The Comparative Method in Evolutionary Biology

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The comparative method for studying adaptation

'we must learn to treat comparative data with the same respect as we would treat experimental results' (Maynard Smith and Holliday 1979, p. vii)

1.1 Introduction

It is second nature for evolutionary biologists to think comparatively because comparisons establish the generality of evolutionary phenomena. How much molecular evolution is neutral? Do large genomes slow down development? Is sperm competition important in the evolution of animal mating systems? What lifestyles select for large brains? Are extinction rates related to body size? These are all questions for the comparative method, and this book is about how such questions can be answered.

Evolutionary biology shares with astronomy and geology the task of interpreting phenomena that cannot be understood today without understanding their past. Stars in the Milky Way, mountains in the Swiss Alps, and finches in the Galápagos Islands each have their own common histories which give them characteristics that set them apart from the stars of other galaxies, mountains in other regions, and the finches of other archipelagos. Much of this book will be devoted to understanding the influence of shared phylogenetic history on the form of contemporary species. But there is something special about organisms such as finches, orchids, and aardvarks which distinguish them from the inorganic world: they have become adapted to their environments through natural selection, a process that gives life to the comparative method in evolutionary biology.

Indeed, organisms are so well adapted that a large part of organismic biology over the centuries has been devoted to the study of adaptation. Before Darwin, it was often argued that a proper understanding of adaptation might give insight into the mind of the creator. Adaptations were thought to be design features, although whether lack of adaptation was to be viewed as 'a paucity of imagination on the part of the creator' (Maynard Smith 1978, p. 136) was not so regularly posed as a serious question. Since Darwin, it has generally been accepted that adaptations have been honed by natural selection. Whichever force was to be praised or blamed, it has been a fact of nature long appreciated that different species often exhibit similar characteristics when they live in similar environments.

If similar characters evolve repeatedly in similar environments, it is reasonable to consider how they might enable their bearers to survive and reproduce in those environments. For example, several species of birds and mammals have evolved white feathers and fur in snowy environments, whereas their close relatives retain what we assume to be the ancestral plain or mottled brown coloration. Presumably, white variants were favoured by natural selection because they were cryptic against a white background of snow. For some species, such as the snowy owl (*Nyctea scandiaca*) or polar bear (*Ursus arctos*), this may have made them more effective predators, although for others, like the ptarmigan (*Lagopus mutus*) or snowshoe hare (*Lepus americanus*), a white coat probably helped to protect them from predators.

From Darwin's time to the present, the comparative method has remained the most general technique for asking questions about common patterns of evolutionary change. The comparative method has, however, changed radically in recent years, and this book is about a new type of comparative study. The major advance has been the development of methods based on explicit evolutionary and statistical models. These techniques take careful stock of the phylogenetic links between species, and marry ideas about evolutionary change with statistical processes in such a way that formal tests of hypotheses about evolution are possible. We describe these new techniques, and how to use them to study evolution and adaptation.

The motivation for many comparative studies is the occurrence of astonishing regularities that require explanation and suggest further ideas. Consider Bonner's (1965) plot of the close relationship between body length and generation time across organisms ranging in length from less then one-thousandth of a centimetre to almost one hundred metres and with generation times that vary from minutes to decades (Fig. 1.1). Could the fact that the relationship is approximately linear when both axes are logarithmically scaled be related to the fact that growth is essentially a logarithmic process? If so, why should organisms of similar size sometimes have quite different generation times (compare the mouse with the horseshoe crab)? Can we think of differences among similar-sized species which might help explain this variation?

Maximum population densities of different species are closely correlated with body mass (Damuth 1987; Fig. 1.2). Across a range of taxa varying in size from viruses and bacteria, to sequoia trees and whales, larger-bodied

