A GENERAL THEORY OF EVOLUTION
By means of selection by density dependent competitive interactions

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By Means of Selection by Density Dependent Competitive Interactions

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To life

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Preface

Since the early 1990s a large number of books have been published on evolutionary ecology reviewing the major theoretical achievements in this field during the last half century (e.g., Rose, 1991; Roff, 1992; Stearns, 1992; Williams, 1992; Charnov, 1993; Andersson, 1994; Bulmer, 1994; Charlesworth, 1994; Crozier and Pamilo, 1996). From these reviews it is apparent that the classical theories have been established relatively independently of one another, and that they treat evolution by natural selection as an optimisation process that has now been described to the extent of a mature theory covering the major traits of the organism. Unfortunately, as shown in this book, these classical theories do not explain the major evolutionary trajectories that have occurred on Earth, and even more unfortunately the classical predictions are evolutionarily unstable in their phenotypic assumptions.

In this book I have integrated the classical theories with the selection pressure of density dependent competitive interactions, and I have done this to avoid the classical paradox of evolutionarily unstable optima. The result is a radically new theory containing the classical equilibria, but based on a new causality. This theory leads to deterministic (directional) evolution, in contrast to classical Darwinism that is based on historical (non-directional) evolution. In consequence, this book contains the first theory of natural selection suggesting that self-replicating molecules automatically evolve toward the complex organisms on Earth.

At first the readers who are educated in the classical theories might find that my theory is entirely crazy because I argue that the selection pressure is propagated through the population in a direction that is opposite to the direction in classical theories. Nevertheless, the interested reader should give my theory a second thought, a thought that is based on the fact that if we take the traditional approach to evolutionary biology and focus on equilibrium predictions, then the critical scientists would generally be unable to detect whether it is the classical theory or my theory that provides the correct description of evolution by natural selection. In other words, in order to test the two theories we need to make comparisons at higher levels than traditionally done, and it is at these levels, beyond the classical approach, that the proposed theory is superior to the classical theories of natural selection.

Altogether, the present study suggests that a major change is a necessity in order to obtain a consistent theory of evolutionary biology. In order to anticipate that such a change is indeed needed I have chosen to write this book in a form where it may be useful as a text book in theoretical evolutionary ecology. I have aimed at this by assuming only some familiarity with basic calculus, and by proceeding through a successive construction of the whole theory starting from the principle of the Malthusian law. I have also aimed at making the book readable without reading the mathematics so that the less mathematically minded should be able to follow the essentials of my arguments. I might have failed in both cases, but at least I have done my very best.

For those of my readers who wonder why my study is published in this non-prestigious way there is only to say that the resistance against my theory was too great among the scientists who control the established scientific literature. This is probably best illustrated by the comments made by a highly established university press: “this book was very interesting but the innovative nature of the ideas would make the research community resistant” . . . “In spite of the interesting content, we would not be able to have such a work passed by our editorial board”. Of approximately thirty different submissions of my theory and parts of it to established journals and publishers it was only the deduction of the body mass allometries (Witting, 1995), which is not in itself controversial, that has been accepted for publication. The rest of the studies were rejected for publication even though they were often considered very important, and even though not one single reviewer could detect one single flaw affecting my conclusions. Despite this lack of firm scientific critique, many of the anonymous reviewers did not hesitate to argue against the publication of my studies, and in all instances they succeeded in convincing the editor not to publish them. For further details on the peer-reviews of my studies see the homepage at http://www.peregrine.dk.

As my theory has floated around in the scientific community in unpublished versions for quite a while, let me set the record straight on the dates where the different parts were released: The part on the evolution of body mass including the directional change was first submitted for publication on May 11, 1994, and the parts on population dynamics on October 27, 1994. Both of these studies were first presented in public 4-8 September 1995 at the Fifth Congress of the European Society for Evolutionary Biology in Edinburgh, together with some essential parts on the evolution of sexual reproduction. In the complete form the theory was first submitted for publication in June 1995, and it was first presented in public in August 1996 at the Fifth International Congress of Systematic and Evolutionary Biology in Budapest, and at the same time some of the essential conclusions were distributed to the members of the mailing list evoldir@evol.biology.mcmaster.ca.

