individual will generally do better if it has more resource, or energy, available.

In Chapter 14 I showed that when selection operates on the exploitation efficiency, then the evolutionary process in a stable environment will equilibrate at an evolutionary steady state where both the exploitation efficiency and the body mass increase exponentially, while the other phenotypic traits evolve in concordance with the exponents of the body mass allometries. Among other things, this implies that Fisherian fitness continues to decline, a result that is diametrically opposite to Fisher's fundamental theorem that predicts a steady increase.

On empirical grounds the continuous increase in body mass is confirmed by Cope's law, which suggests that the majority of phylogenetic lineages tend to increase in size during their history in the fossil record. Another observation, explained by the steady state, is the within-population proportionality between reproduction and body mass. You will recall that it was this relation that was used together with Fisherian selection to explain the evolution of a large body mass in the classical theory. Under the hypothesis of selection by competitive interactions, it is instead the relation between reproduction and body mass that evolves from the evolutionary setting of the selection gradient on body mass, a gradient that is given by the ecological constraints at the evolutionary steady state. As both the ability to

metabolise energy into competitive interactions and the ability to perform complex behavioural interactions are crucial components for the outcome of a competitive encounter both of these traits are expected to increase exponentially at the steady state, just like the body mass. In relation to this general increase in competitive quality it is possible to estimate the evolutionary changes in the metabolic rate by examining the evolutionary trajectory in body mass. This is possible because the shape of the trajectory in body mass reflects the time scaling between the evolutionary process and astronomical time, and because this time scaling depends upon the generation time that is inversely related to the metabolic rate. In Chapter 15 I applied this framework to MacFadden's data on fossil horses and found that, when the metabolic rate is corrected for the allometric relation to body mass, then the metabolic rate of horses is ≈ 10 times larger today than it was 57 million years ago. This estimate implies also that the 25 kg horse 57 million years ago had a lifespan of ≈ 90 years, given that the lifespan of the 500 kg horse of today is ≈ 20 years.

The prediction of a steady increase in competitive quality depends upon the assumptions that the abiotic and biotic factors extrinsic to the population are constant, and that there is no immediate limit to the exploitation efficiency. When instead the exploitation efficiency reaches its upper limit, the body mass will cease to increase, and this levelling-off will occur at lower masses on smaller resources. Hence, we may expect a variety of body masses among natural organisms. Also, if the resource evolves to be less edible, or if competitive interactions with competitively superior individuals from other species causes a decline in the access to resource, then the increase in body mass might even reverse to a decline. Inter-specific interactions and environmental variation may then explain why there always seems to be some organisms that decline in size.

The increase in competitive quality also depends on a sufficiently high influx of energy to the overall biological system. As shown in Chapter 16, when the influx of energy begins to decline there can be a mass extinction that will eliminate predominantly the larger species, while the remaining species will tend to dwarf in size. From the fossil record we know that widespread dwarfing tends to co-occur with events of mass extinction, and that mass extinctions tend to eliminate predominantly the larger species. Finally, if the influx of energy continues to decline and the physical conditions remain suitable for life then most, if not all, species are expected to dwarf until they reach the molecular level. So, in conclusion, the evolutionary process is expected to be reversible with the particular direction being defined by environmental conditions.

25.4 Evolution of derived traits

From the predictions of the evolutionary steady state we expect that a self-replicating molecule in a stable environment with a large resource automatically evolves toward a large-bodied organism with life-histories in accordance with known body mass allometries. Then, from empirical evidence we know that the transition from a negligible to a large body mass is associated with the evolution of a set of derived traits that, among other things, include senescence, males, sexual reproduction, and a diploid genome. The crucial thing is then to show theoretically that the transition to a large body mass is associated with the evolutionary emergence of these derived traits.

As the derived traits tend to be associated with an increase in competitive quality their evolution can be explained by selection due to density dependent competitive interactions. Under this hypothesis, the fitness gained through interference competition is proportional to the number of competitive encounters per individual per unit time and, thus, the evolutionary development of the derived traits is positively related to the level of intra-population interference. This implies that it is essential to show theoretically that the level of intra-population interference associated with a negligible body mass is so low that the derived traits do not evolve in these organisms, and to show theoretically that the level of interference associated with a large body mass is exactly so high that the derived traits will evolve to the level of expression known from large-bodied organisms. In the following three subsections I will summarise how this is possible in relation to respectively the evolution of senescence, the evolution of males and sex ratios, and the evolution of sexual reproduction and a diploid or haplodiploid genome. In the fourth subsection I will turn to the evolution of eusocial colonies and their associated traits, and summarise how these systems can evolve from a body mass that is evolutionarily constrained relative to the exploitation efficiency.

25.4.1 Senescence and soma

To explain the evolution of senescence and soma in mobile organisms we need to explain both why senescence and soma are absent in negligibly sized organisms, like prokaryotes and viruses, and why they are present in large-bodied organisms, like the higher eukaryotes.

The theory on the evolution of senescence reaches back to Weismann (1889), and it was mainly Medawar (1952) and Williams (1957) that developed the traditional view that senescence is a derived trait that evolves from a somatic tissue from which no part is passed on in either sexual or asexual reproduction. This hypothesis coincides with the presence of senescence in the large-bodied eukaryotes that have a soma, and its absence in

the small-bodied prokaryotes that have no soma. This theory does, though, fail on a global scale because it does not explain why the higher eukaryotes have evolved a soma, when prokaryotes have not.

The alternative hypothesis, I developed in Chapter 17, is that the soma is the trait through which senescence is expressed. This hypothesis is based on the notion that senescence cannot evolve without a clear separation between a senescing somatic tissue and a non-senescing reproductive tissue. Senescence and soma can then evolve when it is beneficial to allocate energy from self-repair in the non-reproductive tissue to other processes that can enhance early reproduction and/or survival.

Under the hypothesis of selection by density dependent competitive interactions, the energy that is not used for self-repair can be used to enhance the competitive quality. When this is the case it turns out that the theoretically deduced level of interference in negligibly sized organisms is so low that senescence and a soma are unlikely to evolve, and that the deduced level of interference in large-bodied organisms is so high that senescence and a soma evolve.

25.4.2 Males and sex ratios

To explain the evolution of males and sex ratios we need, among other things, to explain why males are absent in negligibly sized organisms like prokaryotes and viruses, and why there often is one male per female in large-bodied mobile organisms like the mobile higher eukaryotes.

It was Fisher (1930) who developed the classical hypothesis that an even sex ratio is a derived trait that evolves because an average individual of the rare sex is expected to leave more offspring than an average individual of the common sex. This result depends on the assumptions of sexual reproduction between males and females, a diploid or a haplodiploid genome, and random mating at the population level. Hamilton (1967) extended the theory, and showed that the sex ratio will be female biased if mating is local, in the sense that the sons of a single, or related, female/s compete/s with one another for a limited number of matings.

This classical, or Fisherian, sex ratio theory makes sense on a local scale, but it fails on an evolutionary scale because the cost to sexual reproduction implies that the classical sex ratio equilibria are evolutionarily unstable in the assumptions that underlie those equilibria. Traditionally, it has been assumed that sexual reproduction is two-fold costly, but this holds only in a few special cases. More generally, sexual reproduction between a male and a female is four-fold costly, and this is because it is both the male individual and the meiotic division of the genome into haploid gametes that are two-fold costly. The problems with the Fisherian sex ratios then are, (*i*) that the two-fold cost of the male selects for an extreme degree of local mating

and a sex ratio that is biased to the limit where males do not exist, and (ii) that the two-fold cost of meiosis selects for a haploid genome, asexual reproduction, and the absence of males, at least if hermaphrodites are not allowed. If instead, hermaphrodites are allowed, then there may be selection for hermaphrodites, and this is because they have the potential to bypass the four-fold cost of sex. This is possible because hermaphrodites contain no male individuals and because they contribute to reproduction through both the male and the female function. But, in either case, the Fisherian sex ratio theory fails to explain the evolutionary maintenance of sex ratios in mobile organisms with males and females.

If we disregard the classical sex ratio theory, then, under the hypothesis of evolution by density dependent competitive interactions, males can easily evolve by individual selection despite their two-fold cost. This is because the male can invest both energy and time in competitive quality, instead of using it on physiological self-replication as it is done by the female. In this sense the male individual gains fitness not only through sexual reproduction, but also from interference competition where he can prevent that the asexual variant has access to the resource. Hereby the sexual variant can out-reproduce the asexual variant, despite the fact that the sexual variant has the lowest intrinsic growth rate.

In this scenario the number of males per female will depend upon the level of interference in the population. If the level of interference is high, it pays to invest in the competitive quality of the male so that it is optimal to be in relatively large groups containing many males and only a few females. If, on the other hand, the level of interference is low, competitive quality tends to be wasted so that it pays to invest in the female component of numerical replication, generating a female biased sex ratio. The essential point is then to show that the theoretically deduced level of interference will explain the sex ratio patterns that exist among natural species.

From the theoretical deductions in relation to the evolution of body mass, it turns out that the level of interference in negligibly sized organisms, like prokaryotes and viruses, is so low that males cannot evolve. This is in contrast to the deduced level of interference at the evolutionary equilibrium in large-bodied organisms that is exactly so high that the optimal number of males per female is one. Finally, at the evolutionary steady state the deduced number of males per female is approximately two. As shown in Chapter 22, this latter prediction depends upon the assumption that the interfering individuals are males. If, on the other hand, they are allowed also to be the offspring of the female, then the optimal solution is cooperative breeding between a pair and a single offspring. This form of reproduction is widespread in birds and mammals.

Unlike the Fisherian sex ratios, the sex ratios that are predicted by

competitive interactions do not depend upon the presence of sexual reproduction and, therefore, they are also independent of the ploidy level of the genome and of the degree of local mating. However, if we assume sexual reproduction and a diploid, or a haplodiploid, genome, then the two sex ratio theories can be integrated with one another, and it can be shown that the original equilibrium relations will evolve, including the relationship between the degree of female bias and the degree of local mating. The essential differences between the new and the original form of this prediction is (*i*) that the original prediction is evolutionarily unstable while the new prediction is evolutionarily stable, and (*ii*) that the evolutionary causality is turned upside down. This suggests that it is the degree of local mating that evolves from the sex ratio, and not the other way around as it originally was proposed by Hamilton.