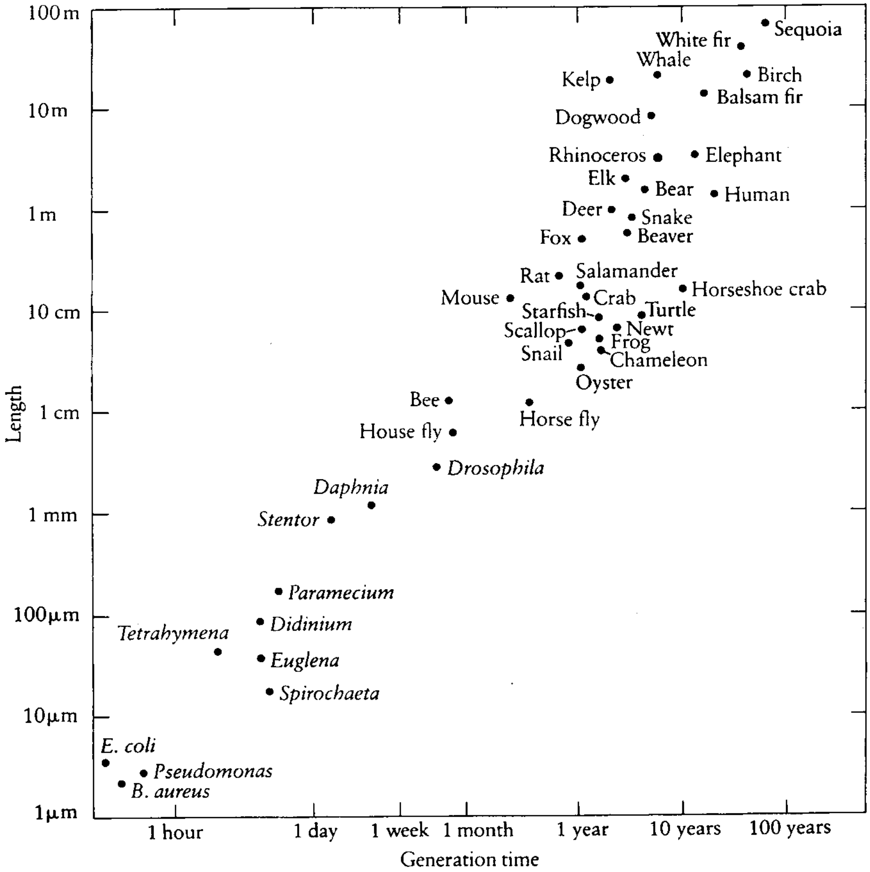

Fig.1.1. The relationship between generation time and body length across species ranging in size from bacteria to sequoia trees and whales. (From McMahon and Bonner 1983, after Bonner 1965).

species live at lower population densities. Perhaps the fact that heavier organisms need more resources to maintain themselves, grow, and reproduce, means that a given area of habitat can sustain fewer of them? However, when different species' energy needs are considered together with the data in Fig. 1.2, a surprising finding emerges. In a given area, the population of each species which exists at its maximum population density uses approximately the same amount of energy (Damuth 1981, 1987). The ecological process that results in populations of different species obtaining approximately equal amounts of energy remains unknown.

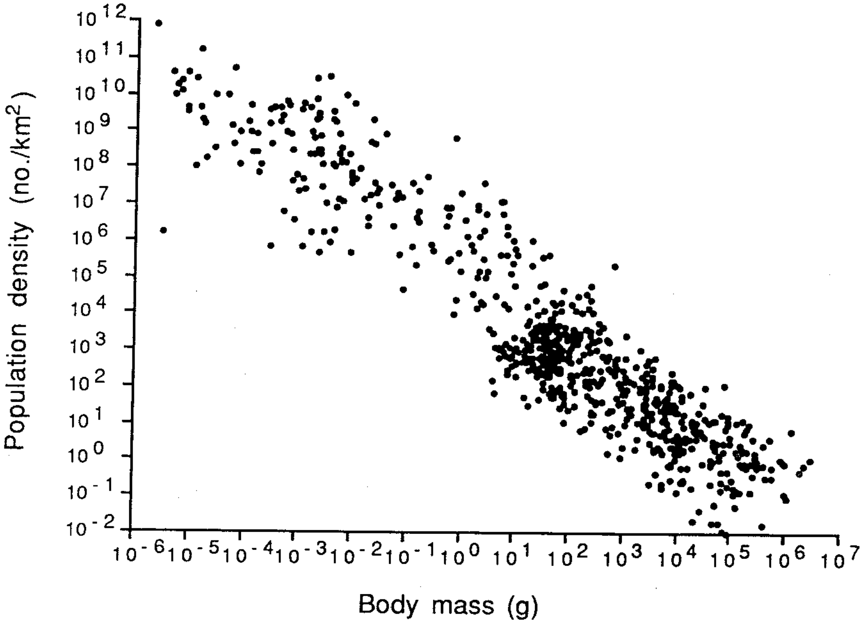

Fig. 1.2. The relationship between population density and body mass across species ranging in size from viruses to sequoia trees and whales. (Data from Damuth 1987).