I want to thank Lev R. Ginzburg at Stony Brook for many stimulating discussions that in the early 1990s turned my thoughts to the field of evolutionary ecology, and I am grateful also to my earlier supervisor Volker Loeschcke at Aarhus University. I also want to thank Bernt Guldbrandtsen and reviewers for helpful comments, John Maynard Smith for being the only reviewer who did not remain anonymous, Richard Barlach for checking my English, and the Department of Ecology and Genetics at Aarhus University for providing a desk during most of the period I used on this study.

Lars Witting
Århus, January 1997

Prologue

Chapter 1

Introduction

Since Darwin rejected Lamarck's notion that organisms have an inherent tendency to climb the ladder of nature evolutionists have agreed that, on the theoretical side, there is no reason to expect that evolution is directional generating an increase in complexity with time. Nevertheless, although there is much noise on smaller scales, evidence actually suggests that large scale evolution is directional. Together with the empirical allometries Cope's law (Cope, 1887) suggests that mobile organisms in a stable environment continue to increase in size while their life-history traits evolve in concordance with the exponents of the body mass allometries. Also, a comparison between prokaryotes and the higher eukaryotes suggests that the transition from a negligible to a relatively large body mass is associated with an evolutionary transition from a haploid organism with no soma, no senescence, and no sexual reproduction, to a diploid organisms with soma, senescence, and sexual reproduction between a male and a female. In a few special cases, mostly in insects, there is an additional transition to eusocial communities, a transition that in some instances may coincide also with a transition from a diploid to a haplodiploid genome. As these major evolutionary trajectories tend to summarise the evolutionary process at a very large scale they require an explanation. It is such an explanation that is the major objective with this book where I develop a new and general theory of evolution that is based on an extension of the mathematical framework behind the classical theory of evolution by natural selection.

1.1 The classical theory of natural selection

In 1859 Darwin proposed that organisms on Earth had evolved by natural selection. It was, however, not until the early 1930s that this hypothesis

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was developed into a formal mathematical theory by the work of Fisher (1930), Haldane (1932), and Wright (1931). This theory, which became known as the genetical theory of natural selection, is a logical unification between Mendelian inheritance and the Darwinian hypothesis of evolution by natural selection. Since then, the ideas that were laid down mainly by Fisher have grown into a mature theory that today covers the evolution of the major components of the phenotype. In this book I refer to this theory as the classical theory of evolution and it is reviewed in the resent books by Roff (1992), Stearns (1992), Charnov (1993), Bulmer (1994), and Charlesworth (1994).

Broadly speaking, classical theory is based on the assumption that the relative fitnesses are constant among genotypes. This implies that it is also assumed that competition is purely exploitative, and that the classical type of selection can be classified as selection by the intrinsic constraints that are inherently part of the organisms itself. More specifically, this type of selection is the hypothesis that we can partition the phenotype into two different sets of traits, where the first set contains the fundamental traits representing the evolutionary constraints that define natural selection, and the second set contains the derived traits that evolve from the selection pressure defined by the fundamental traits. A few examples will illustrate this more clearly. According to Roff (1981) the body mass is a derived trait that evolves from a fundamental and proportional relation that exists between the reproductive rate and body mass. According to Lack (1947) the reproductive rate is a derived trait evolving from a fundamental trade-off that exists between reproduction and either offspring or parent survival. According to Williams (1957) senescence is a derived trait that evolves from the soma, which is more fundamental. According to Fisher (1930) an even sex ratio is a derived trait that evolves from the diploid zygote and random mating that are more fundamental. And according to Hamilton (1964) eusociality is a derived trait evolving from kin selection and a haplodiploid genome, which are seen to be more fundamental.