In many cases males differ from females, e.g., in the size or by the presence of male characters that may include physiological ornaments or a colourful plumage. Traditionally, these differences between females and males have been explained by sexual selection where females choose the large or the more extravagant males. These differences between the two sexes may, however, evolve also by interference competition for other resources than females. According to this latter hypothesis there is a general trend where males tend to be larger than females in species with male biased sex ratios, while the reverse is expected when the sex ratio is female biased. This trend is widespread among natural species where birds and mammals tend to have male biased sex ratios and males that are larger than females, while the reverse often is the case in lower organisms, like insects and other invertebrates.

With respect to male characters there is a difference in the expected pattern depending upon whether they evolve by interference competition for resources or by female choice and sexual selection. If they evolve by interference competition for resources, then, as it was shown in Chapter 20, we expect that they will evolve in many instances when there is overlap between the breeding site and the area in which the organism forages, but only in few instances when there is no overlap between the breeding site and the foraging area. This is in contrast to the situation with female choice where we expect no such differentiation. Bird species generally conform to the situation with interference competition for resources suggesting that female choice for extravagant males is a secondary trait that evolves because it is these males that can supply the females with the largest amount of resource. In other words, it seems that it is female choice and sexual selection that evolve from the presence of male characters, and not the other way around as it traditionally has been thought ever since Darwin introduced the concept of sexual selection.

According to the hypothesis of density dependent competitive interactions this change is not the only major change in the role played by sexual selection. According to the original proposal by Darwin, and all subsequent treatments, sexual selection is seen as the link explaining the non-sexual differences between females and males from the assumption of sexual reproduction. However, as illustrated in the following section, under the hypothesis of competitive interactions sexual selection is the link that explains the evolution of sexual reproduction from the functional differences between males and females. Once again, it seems that the dependent and the independent variables need to be changed around.

25.4.3 Sexual reproduction and ploidy level

To explain the evolution of sexual reproduction we need to explain why sexual reproduction is absent in negligibly sized organisms, like prokaryotes and viruses, why it generally exists among hermaphrodites in sessile organisms, and why it generally exists between males and females in large-bodied mobile organisms. Also, we need to explain why the optimal solution to sexual reproduction is a diploid, or haplodiploid, genome with a meiotic division into haploid gametes.

The problem with sexual reproduction is that the two-fold cost of meiosis selects for a haploid genome and asexual reproduction when sexual reproduction occurs between males and females. In contrast, there is no real paradox associated with the maintenance of sexual reproduction in hermaphrodites, and this is because these species have the potential to avoid both the two-fold cost of the male and the two-fold cost of meiosis. In other words, the difficult task is to explain why we have sexual reproduction between males and females in the large-bodied mobile organisms.

Although at least twenty different theories have been proposed to account for the evolution of sexual reproduction, the case with sexual reproduction in the large-bodied mobile organisms has remained probably the largest paradox in evolutionary biology. A common feature to nearly all the proposed models is that they are based on the idea that genetic diversity is beneficial to the organism per se and, thus, a diploid organism with sexual reproduction is expected to be more fit than a haploid organism with no sex, simply because the diploid organism is genetically more diverse. These hypotheses will, however, not explain the evolution of the male individual at the cost of hermaphrodites, and this is because, even in the presence of genetic variation, the male is still four-fold costly when he is compared with the hermaphrodite. Also, the traditional models will generally not explain why the natural solution to the problem of genetic diversity should be exactly a diploid, or haplodiploid, genome with haploid gametes. In Chapter 21 I was aiming at a more complete solution that could explain

the general patterns associated with sexual reproduction, i.e., a model that could explain why sexual reproduction in natural species takes the particular form with a diploid, or a haplodiploid, genome with haploid gametes, why it generally occurs only in large-bodied organisms and, finally, why in these organisms it generally occurs between males and females when the organism is mobile, while it generally occurs among hermaphrodites when the organism is sessile.

In order to obtain this goal I focused on the hypothesis of evolution by density dependent competitive interactions, where the existence of males and females has been explained independently of the existence of sexual reproduction. In this scenario sexual reproduction can evolve because a pair that contains a female and a male has a higher competitive quality than a lonely female and a pair that contains two females. This implies that it is favourable for the female to attract an unrelated male, and she can do this by sexual reproduction where she can increase the male's fitness by transferring some fraction of his genome to her offspring.

Generally, we expect that the females will choose the males that are competitively superior to other males, and that the competitively superior males will dominate the inferior males in order to choose the females that transfer the largest fraction of their genome on to the offspring. Under this set-up it turns out that, if the body mass is negligible, then the theoretically deduced level of interference is so low that sexual reproduction will not evolve. If instead, the body mass is large and in evolutionary equilibrium, then the deduced level of interference is exactly so high that the female's genome will replicate at the fastest rate when the offspring receives half of its genes from the mother and the other half from a single father. An obvious solution to this mode of sexual inheritance is the form known from diploid organisms, where the diploid offspring receives one set of chromosomes from its mother and an other set from its father, or the form known from haplodiploid organisms, where the diploid female transfers haploid gametes to both daughters and sons, while the haploid male transfers a haploid gamete only to daughters.

The model behind these results is valid only in mobile organisms because it depends upon the implicit assumption that the male can help the female during competitive encounters. This is not the case in sessile organisms where the sessility implies that if a male competes for a female, then he competes also against her. This implies that sessile males are energetically costly, and that the evolutionary optimum to sexual reproduction is hermaphroditic individuals. Moreover, as males generally are absent in sessile organisms there is no male choice to prevent that asexual reproduction and self-fertilization evolve in order to enhance the intrinsic growth rate of the hermaphrodite. Not surprisingly, among sexual organisms, asexual

reproduction and self-fertilization are common in sessile organisms while these traits are rare to absent among mobile organisms.

25.4.4 Eusocial colonies

A eusocial colony is characterised by a large worker caste, and eusociality is known mainly from social insects, where it occurs in one form in ants and bees, and in another form in termites. These two forms of eusociality are characterised by two different sets of co-occurring traits: In ants and bees the queen forms the colony on her own after she has mated with a sexual male, the genome is haplodiploid, the workers are the sterile daughters of the queen, and there are typically three queens per sexual male. In termites the queen forms the colony together with the king, the genome is diploid, the workers are the sterile daughters and sons of the queen, and there typically is one king per queen. Hence, when we explain the evolution of eusociality, it is essential to explain also the evolution of these two patterns of co-occurring traits.

According to the traditional view introduced by Hamilton (1964, 1972), eusocial colonies evolve by kin selection where the sterile workers gain inclusive fitness through the sexual reproduction of their queen. This hypothesis depends on the assumption that the workers are constrained to be the offspring of the queen. If instead, the workers were allowed also be the sexual partners of the queen, then the degree of kin selection is reflected by the proportion of the workers that are offspring workers. In this case eusocial colonies can evolve independently of kin selection when there are no offspring workers. Hence, in order to explain that kin selection is operating in eusocial species, it is essential to relax the assumption of kin selection and show that selection in eusocial species favours offspring workers at the cost of sexual workers.

From Chapter 22 we have that when the assumption of kin selection is relaxed and the workers are allowed to be both offspring and sexual males, then it turns out that the optimal worker caste contains only offspring workers. This is because it is at this limit that each gene in each individual in the colony has the highest probability of being copied to a sexual offspring of the queen. Hence, it seems that it is kin selection that evolves from, and/or is maintained by, eusociality, and not the other way around as it was originally proposed by Hamilton.

As kin selection is not the ultimate cause of the evolution of eusocial colonies they must evolve by other means. According to the hypothesis of selection by density dependent competitive interactions eusocial colonies will evolve when the body mass is upward constrained and there is plenty of resource. This is because, then the energy that cannot be allocated to body mass is selected into reproduction instead, and this results in increased

interference and selection for large groups that can dominate small groups. These groups reach their evolutionary optimum when they contain many interfering individuals (workers), and only a few or a single reproductive females (queens). This result may explain why eusociality is relatively common in insects, where the ecto-skeleton might set an upper limit to the body mass, and why eusociality is almost absent in vertebrates, where the body mass seems to be evolutionarily more flexible.

In relation to the sex ratio in the sexuals produced by a eusocial colony it is likely that it is controlled by the workers because they are numerically far superior to the queen. It was Trivers and Hare (1976) who combined this observation with the genomic selection of the Fisherian sex ratio theory in order to develop the classical explanation of the evolution of the sex ratio in eusocial species. According to this explanation the sex ratio is the derived trait that evolves from the relatedness between the workers and the sexual offspring produced by the queen. This implies that the predicted sex ratio of three queens per sexual male in ants and bees depends upon the assumptions that the genome is haplodiploid and that the workers are the daughters of the queen. Likewise, the prediction of an even sex ratio in termites is the result of the diploid genome.

If we disregard this classical causality on the evolution of sex ratios, then it is possible to relax the traditional assumptions and let both the ploidy level of the genome and the sex ratio in the workers evolve by selection, just like the sex ratio in the sexuals. This is possible because individual selection on the sex ratio in the sexuals dominates over the Fisherian form of genomic selection. This implies that if, as it is the case in ants and bees, the queen establishes the colony on her own, then the two-fold cost of the male selects for a female biased sex ratio. When this prediction is combined with an extended model on Fisherian sex ratios, it turns out that the individual selection on the sex ratio in the sexuals imposes selection on both the ploidy level of the genome and the sex ratio in the worker caste. As shown in Chapter 22, the evolutionary equilibrium of this system is a haplodiploid genome and a worker caste containing only female offspring, i.e., an equilibrium that coincides with the pattern in ants and bees. In this system, the sex ratio in the sexuals is three queens per male at the limit where the force of individual selection is completely diluted by the spread of genes in the population. If instead, the population is substructured and individual selection operates more independently of genomic selection, then the sex ratio in the sexuals will be more female biased.