In addition to the sort of regularities shown in Bonner's and Damuth's comparisons, further patterns are often revealed on closer inspection of the data. For example, testes weight increases with body weight across primate species. However, those adult male primates that belong to species with large testes for their body weight are the ones living in social groups containing several reproductively active males (Fig. 1.3). Why should this be? The answer lies with mating patterns adopted by females, a point we shall return to later in this chapter.

Finally, comparative studies can demonstrate a lack of variation in some characters, despite wide variation in other characters that we might have expected to be correlated with them (see Stearns 1984). For example, for bird and mammal species living in a wide range of social group sizes and with mating patterns that seem to span the range of what is possible (monogamy, polygyny, polyandry, polygynandry, and even promiscuity), the frequency of inbreeding between parent and offspring or between sibs is generally of the order of 1 or 2 per cent of all matings (Fig. 1.4). The exceptions tend to be from populations where mate choice is severely

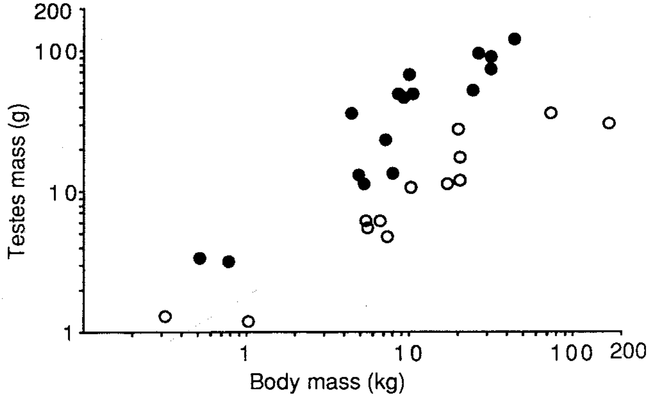

Fig. 1.3. The relationship between testes mass of adult males and body mass across primate species. Males belonging to species in which females are likely to copulate with more than a single partner per oestrus (●) have larger testes for their body weight than those where females invariably mate with only a single male (○). (Data from Harcourt *et al* 1981 and Harvey and Harcourt 1984, with additional material from Terborgh and Goldizen 1985.)

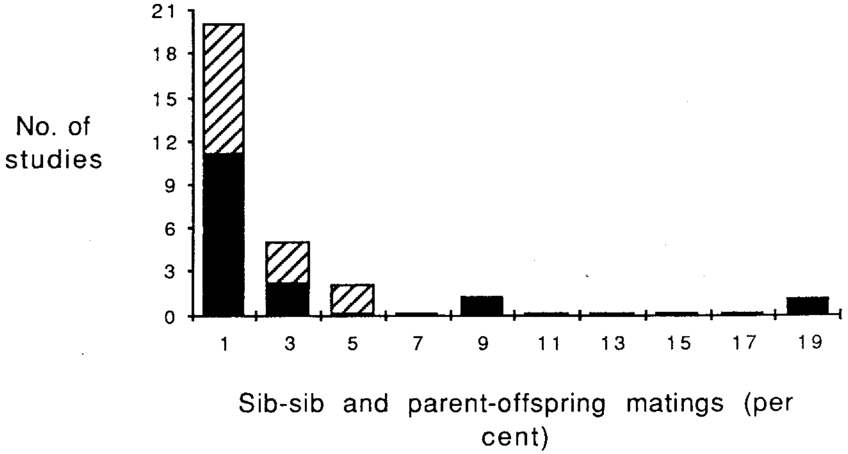

Fig. 1.4. Percentage of matings that are incestuous in populations from different species of birds (solid bars) and mammals (hatched bars). One main feature in the graph is the low frequency of such matings in the vast majority of species. The two outliers are small populations in which mate choice is extremely limited. (After Harvey and Ralls (1986) and Ralls, *et al* 1986.)