1.1.1 Limitations to the classical theory

The classical theory have generally been confirmed to the extent that when the fundamental traits are estimated from the phenotype of a specific organisms, then the predicted setting of the derived traits tends to coincide with the derived traits of that organism. In this sense we might at first think that the classical theory of evolution is firm and solid. However, the interpretation of causality in the classical theory is inherently vulnerable to criticism, and this is because the traits that are assumed to be fundamental in that theory are themselves part of the phenotype. Thus, they have evolved by natural selection, exactly like the traits that are assumed to be more derived. This means that there is selection on both types of traits and, therefore, it is likely that the fundamental traits are no more evolutionarily constrained than the derived traits.

When both the fundamental and the derived traits evolve by selection we have the general problem that, as long as we focus on equilibrium predictions, it is almost impossible to distinguish the case where it is trait A that is fundamental and the cause of the evolution of the derived trait B, from the opposing case where it is the trait B that is fundamental and the cause of the evolution of the derived trait A. In other words, with equal right I can use the classical approach to construct a new theory from which I can propose it is the proportional relation between reproduction and body mass that is the derived trait evolving from the more fundamental selection pressure on body mass. That it is the trade-off between reproduction and survival that evolves from the optimal growth rate that is more fundamental. That it is the soma that is the derived trait evolving from senescence, which is more fundamental. That it is the diploid zygote and random mating that are the derived traits that evolve from the more fundamental sex ratio. And, that it is kin selection and a haplodiploid genome that are the derived traits evolving from eusociality, which is more fundamental.

Such results would not in themselves imply that the classical interpretation of evolutionary causality is wrong. Instead, they imply only that we generally cannot use the classical equilibrium predictions to confirm the traditional explanation instead of the explanation that is diametrically opposite. In other words, we are placed in the uncomfortable situation where we have two opposing theories and where we cannot use simple empirical evidence to confirm which theory is correct and which is false. To avoid this problem I have taken a new approach in this book based on the idea that if we cannot use empirical evidence to confirm whether the fundamental traits in a theory are more fundamental than the derived traits, then we should avoid to base our predictions on the occurrence of fundamental traits that are evolutionarily unexplained.

One way to reach this goal is to extend the theory of selection so that selection operates on all the phenotypic traits that we consider and, then, to show that this complete phenotype is evolutionarily stable given genetic variation in all traits. A theory at this level would be more general than the classical theory, and this is because it will give the same equilibrium predictions as the classical theory while it at the same time will explain also the evolution of the phenotypic assumptions underlying the predictions in the classical theory.

In the construction of such a general or perfect theory we are aiming at a framework predicting evolutionarily stable phenotypes from assumptions that are not in themselves part of the phenotype. Based on this approach we may conclude that a particular theory fails on an evolutionary scale if the phenotype is not evolutionarily stable with respect to all the traits that we consider. Moreover, if we have two, or more, opposing theories to choose among and we cannot use empirical evidence to confirm which theory is correct, then the hypothesis of a perfect theory suggests that the correct theory is likely to be the theory containing the fewest assumptions, i.e., the theory containing the fewest fundamental traits that are evolutionarily unexplained. In this way the construction of a theory of evolution can be seen as a successive process during which the number of assumptions continuously is reduced until we reach the final stage of perfection where the theory contains no biological assumptions besides those that are associated with the origin of living beings.

In other words, in the construction of a perfect theory of evolution we aim at developing the Darwinian hypothesis into a purely deductive theory that is based only on a single biological assumption, namely the assumption that self-replication is the origin from which all living organisms have evolved. It would be possible to reach this goal from the classical theory if we can prove that all the traits that are assumed to be fundamental in that theory evolve from the principle of self-replication independently of the presence versus absence of the traits assumed to be the derived traits. If this is possible we can always trace the evolution of a particular trait back to the common origin of self-replication and we would have a mechanistic explanation for the evolution of all the traits considered in the classical theory.