In the case of termites the situation is different because the sexual male stays with the queen. This implies a constraint of pair formation that induces individual selection for an even sex ratio in the sexuals. When this result is coupled to genomic selection on the ploidy level of the genome, and

to genomic selection on the sex ratio in the worker caste, then it turns out that the evolutionary equilibrium is a diploid genome and a worker caste containing both female and male offspring. In this latter case the sex ratio in the sexuals is always even because an even sex ratio is the equilibrium at the level of both genomic and individual selection.

25.5 Evolutionary population dynamics

The predictions in the previous sections are based on the assumption that the population is in dynamic equilibrium. When this is not the case the population shows dynamic behaviour, and this tends to be inherently cyclic in natural populations. This is unlike the classical theory where population dynamics is inherently non-cyclic, unless there is some sort of delayed regulation caused by over-compensation or by interactions with other species.

Although over-compensatory dynamics have been found in animals as diverse as ungulates and insects, it is now generally agreed that over-compensation cannot explain the general tendency for cyclic dynamics. This is because the single species models, which can over-compensate due to the action of direct density dependence, generally do not explain the observed dynamics, and because the models that may explain the dynamics are based on delayed density regulation, lacking a firm mechanism that can explain why the delay occurs.

At first, these limitations to the single species models in the classical theory suggests that most population cycles are caused by predator-prey interactions in their broadest definition, which includes herb-herbivore and host-parasitoid interactions. However, this hypothesis has always been associated with the problem that many populations apparently continue to cycle even in the absence of the essential interactions. This appears to be the case with *Daphnia*, lemmings, and snow-shoe hares, and with the larch budmoth that has the best documented cycle in forest insects. Due to these limitations it remains questionable whether the mechanisms in the classical theory of population dynamics are sufficient in order to explain the periodic dynamics in natural species.

One obvious limitation to the mechanisms in the classical theory of population dynamics is that they are based on the assumption of no evolutionary changes. I relaxed this assumption in Chapter 24, where I developed a logistic equation based on selection by density dependent competitive interactions. The major result was that the density dependent selection extended the classical theory so that the dynamics of a single species become inherently cyclic, taking a period that coincides with the periods in the forest insects with cyclic dynamics. In other words, we do no longer have to incorporate interactions with other species in order to explain the

cyclic dynamics that occur in natural populations.

According to the action of selection by density dependent competitive interactions the cyclic changes in the population densities are associated with a cycle in the phenotype that, among other things, includes the intrinsic growth rate, the body mass, and the sex ratio. Cyclic changes in body mass have been observed among the *Daphnia* and lemmings that show cyclic dynamics, and evidence suggests that the phenotypic cycle in lemmings also includes the sex ratio and the intrinsic growth rate.

25.6 Conclusion

We have now gone through the major dimensions of the organism, and in nearly all instances obtained the result that the equilibria or predictions in the classical theory are evolutionarily unstable in their phenotypic assumptions. Moreover, we have established a new theory based on a single ADO model that contains nearly all the classical equilibria, only in a new form. The major differences between the new and the classical versions of these equilibria are: (i) that the new versions are evolutionarily stable because they generally do not depend upon phenotypic components that are evolutionarily unstable, and (ii) that the propagation of the selection pressure through the population generally is in opposite directions in the two theories. In the classical theory the propagation is “inside-out” in the sense that it generally is the intrinsic constraints of the genomic and phenotypic systems that determine the selection pressure at higher phenotypic levels. In the proposed theory the propagation is “outside-in” in the sense that it generally is the selection pressure of interference competition that can explain the evolutionary optimum of the major phenotypic dimensions. It is this overall evolutionary optimum together with its behaviour in relation to its position on the major evolutionary trajectory that is the general theory of evolution I propose.

References

- Abrams, P.A. 1989. The importance of intraspecific frequency-dependent selection in modelling competitive coevolution. *Evol. Ecol.* 3:215-220.
- Abrams, P.A. 1994. The fallacies of "ratio-dependent" predation. *Ecology* 75:1842-1850.
- Abrams, P.A. and Matsuda, H. 1994. The evolution of traits that determine ability in competitive contests. *Evol. Ecol.* 8:667-686.
- Adam, K.D., King, C.M. and Köhler, W.H. 1993. Potential ecological effects of escaped transgenic animals: lessons from past biological invasions. In K. Wöhrmann and J. Tomiuk, eds., *Transgenic Organisms*, Birkhäuser Verlag, Basel, pp. 153-173.
- Akçakaya, H.R. 1992. Population cycles of mammals: evidence for a ratio-dependent predation hypothesis. *Ecol. Monogr.* 62:119-142.
- Akçakaya, H.R., Arditi, R. and Ginzburg, L.R. 1995. Ratio-dependent predation: an abstraction that works. *Ecology* 76:995-1004.
- Akçakaya, H.R., Ginzburg, L.R., Slice, D. and Slobodkin, L.B. 1988. The theory of population dynamics-II. Physiological delays. *Bull. Math. Biol.* 50:503-515.
- Alexander, R.D. 1974. The evolution of social behavior. *Ann. Rev. Ecol. Syst.* 4:325-384.
- Anders, E., Shearer, C.K., Papike, J.J., Bell, F.J., Clemett, S.J., Zare, R.N., McKay, D.S., Thomas-Keptra, K.L., Romanek, C.S., Gibson, E.K. Jr., and Vali, H. 1997. Evaluating the evidence for past life on Mars. *Science* 274:2119-2125.
- Anderson, W.W. 1971. Genetic equilibrium and population growth under density-regulated selection. *Am. Nat.* 105:489-498.
- Andersson, M.B. 1994. *Sexual selection*. Princeton University Press, Princeton.
- Andersson, M.B. and Iwasa, Y. 1996. Sexual selection. *Trends. Ecol. Evol.* 11:53-58.
- Arditi, R. and Ginzburg, L.R. 1989. Coupling in predator-prey dynamics: Ratio-dependence. *J. theor. Biol.* 139:311-326.
- Arditi, R., Ginzburg, L.R. and Akçakaya, H.R. 1991. Variation in plankton densities among lakes: a case for ratio-dependent predation models. *Am. Nat.* 138:1287-1296.
- Arditi, R., Ginzburg, L.R. and Perrin, N. 1992. Scale invariance is a reasonable approximation in predation models - reply to Ruxton and Gurney. *Oikos* 65:-

- 336-337.
- Armitage, K.B. 1981. Sociality as a life-history tactic of ground squirrels. *Oecologia* 48:36-49.
- Baltensweiler, W. and Fischlin, A. 1988. The larch budmoth in the alps. In A.A. Berryman, ed., *Dynamics of forest insect populations. Patterns, causes, implications*, Plenum Press, New York, pp. 331-351.
- Banse, K. 1976. Rates of growth, respiration, and photosynthesis of unicellular algae as related to cell size - a review. *J. Phycolgy.* 12:135-140.
- Barbour, D.A. 1990. Synchronous fluctuations in spatially separated populations of cyclic forest insects. In A.D. Watt, S.R. Leather, M.D. Hunter and N.A.C. Kidd, eds., *Population dynamics of forest insects*, Intercept, Andover, Hampshire, pp. 339-346.
- Barnosky, A.D. 1989. The late Pleistocene event as a paradigm for wide spread-mammal extinction. In S.K. Donovan, ed., *Mass extinctions. Processes and evidence*, Columbia University Press, New York, pp. 235-254.
- Bartholomew, G.A. and Casey, T.M. 1978. Oxygen consumption of moths during rest, pre-flight warm up, and flight in relation to body size and wing morphology. *J. Exp. Biol.* 76:11-25.
- Bartholomew, G.A. and Tucker, V.A. 1964. Size, body temperature, thermal conductance, oxygen consumption, and heart rate in Australian varanid lizards. *Physiol. Zool.* 27:341-354.
- Batzli, G.O. 1981. Populations and energetics of small mammals in the tundra ecosystem. In L.C. Bliss, O.W. Heal and J.J. More, eds., *Tundra ecosystems: a comparative analysis*, Cambridge University Press, Cambridge, pp. 377-396.
- Beck, L. 1971. Bodenzoologische gliederung und charakterisierung des amazonischen regenswaldes. *Amazoniana* 3:69-132.
- Beckwith, S.V.W. and Sargent, A.I. 1996. Circumstellar disks and the search for neighbouring planetary systems. *Nature* 383:139-144.
- Begon, M., Harper, J.L. and Townsend, C.R. 1990. *Ecology. Individuals, populations and communities*. Blackwell Scientific Publications, Boston.
- Bejer, B. 1988. The nun moth in european spruce forests. In A.A. Berryman, ed., *Dynamics of forest insect populations. Patterns, causes, implications*, Plenum Press, New York, pp. 211-231.
- Bell, G. 1987. (Review of) Evolution through group selection. V.C. Wynne-Edwards. *Heredity* 59:147-147.
- Bennett, A.F. and Dawson, W.R. 1976. Metabolism. In V.C. Gans and W.R. Dawson, eds., *Biology of the Reptilia. Vol. V*, Academic Press, New York, pp. 127-223.
- Bergmann, C. 1847. Über die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Grösse. *Göttinger Studien* Pt. 1:595-708.
- Berryman, A.A. 1978. Population cycles of the douglasfir tussock moth (*Lepidoptera: Lymantriidae*): the time-delay hypothesis. *Can. Entomol.* 188:775-789.
- Berryman, A.A. 1995. Population cycles: a critique of the maternal and allometric hypotheses. *J. Anim. Ecol.* 64:290-293.