limited (e.g. a breeding population of five swans). There are costs associated with inbreeding because the resultant offspring tend to be homozygous, and the products of rare deleterious recessive genes are thereby expressed. Other things being equal, potential parents would do well to avoid incest. Other things are not always equal, however, and incestuous matings occur. One question posed by Fig. 1.4 is why should the level of inbreeding in birds and mammals generally be of the order of about 1 per cent rather than 0.01 or 10 per cent?

Although we shall often focus on identifying adaptive trends, the absence of correlations between character states and environmental differences may suggest non-adaptive interpretations. Furthermore, we shall describe examples to demonstrate that the repeated evolution of the same character states in similar environments need not necessarily have an adaptationist interpretation. We must relentlessly seek alternative explanations, and we must entertain them seriously, whether they invoke physical laws or genetic constraints. Similarly, we must always be ready to abandon favoured taxonomies, to re-classify phenotypes and environments, and to reconsider tried and tested theories. We have used examples liberally in many parts of this book, hoping that some at least will strike familiar chords with the reader. These are exciting times for comparative biology because most of the issues are clear, much of the groundwork has been laid, and the data are accumulating at least as rapidly as the scientific community can make sense of them.

This book does not attempt an historical survey of the comparative method's many accomplishments. That would have meant reviewing almost all of Darwin's many writings including *On the origin of species by means of natural selection* (Darwin 1859) and *The descent of man and selection in relation to sex* (Darwin 1871); critically summarizing several other landmark texts including D'Arcy Thompson's (1917) *On growth and form* and Julian Huxley's *Problems of relative growth* (Huxley 1932); evaluating the field of animal mechanics (Alexander 1968, 1982; McMahon 1983); and explaining how an amazing diversity of behaviour, morphology, and mating patterns has been related to simple ecological differences in several animal taxa, from weaver birds (Crook 1964), through other birds (Crook 1965; Lack 1968), to ungulates (Jarman 1974), and primates (Crook and Gartlan 1966; Clutton-Brock and Harvey 1977). Even then we should merely have scratched the surface[1].

Instead, as we mentioned above, we have in mind the new rigour that has pervaded the field of comparative biology for a little more than a decade. It matters not at all whether you work with genetic elements, with

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[1] A partial but informative and entertaining history of comparative studies is given in the first chapter of Ridley (1983*a*).

viruses, bacteria, fungi, animals, or plants. The same principles apply if your subject is molecular evolution, the diversity of genetic systems, comparative morphology, physiology, ecology, or behaviour. If you are to interpret organic diversity correctly using comparisons, you need to think carefully about the methods you might use. This book is about those methods and the assumptions that they make.

1.2 The organization of this book

The book consists of seven chapters. This first chapter identifies the sorts of problems that the comparative approach can answer, and shows how it complements other approaches to problem-solving in evolution, such as optimality theory, population genetic models, and experimentation.

The second chapter identifies the biological causes of the most important problem facing comparative biologists, that of similarity among closely related species for almost any character that we look at. Closely related species often inherit traits from common ancestors. Treating species as independent points in statistical analyses may, therefore, greatly overestimate the true number of degrees of freedom. However, if we do not know why closely related species tend to be similar, our arguments will be based on statistical models that have no firm biological foundations—an unsatisfactory state of affairs.

Because the key to comparative analyses depends on understanding the phylogenetic relationships among the sample of species being considered, the third chapter discusses methods for reconstructing phylogenetic trees and ancestral character states. The importance of defining ancestral character states is that they allow us to estimate the amount of evolutionary change in each branch of a phylogenetic tree. This chapter will illustrate the importance of the assumptions we make about the way evolution proceeds: different models of evolution can produce quite different phylogenetic trees and ancestral character states.