Throughout this book I test whether the fundamental traits in the classical theory are evolutionarily stable independently of the derived traits. This is generally done by allowing for genetic variation in the fundamental traits so that their status as evolutionary constraints is relaxed and they evolve by selection, just like the derived traits. When this is done I find that the fundamental traits are evolutionarily unstable, and that the evolutionary predictions of the classical theory collapses in the sense that all organisms evolve to the limit of self-replicating molecules. From these results I conclude that the classical theory fails to explain the evolution of both the fundamental and the derived traits. That is to say that, although the classical explanations are valid according to the traditional framework where it is legitimate to impose evolutionary constraints by assuming the presence of fundamental traits, they fail on an evolutionary scale where it is the complete phenotype that needs to be evolutionarily stable.

It is easy to see why the classical theory fails on an evolutionary scale. This theory has generally been constructed to explain the evolution of traits that require energy that could otherwise be used to enhance numerical replication. Then, as the classical theory defines selection by a continuous increase in the growth rate of the population, the predictions of the theory depend upon the intrinsic constraints preventing the energy contained in the derived traits from being selected into numerical replication. When there is genetic variation in the fundamental traits there is no longer such constraints, and this implies that the phenotype continues to shrink toward an organism of negligible size that replicates at a high rate.

1.1.2 Historical and non-directional evolution

Closely associated with the classical theory of evolution there is the hypothesis that evolution by natural selection is historical, that is to say that it is non-directional. According to this concept there is an almost infinite number of possible evolutionary trajectories and it is historical incidents that determine the actual evolutionary trajectories that can be observed in the fossil record. According to Wright's (1931) theory of shifting balance, historical accidents may resemble unpredictable rearrangements of the genome that generate brief moments of shifting selection pressures.

In the mathematical version of the classical theory the notion of historical evolution is represented in the form of the fundamental traits. In the classical theory these traits represent history in the sense that they have evolved by an unknown form of natural selection that is not included explicitly in the theory. Then, at the current point in the evolutionary history the fundamental traits are assumed to represent evolutionary constraints. It is of course more elegant if the evolution of all traits is modelled explicitly, but this approach does not work in the classical framework, and this is because if we allow for genetic variation in the fundamental traits, then the predictions of the classical theory collapse.

Because of the particular construction, where the fundamental traits are assumed to be fixed, the mathematical version of the classical theory is static in the sense that it does not allow the phenotype to evolve beyond the equilibrium defined by those fundamental traits. This static view has been challenged in the resent books of Buss (1987) and Maynard Smith and Szathmáry (1995) where the authors focus on the evolutionary transitions that have occurred during the history of life on Earth. According to this latter approach evolution is seen as "the elaboration of new self-replicating entities by the self-replicating entities contained within them . . . at each stage in the history of life in which a new self-replicating unit arose–the rules regarding the operation of natural selection changed utterly" Buss (1987:viii). Although this latter approach focuses on transitions instead of static points the concept of evolution remains inherently historical in the sense that the maintenance of the more complex forms of life depends upon evolutionary constraints. In Maynard Smith and Szathmáry (1995) these constraints are referred to as contingent irreversibility and central control.

The whole concept of historical evolution seems to be inseparable from the Darwinian hypothesis of evolution by natural selection. According to Maynard Smith and Szathmáry (1995:4) “It was Lamarck’s notion of an inherent tendency [to climb the ladder of nature], rather than his belief in the inheritance of acquired characters, that Darwin was rejecting”. Today, this rejection is implicit in the thinking of leading evolutionists. For example, by implicitly assuming that evolution on Earth is historical Williams (1992:8) raises the question: “Might there be somewhere a planet on which the biota arises and becomes more complex deterministically?” Along the same line of thought Mayr (1988:20:105) defines natural selection as “a strictly *a posteriori* process” that is not “controlled by any law”. And Maynard Smith and Szathmáry (1995:4) concludes that “On the theoretical side, there is no reason why evolution by natural selection should lead to an increase in complexity”.