- Berryman, A.A. 1996. What causes population cycles of forest Lepidoptera? *Trends. Ecol. Evol.* 11:28-32.
- Berryman, A.A. (ed.). 1988. *Dynamics of Forest Insect Populations: Patterns, Causes, Implications*. Plenum Press, New York.
- Berryman, A.A., Gutierrez, A.P. and Arditi, R. 1995. Credible, parsimonious and useful predator-prey models—A reply to Abrams, Gleeson, and Sarnelle. *Ecology* 76:1980-1985.
- Berryman, A.A., Stenseth, N.C. and Isaev, A.S. 1987. Natural regulation of herbivorous forest insect populations. *Oecologia (Berl.)* 71:174-184.
- Berthelsen, E. 1951. *The ceratioid fishes. Ontogeny, taxonomy, distribution and biology*. Dana-Report No. 39. Carlsberg Foundation, Copenhagen.
- Bjørnstad, O.N., Falck, W. and Stenseth, N.C. 1996. A geographic gradient in small rodent density fluctuations: a statistical modelling approach. *Proc. R. Soc. Lond. B.* 262:127-133.
- Black, D. 1996. Looking for the twilight zone. *Nature* 381:474-475.
- Blum, J.J. 1977. On the geometry of four-dimensions and the relationship between metabolism and body mass. *J. theor. Biol.* 64:599-601.
- Bonner, J.T. 1965. *Size and cycle*. Princeton University Press, Princeton.
- Boomsma, J.J. 1989. Sex-investment ratios in ants: Has female bias been systematically overestimated? *Am. Nat.* 133:517-532.
- Boonstra, R. and Krebs, C.J. 1979. Viability of large- and small-sized adults in fluctuating vole populations. *Ecology* 60:567-573.
- Bowers, M.A. and Brown, J.H. 1982. Body size and coexistence in desert rodents: chance or community structure? *Ecology* 63:391-400.
- Boyce, M.S. and Perrins, C.M. 1987. Optimizing great tit clutch size in a fluctuating environment. *Ecology* 68:142-153.
- Bristowe, W.S. 1929. The mating habits of spiders, with special reference to the problems surrounding sex dimorphism. *Proc. Zool. Soc. Lond.* 21:309-358.
- Brody, S. 1945. *Bioenergetics and growth*. Hafner, New York.
- Brown, J.H., Marquet, P.A. and Taper, M.L. 1993. Evolution of body size: Consequences of an energetic definition of fitness. *Am. Nat.* 142:573-584.
- Brown, J.H. and Maurer, B.A. 1986. Body size, ecological dominance and Cope's rule. *Nature* 324:248-250.
- Brown, J.S. and Vincent, T.L. 1987. Coevolution as an evolutionary game. *Evolution* 41:66-79.
- Bryant, M. 1988. Lifetime reproductive success of house martin. In T.H. Clutton-Brock, ed., *Reproductive success. Studies of individual variation in contrasting breeding systems*, University of Chicago Press, Chicago, pp. 173-188.
- Bulmer, M.J. 1974. A statistical analysis of the 10-year cycle in Canada. *J. Anim. Ecol.* 43:701-718.
- Bulmer, M. 1994. *Theoretical evolutionary ecology*. Sinauer Associates Publishers, Massachusetts.
- Buss, L.W. 1987. *The evolution of individuality*. Princeton University Press, Princeton.

- Calder, W.A. III. 1974. Consequences of body size for avian energetics. In R.A. Paynter, ed., *Avian Energetics*, Nuttall Ornithological Club, Cambridge, pp. 86-151.
- Calder, W.A. III. 1983. An allometric approach to population cycles of mammals. *J. theor. Biol.* 100:275-282.
- Calder, W.A. III. 1984. *Size, function, and life history*. Harvard University Press, Cambridge.
- Case, T.J. 1979. Optimal body size and an animal's diet. *Acta Biotheor.* 28:54-69.
- Caswell, H. 1989a. *Matrix population models*. Sinauer, Sunderland, Massachusetts.
- Caswell, H. 1989b. Life-history strategies. In J.M. Cherrett, ed., *Ecological concepts. The contribution of ecology to an understanding of the natural world*, Blackwell Scientific Publications, Oxford, pp. 285-307.
- Charlesworth, B. 1994. *Evolution in age-structured populations. 2nd ed.* Cambridge University Press, Cambridge.
- Charnov, E.L. 1978. Sex-ratio selection in eusocial hymenoptera. *Am. Nat.* 112:317-326.
- Charnov, E.L. 1982. *The theory of sex allocation*. Princeton University Press, Princeton.
- Charnov, E.L. 1993. *Life history invariants. Some explorations of symmetry in evolutionary ecology*. Oxford University Press, New York.
- Charnov, E.L. 1995. A note on dimensionless life histories for birds versus mammals. *Evol. Ecol.* 9:288-291.
- Chesson, P.L. and Warner, R.R. 1981. Environmental variability promotes coexistence in lottery competitive systems. *Am. Nat.* 117:923-943.
- Chesson, P. 1991. A need for niches? *Trends Ecol. Evol.* 6:26-28.
- Chitty, D. 1960. Population processes in the voles and their relevance to general theory. *Can. J. Zool.* 38:99-113.
- Clarke, B. 1972. Density-dependent selection. *Am. Nat.* 106:1-13.
- Clarke, J.M. and Maynard Smith, J. 1961a. Independence of temperature of the rate of aging in *Drosophila subobscura*. *Nature* 190:1027-1028.
- Clarke, J.M. and Maynard Smith, J. 1961b. Two phases of aging in *Drosophila subobscura*. *J. Exp. Biol.* 38:679-684.
- Cody, M. 1974. *Competition and the structure of Bird Communities*. Princeton University Press, Princeton.
- Cosmides, L.M. and Tooby, J. 1981. Cytoplasmic inheritance and intragenomic conflict. *J. theor. Biol.* 89:83-129.
- Costantino, R.F., Cushing, J.M., Dennis, B. and Desharnais, R.A. 1995. Experimentally induced transitions in the dynamic behavior of insect populations. *Nature* 375:227-230.
- Cope, E.D. 1887. *The origin of the fittest*. D. Appleton and Co, New York.
- Cowan, I.M. 1947. The timber wolf in the Rocky Mountain National Parks of Canada. *Can. J. Res.* 25:139-174.
- Cramp, S. 1985, 1988, & 1992. *Handbook of the birds of Europe the middle east and north africa. The birds of the western palearctic. Vol. IV-VI*. Oxford

- University Press, Oxford.
- Cramp, S. and Perrins, C.M. 1993. *Handbook of the birds of Europe the middle east and north africa. The birds of the western palearctic. Vol VII.* Oxford University Press, Oxford.
- Cramp, S. and Simmons, K.E.L. 1977, 1980, & 1983. *Handbook of the birds of Europe the middle east and north africa. The birds of the western palearctic. Vol I-III.* Oxford University Press, Oxford.
- Crespi, B.J. 1992. Eusociality in Australian gall thrips. *Nature* 359:724-726.
- Crozier, R.H. and Pamilo, P. 1996. *Evolution of social insect colonies. Sex allocation and kin selection.* Oxford University Press, Oxford.
- Cuellar, O. 1977. Animal parthenogenesis. A new evolutionary-ecological model is needed. *Science* 144:837-843.
- Currie, D.J. and Fritz, J.T. 1993. Global patterns of animal abundance and species energy use. *Oikos* 67:56-68.
- Dahlsten, D.L., Rowney, D.L., Copper, W.A., Tait, S.M., and Wenz, J.M. 1990. Long-term population studies of the douglas-fir tussock moth in California In A.D. Watt, S.R. Leather, M.D. Hunter and N.A.C. Kidd, eds., *Population dynamics of forest insects*, Intercept, Andover, Hampshire, pp. 45-58.
- Damuth, J. 1981. Population density and body size in mammals. *Nature* 290:699-700.
- Damuth, J. 1987. Interspecific allometry of population density in mammals and other animals: the independence of body mass and population energy-use. *Biol. J. Linnean Society.* 31:193-246.
- Darwin, C. 1859. *The origin of species.* John Murray, London.
- Darwin, C. 1871. *The descent of Man, and selection in relation to sex.* John Murray, London.
- Darwin, C. 1958. *The autobiography of Charles Darwin. Ed. Barlow, N.* Collins, London.
- Darwin, F. 1888. *The life and letters of Charles Darwin.* Murray, London.
- Day, T. and Taylor, P.D. 1996. Evolutionarily stable versus fitness maximizing life histories under frequency-dependent selection. *Proc. R. Soc. Lond. B.* 263:333-338.
- Dekker, H. 1975. A simple mathematical model of rodent population cycles. *J. Math. Biol.* 2:57-67.
- del Hoyo, J., Elliott, A. and Sargatal, J. eds. 1992. *Handbook of the birds of the world. Vol. 1.* Lynx Edicions, Barcelona.
- Depéret, C. 1909. *The transformation of the animal world.* D. Appleton and Co, New York.
- Desharnais, R.A. and Liu, L. 1987. Stable demographic limit cycles in laboratory populations of *Tribolium castaneum*. *J. Anim. Ecol.* 56:885-906.
- De Vita, J. 1979. Mechanisms of interference and foraging among colonies of the harvesting ant *Pogonomyrmex californicus* in the Mojave Desert. *Ecology* 60:729-737.
- Diamond, J.M. 1973. Distributional ecology of New Guinea birds. *Science* 179:759-769.