The ultimate conclusion from non-directional evolution is that the occurrence of intelligent and large-bodied animals with a high metabolic rate, senescence, soma, and sexual reproduction is more of a coincidence than a consequence of natural selection. This conclusion is somewhat ironical for a theory of evolution by natural selection, and it means that if extraterrestrial life exists, then it may not at all resemble life on Earth. It is obvious that these results are the consequence of an evolutionary theory that lacks a unifying force of selection that can explain the general structuring of organic matter. Just like the structuring of inert matter into planets and solar systems was mysterious prior to Newton’s theory of gravity, so does it seem that the mechanisms behind the structuring of organic matter will remain largely obscure until a unifying force of selection has been identified. With the theory that I propose in this book I have aimed at identifying a unifying force of selection in order to explain the general structuring of organic matter.

1.2 The proposed theory of natural selection

As the predictions of the classical theory fail when there is genetic variation in the fundamental traits we need a new type of selection if we want to explain the evolution of both the fundamental and the derived traits. As the classical theory is based on selection by intrinsic constraints an obvious way to proceed is to include selection by some sort of ecological constraint existing extrinsic to the organism. It is this route I have taken in this book where I develop a new theory of evolution based on a unifying force of selection arising from the density dependent competitive interactions that exist among the individuals within populations. As this leads to a special type of density and frequency dependent relativity among the relative fitness values defined by the Malthusian parameters I refer to my theory as the theory of Malthusian relativity.

Up to now the hypothesis of evolution by competitive interactions has been treated in relation to specific topics like game theory (e.g., Maynard Smith and Price, 1973; Maynard Smith, 1982; Vincent and Brown, 1988), coevolution (e.g., Lawlor and Maynard Smith, 1976; Brown and Vincent, 1987; Abrams, 1989), the evolution of plant height (e.g., Mirmirani and Oster, 1978; Mäkela, 1985; King, 1990), and the evolution of competitive traits, especially in relation to selection for sexual mates (e.g., Parker, 1979, 1983; Haigh and Rose, 1980; Maynard Smith and Brown, 1986; Abrams and Matsuda, 1994; Day and Taylor, 1996). These earlier studies differ from the theory that I develop in this book in the way that they generally are based on the simplifying assumption that the number of competitive interactions per individual is density independent. They differ also in the sense that they tend to operate with "classical phenotypes" where the evolutionary predictions depend on fundamental traits that are evolutionarily unexplained. Furthermore, in the earlier studies there has been only sporadic interest in developing the hypothesis of evolution by competitive interactions into a general theory of evolution (Day and Taylor, 1996). With this book I have developed a general theory that covers the evolution of many of the major phenotypic patterns observed among and within mobile organisms.

1.2.1 Integrating the two theories

The theory of Malthusian relativity has a restricted or special version and an extended or general version, which are distinguished from one another by the degree to which the intrinsic selection procedures of the classical theory are integrated with the ecological selection pressure of density dependent competitive interactions. In the restricted, or special, form of Malthusian relativity the predictions are based almost exclusively upon the selection pressure of density dependent competitive interactions. This is in contrast to the general form of the theory where the predictions are based also on an integration between the intrinsic selection procedures in the classical theory and the proposed selection pressure of density dependent competitive interactions. The major difference between the predictions made by these two versions of the theory is on the number of phenotypic traits included in the predictions.

In the restricted form of Malthusian relativity the selection pressure of density dependent competitive interactions is used to predict the evolution of the traits that generally are treated as the derived traits in the classical theory. As these predictions are made independently of fundamental traits they are evolutionarily stable, and this is in contrast to the classical predictions, which are evolutionarily unstable in the dimension of the traits that are fundamental in the classical theory.

These new and restricted predictions do not in themselves establish the classical equilibrium relations between the traits that are fundamental and derived in the classical theory, i.e., they do not establish the relations that traditionally have been confirmed by empirical evidence. Instead, these relations are generally established by the transition from the restricted to the general form of Malthusian relativity, a transition carried out by superimposing the intrinsic selection procedures of the classical theory on top of the restricted form of Malthusian relativity.

Although the classical equilibrium relations between the fundamental and the derived traits are reestablished in the general form of Malthusian relativity, there are two major differences between the new and the old form of the classical predictions. The first difference is that the evolutionary causality underlying the new predictions most often is diametrically opposite to the causality underlying the original predictions. That is to say that it is the traits that are fundamental in the classical theory that are the derived traits in Malthusian relativity, while the traits that originally were derived are fundamental.

This change in causality is induced when we apply the classical selection procedures to the restricted form of Malthusian relativity because, then, we have a situation where the derived traits are explained already while the setting of the fundamental traits is unexplained. It is therefore most obvious to let the selection pressure of the classical selection procedures operate, not on the traits that are the derived traits in the classical theory, but instead on the traits traditionally assumed to be fundamental. Then, it is the assumptions in the original version of the classical theory that become the evolutionary predictions in the new version. For example, with Lack's theory on clutch size we will conclude that it is the trade-off between reproduction and survival that evolves from the optimal growth rate, and not the optimal growth rate that evolves from the trade-off as it was originally proposed by Lack.

This change in causality is possible because the causality in the classical selection procedures generally is defined not by the selection procedures in themselves, but by assumptions where it is the traits that are assumed to be fixed that impose selection on the traits allowed to evolve by selection. Hence, when the fixed and the evolving traits are switched around the selection procedure remains the same while the action of selection is turned upside down in the sense that it is now the original prediction that imposes selection on the original assumption.

The second difference between the new and the old forms of the classical predictions is that the new predictions are evolutionarily stable while the original predictions are evolutionarily unstable in the dimension of the traits that are fundamental in the classical theory. This new form of evolutionary stability arises because the evolution of the traits that are fundamental in the new theory have been explained prior to their use as the assumptions that explain the evolution of the derived traits. In this way the evolutionary stability of the fundamental trait is transferred to the derived trait in the sense that the new prediction is stable in the dimension of the fundamental trait. It is due to this hierarchical propagation of the selection pressure and, thus, also of the evolutionary stability, to the different levels of the phenotype that we can reach a theoretically based conclusion on the causality that links the evolution of the different traits together, namely that it is because we can explain the evolution of trait A independently of trait B, and because we cannot explain the evolution of trait B independently of trait A, that it is A that induces the evolution of B, and not B that induces the evolution of A.

1.2.2 Deterministic and directional evolution

When we have constructed a theory where the evolutionary optima do not depend on phenotypic assumptions, then we have a situation where phenotypic variation necessarily must be given either by differences in initial conditions, by differences in environmental conditions, and/or differences in the degree to which the organisms have evolved along the evolutionary trajectory defined by natural selection.

The theory in this book suggests that many of the major phenotypic patterns existing among the mobile organisms on Earth are explained by differences in the degree that the organisms have evolved along a major evolutionary trajectory. The proposed theory also suggests that these differences are maintained because the different organisms are exposed to different environmental conditions, and that inter-specific interference competition probably is the major factor maintaining these differences in environmental conditions among species.

This hypothesis implies that evolution is deterministic, or directional, in the sense that organisms in a stable environment have an inherent tendency to evolve in particular directions because natural selection is selecting for directional changes. In the proposed theory the directional component is not in itself the result of selection by density dependent competitive interactions. Instead, the directionality requires the additional notion of selection for an increase in the ability by which an individual exploits the resource. This increase implies an exponential increase in the amount of resource, or energy, that is assimilated by the individual, and it is then selection by density dependent competitive interactions that allocates these resources to the different components of the phenotype generating a major evolutionary trajectory.

For mobile organisms the predicted trajectory includes an exponential increase in body mass, metabolic rate, and the complexity of behavioural interactions. Associated to the transition from a negligible to a relatively large body mass there is a transition from a haploid organism with no soma, no senescence, and no sexual reproduction, to a diploid organism with soma, senescence, and sexual reproduction between a male and a female. In the special case where the body mass is constrained relatively to the ability by which the individual can assimilate resource the trajectory also includes a transition to eusocial communities, and dependent upon the role played by the sexual male this transition can be associated with a transition from a diploid to a haplodiploid genome. The evolutionary trajectory also explains the across-species exponents of the body mass allometries and the within-species exponent between reproduction and body mass. In other words, the predicted trajectories resemble the major evolutionary trajectories of the evolutionary process that has occurred on Earth. In Table 1.1 the major predictions of Malthusian relativity are listed and compared with the corresponding predictions in the classical theory.