- Diamond, J.M. 1975. Assembly of species communities. In M.L. Cody and J.M. Diamond, eds., *Ecology and evolution of communities*, Harvard University Press, Cambridge, pp. 342-344.
- Donovan, S.K. (ed.). 1989. *Mass extinctions: Processes and evidence*. Columbia University Press, New York.
- Duffy, J.E. 1996. Eusociality in a coral-reef shrimp. *Nature* 381:512-514.
- Ebert, D. and Hamilton, W.D. 1996. Sex against virulence: the coevolution of parasitic diseases. *Trends Ecol. Evol.* 11:79-82.
- Elgar, M.A. and Pierce, N.E. 1988. Mating success and fecundity in an ant-tended lycaenid butterfly. In T.H. Clutton-Brock, ed., *Reproductive success. Studies of individual variation in contrasting breeding systems*, University of Chicago Press, Chicago, pp. 59-75.
- Elton, C. 1927. *Animal Ecology*. Sidgwick & Jackson, London.
- Emlen, J.M. 1970. Age specificity and ecological theory. *Ecology* 51:588-601.
- Emmons, L.H. 1980. Ecology and resource partitioning among nine species of African rain forest squirrels. *Ecol. Monogr.* 50:31-54.
- Feder, M.E. 1976. Oxygen consumption and body temperature in neotropical and temperature zone lungless salamanders (*Amphibia: Plethodontidae*). *J. Comp. Physiol.* 110:197-208.
- Fenchel, T. 1974. Intrinsic rate of natural increase: The relationship with body size. *Oecologia (Berl.)* 14:317-326.
- Fisher, R.A. 1930. *The genetical theory of natural selection*. Dover publisher, Inc., New York.
- Fittkau, E.J. and Klinge, H. 1973. On biomass and trophic structure of the central Amazonian rain forest ecosystem. *Biotropica* 5:2-14.
- Foster, J.B. 1964. The evolution of mammals on islands. *Nature* 202:234-235.
- Fry, C.H., Fry, K. and Harris, A. 1992. *Kingfishers, bee-eaters & rollers. A handbook*. Princeton University Press, Princeton.
- Gadgil, M. and Bossert, P.W. 1970. Life-historical consequences of natural selection. *Am. Nat.* 104:1-24.
- Garland, T. 1983. Scaling the ecological cost of transport to body mass in terrestrial mammals. *Am. Nat.* 121:571-587.
- Gause, G.F. 1934. *The struggle for existence*. Williams and Wilkins, Baltimore.
- Geist, V. 1986. Bergmann's rule is invalid. *Can. J. Zool.* 65:1035-1038.
- Gerritsen, J. 1984. Size efficiency reconsidered: a general foraging model for free swimming aquatic animals. *Am. Nat.* 123:450-467.
- Ghiselin, M. 1974. *The economy of nature and the evolution of sex*. University of California Press, Berkeley.
- Ginzburg, L.R. 1992. Evolutionary consequences of basic growth equations. *Trends Ecol. Evol.* 7:133.
- Ginzburg, L.R. and Akçakaya, H.R. 1992. Consequences of ratio-dependent predation for steady-state properties of ecosystems. *Ecology* 73:1536-1543.

- Ginzburg, L.R. and Taneyhill, D.E. 1994. Population cycles of forest Lepidoptera: a maternal effect hypothesis. *J. Anim. Ecol.* 63:79-92.
- Ginzburg, L.R. and Taneyhill, D.E. 1995. Higher growth rate implies shorter cycle, whatever the cause: a reply to Berryman. *J. Anim. Ecol.* 64:294-295.
- Gleeson, S.K. 1994. Density dependence is better than ratio dependence. *Ecology* 75:1834-1835.
- Godfray, H.C.J., Partridge, L. and Harvey, P.H. 1991. Clutch size. *Ann. Rev. Ecol. Syst.* 22:409-429.
- Godfrey, G.K. 1955. Observations on the nature of the decline in numbers of two *Microtus* populations. *J. Mamm.* 36:209-214.
- Gould, S.J. 1988. Trends as changes in variance: a new slant on progress and directionality in evolution. *J. Paleont.* 62:319-329.
- Gould, S.J. 1989. *Wonderful life*. Norton, New York.
- Gould, S.J. 1997. Cope's rule as psychological artefact. *Nature* 385:199-200.
- Graften, A. 1990. Sexual selection unhandicapped by the Fisher process. *J. theor. Biol.* 144:517-546.
- Greenstone, M.H. and Bennett, A.F. 1980. Foraging strategy and metabolic rate in spiders. *Ecology* 61:1255-1259.
- Guthrie, R.D. 1984. Mosaic, allelochemicals and nutrients. An ecological theory of late Pleistocene megafaunal extinctions. In P.S. Martin and R.G. Klein, eds., *Quaternary extinctions. A prehistoric revolution*, The University of Arizona Press, Tucson, pp. 259-298.
- Haigh, J. and Rose, M.R. 1980. Evolutionary game auctions. *J. theor. Biol.* 85:381-397.
- Hairston, N.G. Jr. and Hairston, N.G. Sr. 1993. Cause-effect relationships in energy flow, trophic structure, and interspecific interactions. *Am. Nat.* 142:379-411.
- Hairston, N.G. Sr., Smith, F.E. and Slobodkin, L.B. 1960. Community structure, population control, and competition. *Am. Nat.* 94:421-425.
- Hamilton, W.D. 1964. The genetical evolution of social behavior. *J. theor. Biol.* 7:1-52.
- Hamilton, W.D. 1966. The moulding of senescence by natural selection. *J. theor. Biol.* 12:12-45.
- Hamilton, W.D. 1967. Extraordinary sex ratios. *Science* 156:477-488.
- Hamilton, W.D. 1972. Altruism and related phenomena, mainly in social insects. *Ann. Rev. Ecol. Syst.* 3:193-232.
- Hamilton, W.D., Axelrod, R. and Tanese, R. 1990. Sexual reproduction as an adaptation to resist parasites. *Proc. Nat. Acad. Sci. USA* 87:3566-3573.
- Haldane, J.B.S. 1932. *The causes of evolution*. Longmans, London.
- Hanski, I. and Korpimäki, E. 1995. Microtine rodent dynamics in northern Europe: Parameterized models for the predator-prey interaction. *Ecology* 76:840-850.
- Hanski, I., Turchin, P., Korpimäki, E. and Henttonen, H. 1993. Population oscillations of boreal rodents: regulation by mustelid predators leads to chaos. *Nature* 364:232-235.

- Hansson, L. 1987. An interpretation of rodent dynamics as due to tropical interactions. *Oikos* 50:308-318.
- Hansson, L. and Henttonen, H. 1985. Gradients in density variations of small rodents: the importance of latitude and snow cover. *Oecologia (Berl.)* 67:394-402.
- Harestad, A.S. and Bunell, F.L. 1979. Home range and body weight - a re-evaluation. *Ecology* 60:389-402.
- Harrison, P. 1985. *Seabirds. An identification guide*. Croom & Helm Ltd, Beckenham.
- Hassell, M.P. and Anderson, R.M. 1989. Predator-prey and host-pathogen interactions. In J.M. Cherrett, ed., *Ecological concepts. The contribution of ecology to an understanding of the natural world*, Blackwell Scientific Publications, Oxford, pp. 147-196.
- Hassell, M.P., Lawton, J.H. and May, R.M. 1976. Patterns of dynamical behavior in single species populations. *J. Anim. Ecol.* 45:471-486.
- Heaney, L.R. 1978. Island area and body size of insular mammals: evidence from the tri-colored squirrel (*Callosciurus prevosti*) of Southeast Asia. *Evolution* 32:29-34.
- Herre, E.A. 1985. Sex ratio adjustment in fig wasps. *Science* 228:896-900.
- Heywood, J.S. 1989. Sexual selection by the handicap mechanism. *Evolution* 43:1387-1397.
- Hoelzer, G.A. 1989. The good parent process of sexual selection. *Aim. Behav.* 38:1067-1078.
- Holekamp, K.E. and Smale, L. 1995. Rapid change in offspring sex ratios after clan fission in the spotted hyena. *Am. Nat.* 145:261-278.
- Horn, H.S. and MacArthur, R.H. 1972. Competition among fugitive species in a harlequin environment. *Ecology* 53:749-752.
- Howell, A.B. 1923. Periodic fluctuations in the numbers of small mammals. *J. Mamm.* 4:149-155.
- Huffaker, C.B. 1958. Experimental studies on predation: dispersion factors and predator-prey oscillations. *Hilgardia* 27:343-383.
- Hunt, F. 1982. Regulation of population cycles by genetic feedback. Existence of period solutions of a mathematical model. *J. Math. Biol.* 13:271-282.
- Hurst, L.D. and Peck, J.R. 1996. Recent advances in understanding of the evolution and maintenance of sex. *Trends Ecol. Evol.* 11:46-52.
- Hutchinson, G.E. 1948. Circular causal systems in ecology. *Ann. N.Y. Acad. Sci.* 50:221-246.
- Hutchinson, G.E. 1959. Homage to Santa Rosalia, or why are there so many kinds of animals? *Am. Nat.* 93:145-159.
- Hutchinson, V.H., Whitford, W.G. and Kohl, M. 1968. Relation of body size and surface area to gas exchange in anurans. *Physiol. Zool.* 41:65-85.
- Hölldobler, B. and Wilson, E.O. 1990. *The ants*. Springer-Verlag, Berlin.
- Hörnfeldt, B. 1994. Delayed density dependence as a determinant of vole cycles. *Ecology* 73:791-806.

- Itô, Y. 1989. The evolutionary biology of sterile soldiers in Aphids. *Trends Ecol. Evol.* 4:69-73.
- Jablonski, D. 1995. Extinctions in the fossil record. In J.H. Lawton and R.M. May, eds., *Extinction rates*, Oxford University Press, Oxford, pp. 25-44.
- Jablonski, D. 1997. Body-size evolution in Cretaceous molluscs and the status of Cope's rule. *Nature* 385:250-252.
- Jarvis, J.U.M. 1981. Eusociality in a mammal: Cooperative breeding in naked mole-rat colonies. *Science* 212:571-573.
- Kaspari, M. and Vargo, E.L. 1995. Colony size as a buffer against seasonality: Bergmann's rule in social insects. *Am. Nat.* 145:610-632.
- Kayser, C. and Heusner, A. 1964. Etude comparative du métabolisme énergétique dans la série animale. *J. Physiol. (Paris)* 56:489-524.
- Keith, L.B. 1963. *Wildlife's ten year cycle*. University of Wisconsin Press, Madison.
- Kelsall, A.P. 1968. *The migratory barren-ground caribou of Canada*. Canadian Wildlife Service, Ottawa.
- Kerr, W.E. 1990. Why are workers in social hymenoptera not males? *Rev. Brasil. Genet.* 13:133-136.
- King, D.A. 1990. The adaptive significance of tree height. *Am. Nat.* 135:809-828.
- King, J.E. and Saunders, J.J. 1984. Environmental insularity and the extinction of the American mastodont. In P.S. Martin and R.G. Klein, eds., *Quaternary extinctions. A prehistoric revolution*, The University of Arizona Press, Tucson, pp. 315-344.
- Kirkpatrick, M. 1982. Sexual selection and the evolution of female choice. *Evolution* 36:1-12.
- Kirkwood, T.B.L. 1977. Evolution of ageing. *Nature* 270:301-304.
- Kirkwood, T.B.L. and Rose, M.R. 1991. Evolution of senescence: late survival sacrificed for reproduction. *Phil. Trans. R. Soc. Lond.* 332:15-24.
- Kleiber, M. 1932. Body and size and metabolism. *Hilgardia* 6:315-353.
- Klomp, H. 1970. The determination of clutch size in birds: a review. *Ardea* 58:1-124.
- Kolman, W. 1960. The mechanism of natural selection for the sex ratio. *Am. Nat.* 94:373-377.
- Kondrashov, A.S. 1982. Selection against harmful mutations in large sexual and asexual populations. *Genet. Res.* 40:325-332.
- Kondrashov, A.S. 1994. Sex and deleterious mutations. *Nature* 369:99-100.
- Konoplev, V.A., Sokolov, V.E. and Zotin, A.L. 1978. Criterion of orderliness and some problems of taxonomy. In I. Lamprecht and A.L. Zotin, eds., *Thermodynamics of Biological Processes*, deGruyter, Berlin, pp. 349-359.
- Krebs, C.J. 1978. A review of the Chitty hypothesis of population regulation. *Can. J. Zool.* 56:2464-2480.
- Krebs, C.J., Boutin, S., Boonstra, R., Sinclair, A.R.E., Smith, J.N.M., Dale, M.R.T., Martin, K., and Turkington, R. 1995. Impact of food and predation on the snowshoe hare cycle. *Science* 269:1112-1115.