Evidently there are some taxa that have been left aside from the predicted trajectory and this might at first appear to be contradictory to a theory on directional evolution. This is, however, not the case, and this is because the predicted trajectory depends upon an assumption of a stable environment with a sufficiently large resource. If, instead, the resource is extremely sparse, then the upper boundary to resource consumption is low and the organism may not be able to evolve away from a simple self-replicator. Also, for such organisms it might not be possible to invade environments with more abundant resources, and this is because these environments are likely to be dominated by larger species that can exclude the former species by direct interference. In this way there may be a relatively fixed pattern in which the different resources are distributed among different organisms, and this pattern may allow for a variety of variation in the degree to which natural organisms can evolve along the major evolutionary trajectory.

As the predicted evolutionary unfolding depends on a stable environment with a sufficiently high influx of energy to the underlying resource, we will find that the predicted trajectory is reversible in the sense that it may reverse if the influx of energy begins to decline. Also, at points where the influx of energy begins to decline there may be a mass extinction that will eliminate predominantly the larger species. And, if the influx continues to decline we expect a deterministic back-folding characterised by a decline in body mass, metabolic rate, and the complexity of behavioural interactions. As the back-folding continues males and eusocial communities will vanish together with senescence and soma and, given that the physical conditions remain suitable for life, the decline is expected to continue until the point of simple self-replicators.

Table 1.1 Some major predictions of the general theory of Malthusian relativity, and the corresponding predictions of the classical theory. The predictions of Malthusian relativity include all the traits mentioned, while the classical predictions include only the traits marked with a numbered $*$. These classical predictions depend on the fundamental traits with the superscript $\#$ and the corresponding number. A $+$ or $-$ indicates respectively the presence or absence of the main trait.

Main trait	Related patterns
Body mass^{*1}	Intra-specific relation to reproductive rate$^{\#1}$, Bergmann's rule, Island rule, Cope's law, Dwarfing
Body mass allometry	For metabolic rate, lifespan, population density, home-range, reproductive rate, intrinsic growth rate, population energy use, biomass, level of sociality
Metabolism	Increase in metabolic rate
Behaviour	Increase in complexity of interactions
Reproductive rate^{*2}	Trade-offs between reproduction and survival$^{\#2}$, balance against extrinsic mortality, difference between homeo- and poikilotherms
Population density	Difference between homeo- and poikilotherms
Senescence^{*3} & soma$^{\#3}$	- in negligibly sized organisms, + in large organisms
Male individual	- in negligibly sized organisms, + in large mobile organisms, - in large sessile organisms, sex dimorphism's
Sex ratio^{*4}	Mating structure$^{\#4}$, parthenogenesis
Sexual reproduction	- in negligibly sized organisms, + in large organisms, differences between sessile and mobile organisms
Genome	Haploid in negligibly sized organisms, diploid or haplodiploid in large organisms $^{\#4}$, diploid in eusocial termites$^{\#4}$, haplodiploid in eusocial ants and bees$^{\#4}$
Eusociality^{*5}	Offspring workers$^{\#5}$, kin selection$^{\#5}$, - in vertebrates and + in insects, female biased sex ratio^{*6}, female workers$^{\#6}$, and a haplodiploid genome$^{\#6}$ in ants and bees, even sex ratio^{*7}, male and female workers$^{\#7}$, and a diploid genome$^{\#7}$ in termites
Dynamics	Population cycles, phenotypic cycles in, e.g., body mass & sex ratio

1.2.3 Extraterrestrial life

The idea that extraterrestrial intelligent beings may inhabit planets in other stellar systems have been a common subject of books and films, but until recently there has been very little scientific evidence that could support such ideas. Nevertheless, the accumulation of evidence seems now to suggest that extraterrestrial intelligent beings might exist quite commonly on other planets.