- Krebs, C.J., Gaines, M.S., Keller, B.L., Myers, J.H., and Tamarin, R.H. 1973. Population cycles in small rodents. *Science* 179:35-41.
- Krukonis, G. and Schaffer, W.M. 1991. Population cycles in mammals and birds: does periodicity scale with body size? *J. theor. Biol.* 148:469-493.
- Kukuk, P.F., Eickwort, G.C., Raveret-Richter, M., Alexander, B., Gibson, R., Morse, R.A., and Ratnieks, F. 1989. Importance of the sting in the evolution of sociality in the hymenoptera. *Ann. Entomol. Soc. Am.* 82:1-5.
- Kurtén, B. 1953. On the variation and population dynamics of fossil and recent mammal populations. *Acta Zool. Fenn.* 76:1-122.
- LaBarbera, M. 1986. The evolution and ecology of body size. In D.M. Raup and D. Jablonski, eds., *Patterns and processes in the history of life*, Springer-Verlag, Berlin, pp. 69-98.
- Lack, D. 1947. The significance of clutch size. *Ibis* 89:302-352.
- Lack, D. 1954. *The natural regulation of animal numbers*. Oxford University Press, Oxford.
- Lack, D. 1966. *Population studies of birds*. Clarendon Press, Oxford.
- Lamarck, J.-B. 1809. *Philosophie zoologique*. Paris.
- Lande, R. 1976. Natural selection and random genetic drift in phenotypic evolution. *Evolution* 30:314-334.
- Lande, R. 1981. Models of speciation by sexual selection on polygenic traits. *Proc. Natl. Acad. Sci. USA* 78:3721-3725.
- Law, R. and Hutson, V. 1992. Intracellular symbionts and the evolution of uniparental cytoplasmic inheritance. *Proc. Roy. Soc. Lond.* 248:69-77.
- Lawlor, L.R. and Maynard Smith, J. 1976. The coevolution and stability of competing species. *Am. Nat.* 110:79-99.
- Levin, S.A. 1970. Community equilibria and stability, and an extension of the competitive exclusion principle. *Am. Nat.* 104:413-423.
- Lewin, R. 1983. Santa Rosalia was a goat. *Science* 221:636-639.
- Lister, A.M. 1989. Rapid dwarfing of red deer on Jersey in the Last Interglacial. *Nature* 342:539-543.
- Lockie, J.D. 1955. The breeding habits and food of short-eared owls after a vole plague. *Bird Study* 2:53-69.
- Lomolino, M. 1985. Body size of mammals on islands: the island rule reexamined. *Am. Nat.* 125:310-316.
- Lotka, A.J. 1925. *Elements of physical biology*. Williams and Wilkins, Baltimore.
- Lunberg, S. and Persson, L. 1993. Optimal body size and resource density. *J. theor. Biol.* 164:163-180.
- Lynch, M. 1984. Destabilizing hybridization, general-purpose genotype and geographic parthenogenesis. *Quart. Rev. Biol.* 59:257-290.
- MacArthur, R.H. 1962. Some generalized theorems of natural selection. *Proc. Natl. Acad. Sci. USA* 46:1893-1897.
- MacArthur, R. and Levins, R. 1967. The limiting similarity, convergence, and divergence of coexisting species. *Am. Nat.* 101:377-385.

- MacFadden, B.J. 1986. Fossil horses from "Eohippus" (Hyracotherium) to Equus: scaling, Cope's Law, and the evolution of body size. *Paleobiology* 12:355-369.
- Mäkela, A. 1985. Differential games in evolutionary theory: Height growth strategies of trees. *Theor. Pop. Biol.* 27:239-267.
- Manning, J.T. and Thompson, D.J. 1984. Muller's ratchet accumulation of favorable mutations. *Acta Biotheor.* 33:219-225.
- Malthus, T.R. 1798. *An essay on the principle of population*. Johnson, London.
- Martin, P.S. and Klein, R.G. (eds.). 1984. *Quaternary extinctions. A prehistoric revolution*. University of Arizona Press, Tucson, Arizona.
- Mathew, A.L. 1995. The niche concept revisited: mechanistic models and community context. *Ecology* 76:1371-1382.
- Matson, P.A. and Berryman, A.A., eds. 1992. Special feature: ratio-dependent predator-prey theory. *Ecology* 73:1539-1566.
- May, R.M. 1974. Biological populations with nonoverlapping generations: stable points, stable cycles and chaos. *Science* 186:645-647.
- May, R. and MacArthur, R. 1972. Niche overlap as a function of environmental variability. *Proc. Nat. Acad. Sci. USA* 69:1109-1113.
- Maynard Smith, J. 1958. The effects of temperature and of egg-laying on the longevity of *Drosophila subobscura*. *J. Exp. Biol.* 35:832-842.
- Maynard Smith, J. 1963. Temperature and the rate of aging in poikilotherms. *Nature* 199:400-402.
- Maynard Smith, J. 1964. Group selection and kin selection. *Nature* 201:1145-1147.
- Maynard Smith, J. 1971. The origin and maintenance of sex. In G.C. Williams, ed., *Group selection*, Aldine Atherton, Chicago, pp. 163-175.
- Maynard Smith, J. 1978. *The evolution of sex*. Cambridge University Press, Cambridge.
- Maynard Smith, J. 1982. *Evolution and the theory of games*. Cambridge University Press, Cambridge.
- Maynard Smith, J. and Brown, R.L.W. 1986. Competition and body size. *Theor. Pop. Biol.* 30:166-179.
- Maynard Smith, J. and Price, G.R. 1973. The logic of animal conflict. *Nature* 246:15-18.
- Maynard Smith, J. and Szathmáry, E. 1995. *The major transitions in evolution*. W.H. Freeman Spektrum, Oxford.
- Mayor, M. and Queloz, D. 1995. A Jupiter-mass companion to a solar-type star. *Nature* 378:355-359.
- Mayr, E. 1988. *Toward a new philosophy of biology. Observations of an evolutionist*. Harvard University Press, Cambridge.
- Mayr, E. 1991. *One long argument. Charles Darwin and the genesis of modern evolutionary theory*. Harvard University Press, Cambridge.
- McCarthy, M.A., Ginzburg, L.R. and Akçakaya, H.R. 1995. Predator interference across trophic chains. *Ecology* 76:1310-1319.
- McKay, D.S., Gibson Jr, E.K., Thomas-Keppta, K.L., Vali, H., Romanek, C.S., Clemett, S.J., Chillier, D.F., Maechling, C.R., and Zare, R.N. 1996. Search for past life on Mars: Possible relic biogenic activity in Martian meteorite

- ALH84001. *Science* 273:924-930.
- McKinney, M.L. 1990. Trends in body-size evolution. In K.J. McNamara, ed., *Evolutionary Trends*, The University of Arizona Press, Tucson, pp. 75-118.
- McLaren, I.A. 1966. Adaptive significance of large size and long life of the *Chaetognath sagitta elegans* in the Arctic. *Ecology* 47:852-855.
- McMahon, T.A. 1973. Size and shape in biology. *Science* 179:1201-1204.
- McMahon, T.A. 1975. Allometry and biomechanics: limb bones in adult ungulates. *Am. Nat.* 109:547-563.
- McNab, B.K. 1969. The economics of temperature regulation in neotropical bats. *Comp. Bioch. Physiol.* 32:227-348.
- McNab, B.K. 1971. On the ecological significance of Bergmann's rule. *Ecology* 52:845-854.
- McNab, B.K. 1994. Resource use and the survival of land and freshwater vertebrates on oceanic islands. *Am. Nat.* 144:643-660.
- Medawar, P.B. 1952. *An unsolved problem of biology*. Lewis, London.
- Metcalf, R.A. 1980. Sex ratio, parent-offspring conflict, and local competition for mates in the social wasps *Polistes metricus* and *Polistes variatus*. *Am. Nat.* 116:642-654.
- Michod, R.E. and Levin, B.R. 1988. *The evolution of sex*. Sinauer Ass. Inc. Publishers, Sunderland, Massachusetts.
- Mirmirani, M. and Oster, G. 1978. Competition, kin selection, and evolutionary stable strategies. *Theor. Pop. Biol.* 13:304-339.
- Moran, P.A.P. 1953. The statistical analysis of the Canadian lynx cycle. *Aust. J. Zool.* 1:163-173.
- Morris, R.F. 1959. Single-factor analysis in population dynamics. *Ecology* 40:580-588.
- Morris, R.F. 1964. The value of historical data in population research, with particular reference to *Hyphantria cunea drury*. *Can. Entomol.* 96:356-368.
- Muller, H.J. 1932. Some genetic aspects of sex. *Nature* 66:118-138.
- Murdoch, W.W. and McCauley, E. 1985. Three distinct types of dynamic behavior shown by a single planktonic system. *Nature* 316:628-630.
- Møller, A.P. 1994. *Sexual selection and the barn swallow*. Oxford University Press, New York.
- Naumov, S.P., Gibet, L.A. and Shatalova, S.P. 1969. Dynamics of sex ratio in respect to changes in numbers of mammals. *Zh. Obshch. Biol.* 30:673-680.
- Nee, S., Read, A.F., Greenwood, J.J.D. and Harvey, P.H. 1991. The relationship between abundance and body size in British birds. *Nature* 351:312-313.
- Newell, N.D. 1949. Phyletic size increase, an important trend illustrated by fossil invertebrates. *Evolution* 3:103-124.
- Nicholson, A.J. 1933. The balance of animal populations. *J. Anim. Ecol.* 2:132-178.
- Noirot, C. and Pasteels, J.M. 1987. Ontogenetic development and evolution of the worker caste in termites. *Experientia* 43:851-860.
- Nonacs, P. 1986. Ant reproductive strategies and sex allocation theory. *Quart. Rev. Biol.* 61:1-21.