In order to conclude on the occurrence of extraterrestrial intelligent life there are at least four independent questions that we need to address. The first three of these belong to the physical sciences, while it is only the last question that belongs to the domain of biology. The first three questions are: (*i*) Whether stars generally have planetary systems, (*ii*) whether such planetary systems generally have planets that are potentially habitable by life, and (*iii*) whether the origin of simple self-replicators is so common a phenomena that they are likely to have arisen on the planets suitable for life. When we know the answer to these questions the final and biological question is whether simple self-replicators on suitable planets will evolve toward complex and intelligent beings.

The theory that is developed in this book is related only to the last question where it suggests that intelligent beings are expected because the predicted evolutionary unfolding is the result of self-replication in a stable environment suitable for life. This suggests that the evolutionary process we know from Earth is only a single example of a general process that is driven by universal laws.

In relation to the three questions in the physical domain there have recently been a number of studies that for the first time suggest that the three physical conditions required for extraterrestrial life may also be fulfilled: (*i*) The observations of a handful of stars with planet-like companions (e.g., Wolszczan and Frail, 1992; Mayor and Queloz, 1995; reviewed by Beckwith and Sargent, 1996) suggest that planetary systems are common, especially when we consider the technical problems associated with the detection of such systems. (*ii*) The theoretical studies of Wetherill (1996) and others (see Black, 1996) suggest that planetary systems have a rather high probability of containing planets that are potentially habitable by living organisms. And finally, (*iii*) if the resent hypothesis of ancient life on Mars (McKay et al., 1996; see also Anders et al., 1997) is true it suggests that the origin of simple self-replicators is a common phenomenon that is not unique to Earth. Hence, it seems to be likely that extraterrestrial intelligent beings are widespread within the universe.

1.3 Evolutionary population dynamics

Apart from defining a new theory of evolution, Malthusian relativity also provides an extension of the classical theory of population dynamics. This latter theory arose from Malthus (1798) and it is based on the assumption of no evolutionary changes in the growth rates of populations. This assumption leads to the population dynamics described by the Malthusian law of exponential increase, the logistic equation, and the Lotka-Volterra predator-prey equations.

In the theory of Malthusian relativity population dynamics is inherently associated with evolutionary changes in the growth rates, and this implies that the proposed theory merges into the classical theory only in the special case where genetic variation is absent. The major implication of the new theory is that it can explain the cyclic dynamics that is widespread throughout the animal kingdom and which have remained a mystery throughout this century. Not only does the predicted dynamics include a cycle in the abundance of the population, but it also includes a cycle in the phenotype. Among other things, this latter cycle can include periodic changes in the body mass and the sex ratio.

1.4 The structure of the book

The book contains six parts that each contain a set of chapters on related subjects. Apart from the deduction of Hutchinson's rule in Chapter 6, the first part is mainly a review describing the classical tradition in theoretical ecology, i.e., the tradition based on the classical theory of population dynamics. This part introduces the inexperienced reader to the theoretical framework used throughout the book. It also illustrates that the structuring of ecological communities is highly influenced by interference competition. The second part is an introduction to evolutionary analysis, and the third part describes the evolution of basic traits like body mass, population abundance, and reproduction. In the last chapter of this part I deduce the exponents of the body mass allometries. Then, in the fourth part I show that the evolutionary process is expected to equilibrate at an evolutionary steady state with exponential increase in the exploitation efficiency, body mass, and metabolic rate. In that part I also focus on evolution during environmental crises and on extinctions. In the fifth part I leave the basic traits and describe the evolution of derived traits like senescence, soma, group size, sexual reproduction, ploidy level of the genome, and eusocial communities. Finally, in the last part the assumption of population dynamic equilibria is relaxed and focus is shifted toward evolutionary population dynamics.