- Nowak, R.M. 1991. *Walker's mammals of the world. 5th ed. Vol I-II.* The Johns Hopkins University Press, Baltimore.
- O'Donald, P. 1962. The theory of sexual selection. *Heredity* 17:541-552.
- O'Donald, P. 1980. *Genetic models of sexual selection.* Cambridge University Press, Cambridge.
- Oksanen, L., Moen, J. and Lundberg, P.A. 1992. The time-scale problem in exploiter-victim models: does the solution lie in ratio-dependent exploitation? *Am. Nat.* 140:938-960.
- Parker, G.A. 1979. Sexual selection and sexual conflict. In M.S. Blum and N.A. Blum, eds., *Sexual selection and reproductive competition in insects*, Academic Press, New York, pp. 123-166.
- Parker, G.A. 1983. Arms races in evolution—an ESS to the opponent-independent cost game. *J. theor. Biol.* 101:619-648.
- Parker, G.A., Baker, R.R. and Smith, V.G.F. 1972. The origin and evolution of gamete dimorphism and the male-female phenomenon. *J. theor. Biol.* 36:529-533.
- Parry, G.D. 1981. The meanings of r- and K-selection. *Oecologia* 48:260-264.
- Pearl, R. 1928. *The rate of living.* Alfred A. Knopf, New York.
- Pearson, O.P. 1966. The prey of carnivores during one cycle of mouse abundance. *J. Anim. Ecol.* 35:217.
- Peck, J.R. 1994. A ruby in the rubbish: beneficial mutations and the evolution of sex. *Genetics* 137:597-606.
- Peters, R.H. 1983. *The ecological implication of body size.* Cambridge University Press, Cambridge.
- Peterson, B. 1950. The relation between size of mother and number of eggs and young in some spiders and its significance for the evolution of size. *Experimentia* 6:96-98.
- Peterson, R.O., Page, R.E. and Dodge, K.M. 1984. Wolves, moose, and the allometry of population cycles. *Science* 224:1350-1352.
- Pianka, E.R. 1970. On r- and K-selection. *Am. Nat.* 104:592-596.
- Pimlot, D.H. 1967. Wolf predation and ungulate populations. *Amer. Zool.* 7:267-278.
- Pollard, E., Lakhani, K.H. and Rothery, P. 1987. The detection of density-dependence from a series of annual censuses. *Ecology* 68:2046-2055.
- Press, W.H., Flannery, B.P., Teukolsky, S.A. and Vetterling, W.T. 1986. *Numerical recipes. The art of scientific computing.* Cambridge University Press, Cambridge.
- Price, G.R. 1970. Selection and covariance. *Nature* 227:520-521.
- Pyke, G.H. 1982. Local geographic distributions of bumblebees near Crested Butte, Colorado: Competition and community structure. *Ecology* 63:555-573.
- Reiss, M.J. 1989. *The allometry of growth and reproduction.* Cambridge University Press, Cambridge.

- Rensch, B. 1960. *Evolution above the species level*. Columbia University Press, New York.
- Reznick, D.N. and Bryga, H. 1987. Life-history evolution in guppies. 1. Phenotypic and genotypic changes in an introduction experiment. *Evolution* 41:1370-1385.
- Reznick, D.N., Bryga, H. and Endler, J.A. 1990. Experimentally induced life-history evolution in a natural population. *Nature* 346:357-359.
- Reznick, D.N., Butler IV, M.J., Rodd, F.H. and Ross, P. 1996. Life-history evolution in guppies (*Poecilia reticulata*) 6. Differential mortality as a mechanism for natural selection. *Evolution* 50:1651-1660.
- Reznick, D.N., Rodd, F.H. and Cardenas, M. 1996. Life-history evolution in guppies (*Poecilia reticulata*: Poeciliidae). IV. Parallelism in life-history phenotypes. *Am. Nat.* 147:319-338.
- Ricklefs, R.E. 1990. *Ecology*. 3rd ed. W.H. Freeman & Company, New York.
- Ridely, M. and Thompson, D.J. 1979. Size and mating in *Asellus aquaticus* (Crustacea: Isopoda). *Z. Tierpsychol.* 51:380-397.
- Robertson, A. 1955. Selection in animals: Synthesis. *Cold Spring Harbor Symp. Quant. Biol.* 20:225-229.
- Robertson, F.W. 1957. Studies in quantitative inheritance. XI. Genetic and environmental correlation between body size and egg production in *Drosophila melanogaster*. *J. Gen.* 55:428-443.
- Robertson, A. 1968. The spectrum of genetic variation. In R.C. Lewontin, ed., *Population Biology and Evolution*, Syracuse University Press, New York, pp. 5-16.
- Robinson, W.R., Peters, R.H. and Zimmermann, J. 1983. The effects of body size and temperature on metabolic rate of organisms. *Can. J. Zool.* 61:281-288.
- Roff, D.A. 1981. On being the right size. *Am. Nat.* 118:405-422.
- Roff, D.A. 1982. Reproductive strategies in flatfish: a first synthesis. *Can. J. Fish. Aquat. Sci* 38:968-977.
- Roff, D.A. 1986. Predicting body size with life history models. *BioSci.* 836:316-323.
- Roff, D.A. 1992. *The evolution of life histories. Theory and analysis*. Chapman & Hall, New York.
- Roques, A. 1988. The larch cone fly in the French alps. In A.A. Berryman, ed., *Dynamics of forest insect populations. Patterns, causes, implications*, Plenum Press, New York, pp. 1-28.
- Rose, M.R. 1991. *Evolutionary biology of aging*. Oxford University Press, New York.
- Roth, V.L. 1981. Constancy in the size ratios of sympatric species. *Am. Nat.* 118:394-404.
- Roughgarden, J. 1971. Density-dependent natural selection. *Ecology* 5:453-468.
- Roughgarden, J. 1976. Resource partitioning among competing species—a coevolutionary approach. *Theor. Pop. Biol.* 9:388-424.
- Roughgarden, J. 1989. The structure and assembly of communities. In *Perspectives in ecological theory*, J. Roughgarden, R.M. May and S.A. Levin, eds. Princeton University Press, Princeton, pp. 203-226.

- Royama, T. 1984. Population dynamics of the spruce budworm *Choristoneura fumiferana*. *Ecol. Monogr.* 54:429-462.
- Royama, T. 1992. *Analytical population dynamics*. Chapman & Hall, New York.
- Rubner, M. 1883. Über den einfluss der körper grosse auf stoff-und kraft-wechsel. *Z. Biol.* 19:535-562.
- Ruxton, G.D. and Gurney, W.S.C. 1992. The interpretation of tests for ratio-dependence. *Oikos* 65:334-335.
- Salthe, S.N. 1989. Untitled. In M.K. Hecht, ed., *Evolutionary biology at the crossroads*, Queens College Press, New York, pp. 174-176.
- Sarnelle, O. 1994. Inferring process from pattern: trophic level abundances and imbedded interactions. *Ecology* 75:1835-1841.
- Schaffer, W.M. 1983. The application of optimal control theory to the general life history problem. *Am. Nat.* 121:418-431.
- Schoener, T.W. 1968. Sizes of feeding territories among birds. *Ecology* 49:123-131.
- Schoener, T.W. 1969. Models of optimal size for solitary predators. *Am. Nat.* 103:277-313.
- Schoener, T.W. 1971. Theory of feeding strategies. *Ann. Rev. Ecol. Syst.* 2:369-401.
- Schoener, T.W. 1976. Alternatives to Lotka-Volterra Competition: Models of intermediate complexity. *Theor. Pop. Biol.* 10:309-333.
- Sinclair, A.R.E. 1989. Population regulation in animals. In J.M. Cherrett, ed., *Ecological concepts. The contribution of ecology to an understanding of the natural world*, Blackwell Scientific Publications, Oxford, pp. 197-241.
- Slatkin, M. 1979. Frequency- and density-dependent selection on a quantitative character. *Genetics* 93:755-771.
- Smith, H.S. 1935. The role of biotic factors in the determination of population densities. *J. Econ. Entom.* 28:873-898.
- Sober, E. 1993. *Philosophy of biology*. Oxford University Press, Oxford.
- Sokal, R.R. and Rohlf, F.J. 1981. *Biometry, 2. ed.* W.H. Freeman & Company, New York.
- Southwood, T.R.E. 1967. The interpretation of population change. *J. Anim. Ecol.* 36:519-529.
- Stacey, P.B. and Koenig, W.D. 1990. *Cooperative breeding in birds: long-term studies of ecology and behavior*. Cambridge University Press, Cambridge.
- Stahl, W.R. 1967. Scaling of respiratory variables in mammals. *J. A. Physiol.* 22:453-460.
- Stanley, S.M. 1973. An explanation for Cope's rule. *Evolution* 27:1-26.
- Starr, C.K. 1985. Enabling mechanisms in the origin of sociality in the hymenoptera-the sting's the thing. *Ann. Entomol. Soc. Am.* 78:836-840.
- Stearns, S.C. 1976. Life-history tactics: A review of the ideas. *Quart. Rev. Biol.* 51:3-47.
- Stearns, S.C. 1977. The evolution of life-history traits: A critique of the theory and a review of the data. *Ann. Rev. Ecol. Syst.* 8:145-171.

- Stearns, S.C. 1992. *The evolution of life histories*. Oxford University Press, Oxford.
- Stearns, S.C. and Koella, J. 1986. The evolution of phenotypic plasticity in life-history traits: Predictions for norms of reaction for age- and size-at-maturity. *Evolution* 40:893-913.
- Stenseth, N.C. 1978. Demographic strategies in fluctuating populations of small rodents. *Oecologia* 33:149-172.
- Stenseth, N.C. 1981. On Chitty's theory for fluctuating population: the importance of genetic polymorphism in the generation of regular density cycles. *J. theor. Biol.* 90:9-36.
- Stenseth, N.C. 1982. Causes and consequences of dispersal in small mammals. In I. Swingland and P. Greenwood, eds., *The ecology of animal movement*, Oxford University Press, Oxford, pp. 62-101.
- Stenseth, N.C. 1995. Snowshoe hare populations: Squeezed from below and above. *Science* 269:1061-1062.
- Stenseth, N.C., Bjørnstad, O.N. and Saitoh, T. 1996. A gradient from stable to cyclic populations of *Clethrionomys rufocanus* in Hokkaido, Japan. *Proceedings of the Royal Society of London: Biological Sciences* Proc. R. Soc. Lond. B.263:1117-1126
- Stewart, F.M. and Levin, B.R. 1973. Partitioning of resources and the outcome of interspecific competition: A model and some general considerations. *Am. Nat.* 107:171-198.
- Taylor, P.D. 1988. Inclusive fitness models with two sexes. *Theor. Pop. Biol.* 34:145-168.
- Thompson, D.Q. 1952. Travel, range and food habits of timber wolves in Wisconsin. *J. Mammal.* 33:429-442.
- Thue Poulsen, E. 1979. A model for population regulation with density- and frequency-dependent selection. *J. Math. Biol.* 8:325-343.
- Trivers, R.L. and Hare, H. 1976. Haplodiploidy and the evolution of social insects. *Science* 191:249-263.
- Turchin, P. 1990. Rarity of density dependence or population regulation with lags? *Nature* 344:660-663.
- Turchin, P., Lorio, P.L., Jr., Taylor, A.D. and Billings, R.F. 1991. Why do populations of southern pine beetles (Coleoptera: Scolytidae) fluctuate? *Environ. Entomol.* 20:401-409.
- Turchin, P. and Taylor, A.D. 1992. Complex dynamics in ecological time series. *Ecology* 73:289-305.
- Turner, F.B., Jennrich, R.I. and Weintraub, J.D. 1969. Home range and body size of lizards. *Ecology* 50:1076-1081.
- Utida, S. 1957. Population fluctuation, an experimental and theoretical approach. *Cold Spring Harbor Symp. Quant. Biol.* 22:139-151.
- Vance, R.R. 1985. The stable coexistence of two competitors for one resource. *Am. Nat.* 126:72-86.

- Van Groenendael, J., de Kroon, H. and Caswell, H. 1988. Projection matrices in population biology Trends. Ecol. Evol. 3:264-269.
- Vandel, A. 1928. La parthénogénèse géographique. Contribution à l'étude biologique et cytologique de la parthénogénèse naturelle. Bull. Biol. France. Belg. 62:164-281.
- Varley, G.C., Gradwell, G.R. and Hassell, M.P. 1973. *Insect population ecology: An analytical approach*. Blackwell Scientific Publications, Oxford.
- Verhulst, P.F. 1838. Notice sur la loi que la population suit dans son accroissement. Corresp. Math. Phys. 10:113-121.
- Vincent, T.L. and Brown, J.S. 1988. The evolution of ESS theory. Ann. Rev. Ecol. Syst 19:423-443.
- Vincent, T.L.S. and Vincent, T.L. 1996. Using the ESS maximum principle to explore root-shoot allocation, competition and coexistence. J. theor. Biol. 180:111-120.
- Vollrath, F. 1980. Male body size and fitness in the web-building spider *Nephila clavipes*. Z. Tierpsychol. 53:61-78.
- Volterra, V. 1926. Variazioni e fluttuazioni del numero d'individui in specie animali conviventi. Mem. Acad. Lincei. 2:31-113.
- Volterra, V. 1926. Variations and fluctuations of the numbers of individuals in animal species living together. Reprinted 1931. In R.N. Chapman, ed., *Animal Ecology*, McGraw-Hill, New York, pp. .
- Watt, A.D., Leather, S.R., Hunter, M.D. and Kidd, N.A.C. 1990. *Population dynamics of forest insects*. Intercept, Andover, Hampshire.
- Weismann, A. 1889. *Essays upon heredity and kindred biological problems*. Clarendon Press, Oxford.
- Werren, J.H. 1983. Sex ratio evolution under local mate competition in a parasitic wasp. Evolution 50:1-33.
- West-Eberhard, M.J. 1975. The evolution of social behavior by kin selection. Quart. Rev. Biol. 59:257-290.
- Wetherill, G.W. 1996. Icarus 119:219-238.
- Whitford, W.G. and Hutchinson, V.H. 1967. Body size and metabolic rate in salamanders. Physiol. Zool. 40:127-133.
- Wiegert, R.G. and Owen, D.F. 1971. Trophic structure, available resources and population density in terrestrial vs. aquatic ecosystems. J. theor. Biol. 30:69-81.
- Wiens, J.A. 1966. On group selection and Wynne-Edwards' hypothesis. Am. Sci. 54:273-287.
- Wilbur, H.M. and Collins, J.P. 1973. Ecological aspects of amphibian metamorphosis. Science 182:1305-1314.
- Wilbur, H.M. and Morin, P.J. 1988. Life history evolution in turtles. In C. Gans and R.B. Huey, eds., *Biology of the reptilia. vol 16, B. Defence and life history*, Alan R. Liss, Inc., New York, pp. 387-439.
- Williams, G.C. 1957. Pleiotropy, natural selection and the evolution of senescence. Evolution 11:398-411.

- Williams, G.C. 1966. *Adaptation and natural selection. A critique of some current evolutionary thought*. Princeton University Press, Princeton.
- Williams, G.C. 1975. *Sex and evolution*. Princeton University Press, Princeton.
- Williams, G.C. 1992. *Natural selection. Domains, levels, and challenges*. Oxford University Press, New York.
- Winberg, G.G. 1960. *Rate of metabolism and food requirement of fishes*. Fisheries Research Board Translation Services, No 194.
- Witteman, G.J., Redfearn, A. and Pimm, S.L. 1990. The extent of complex population changes in nature. *Evol. Ecol.* 4:173-183.
- Witting, L. 1995. The body mass allometries as evolutionarily determined by the foraging of mobile organisms. *J. theor. Biol.* 177:129-137.
- Woiwod, I.P. and Hanski, I. 1992. Patterns of density dependence in moths and aphids. *J. Anim. Ecol.* 61:619-629.
- Wolszczan, A. and Frail, D.A. 1992. A planetary system around the millisecond pulsar PSR1257+12. *Nature* 355:145-147.
- Wootton, R.J. 1979. Energy cost of egg production and environmental determinants of fecundity in teleost fishes. *Symp. Zool. Soc. Lond.* 44:133-159.
- Wrensch, D.L. and Ebbert, M. (eds.). 1993. *Evolution and diversity of sex ratio in insects and mites*. Chapman & Hall, London.
- Wright, S. 1931. Evolution in Mendelian populations. *Genetics* 16:97-159.
- Wynne-Edwards, V.C. 1962. *Animal dispersion in relation to social behavior*. Oliver & Boyd, Edinburgh.
- Wynne-Edwards, V.C. 1986. *Evolution through group selection*. Blackwell Scientific Publications, Oxford.
- Wynne-Edwards, V.C. 1993. A rationale for group selection. *J. theor. Biol.* 162:1-22.
- Young, J.P.W. 1981. Sib competition can favor sex in two ways. *J. theor. Biol.* 88:755-756.
- Zar, J.H. 1969. The use of the allometric model for avian standard metabolism-body weight relationships. *Comp. Bioch. Physiol.* 29:227-234.
- Zotin, A.I. and Konoplev, V.A. 1978. Direction of the evolutionary progress of organisms. In I. Lamprecht and A.I. Zotin, eds., *Thermodynamics of Biological Processes*, deGruyter, Berlin, pp. 341-347.

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Symbols

<i>S</i>	Trait	Relations
w	Body mass	
B	Metabolic rate per unit mass	
ω	Senescence parameter	
T	Lifespan	$T = \omega/B$
q	Energetic and competitive quality	$q = wTB$
θ	Proportion of females	
ϕ	Proportion of males	$\phi = 1 - \theta$
ϕ/θ	Sex ratio	
H	Home-range	
N	Population density	$N^* = \sqrt[3]{\lambda_m}$
ι	Intra-population interference, also I	$I = e^\iota$
γ_α	Density regulation by exploitation	$-\gamma_\alpha \ln N$
γ_ι	Density dependence in interference	$\iota = \gamma_\iota \ln N$
μ	Regulation by interference	$-\mu\iota, \cdot g(I)$
γ	Total density regulation	$\gamma = \gamma_\alpha + \mu\gamma_\iota$
f	Regulation by foraging self-inhibition	$\cdot f$
α	Exploitation efficiency	
κ	Realised foraging efficiency	$\kappa = fg\alpha$
r_e	Rate of increase in the resource	
γ_e	Density regulation in the resource	
E	Resource density	$E^* = (r_e - \kappa N^*)/\gamma_e$
ϵ	Energy used on reproduction	$\epsilon = \kappa E^*$
R	Lifetime reproduction	$R = T\epsilon/q = \epsilon/wB$
p	Survival scalar	
R_0	Net lifetime reproduction	$R_0 = pR$
λ	Discrete Malthusian parameter	$\lambda = R_0$
r	Intrinsic Malthusian parameter	$r^* = \ln(p\alpha E^*/wB)$
x	Extrinsic Malthusian parameter	$x^* = \ln(p\kappa E^*/wB)$
d	Spatial dimensionality of behaviour	
$\sigma_{\ln q}^2$	Genetic variance in \ln quality	
ψ	Within population slope in μ	
Q	Fitness, or resource, quanta	$\psi \propto Q$

The most important symbols (S). The superscript star indicates the population equilibrium, and the subscript m maximal values