On the assumption that phylogenetic trees and ancestral character states are known, the fourth chapter sets out to develop statistical tests that will determine whether different characters that exist in discrete states show evidence for correlated evolution. For example, caterpillars have sometimes evolved from being cryptic to being warningly coloured and, on occasion, they have also become distasteful to predators. Have the two traits, warning coloration and distastefulness, evolved independently of each other? After reviewing alternative methods, we develop a more general model for the evolution of characters that change state from time to time. That model, which assumes that characters evolve independently, can be used as a null hypothesis against which to test real data which, we might suspect, can demonstrate that correlated evolution has occurred. To pursue the noxious caterpillars for a moment, we might demonstrate that the phylogenetic ancestry of warning coloration and distastefulness does not accord with our model of the two characters evolving independently. We then return to the alternative methods that have been developed to detect correlated evolution between discrete character states. We show how they can be viewed as special cases of our more general model which make particular assumptions about branch lengths in phylogenetic trees and about similarity in rates of character change.

The fifth chapter turns to comparative analyses of continuously varying characters. On the basis of such characters, every species differs, however minimally, from every other species. As a consequence, there must have been change in the character states along all branches of the phylogenetic tree that relates the species in a sample. Two problems are posed by such characters. We must first define independent comparisons for statistical testing, and then we must devise appropriate tests that can detect correlated evolution. Over the last few years, many ways of seeking independence have been suggested and a number of tests have been devised. We assess the different tests in the light of the evolutionary and statistical models they are based on and we conclude that one particular approach, that of independent comparisons either between species and higher nodes or along the branches of the phylogeny, is the most satisfactory. Again, we stress the relationship between statistical models and the process of evolution. Each statistical model makes assumptions about the way evolution has occurred, and the choice of a statistical method is really the choice of a model of evolution.

The sixth chapter deals not with *whether* characters have evolved together, but with the *way* in which they show correlated evolution. The form of the relationship between two continuously varying characters can suggest to us reasons for the relationship. Allometry provides good examples because many characters vary with body size in ways that are dictated by physical processes. We shall describe a general statistical model that can be used to identify the forms of allometric relationships, and show how the more usual procedures for line fitting are special cases of the general model, each making different assumptions about sources of variation in the sample of organisms used. Those assumptions may or may not be valid in any particular case. We also show how independent evolutionary occurrences of functional relationships, such as allometric relationships, can be identified and used to estimate the general relationship. Finally, we discuss statistical models for identifying allometric relationships when the variable to be predicted is represented as a function of two or more predictor variables.

The seventh and concluding chapter argues that comparative analyses will be used more widely in molecular biology on the one hand and ecology on the other, but that many future developments of comparative methodology await more accurate understanding of evolutionary processes.

Comparisons are not made simply to help understand adaptation. In the next section of this chapter (Section 1.3) we discuss how the comparative method works at the interface between the two classic traditions in comparative biology—reconstructing phylogenetic trees and studying adaptation. We then examine more carefully the different types of question that comparative biologists might attempt to answer, and the types of comparison that can be used to answer them (Section 1.4). In particular, we discuss how adaptation can be inferred from comparative studies, and we distinguish between the two main types of comparative study which differ in the comparisons made. Directional studies compare ancestors with descendants, whereas non-directional studies compare character states among daughter taxa without considering explicitly the character state of their most recent common ancestor.

Having laid the groundwork for comparative studies, we then show how they can complement other approaches to problem-solving in evolutionary biology (Section 1.5). Comparative studies can be based on both the kinematic models of population geneticists and the optimality approaches favoured by behavioural ecologists. We use the two case studies of sex ratio and home range evolution to illustrate the complementary role of the comparative, experimental, and observational methods for tackling evolutionary problems (Section 1.6).

We conclude this introductory chapter with a short account of the atomization of characters and environments (Section 1.7): organisms can be butchered in many ways, but some cuts are more natural than others.

1.3 Two traditions in comparative biology: descent and guilds

There are two traditions of comparative biology (see Ridley 1983*a*), which might be called the descent and guild schools. For the most part, taxonomists belong to the descent school, whereas ecologists belong to the guild school. Taxonomists search for natural ways of classifying organisms and phylogenetic relationship forms the obvious unifying principle: organisms are classified on the basis of common ancestry[2]. Ecologists, on the other hand, recognize guilds as groups of animals that share a common way of life (Root 1967). Members of a guild may be close phylogenetic

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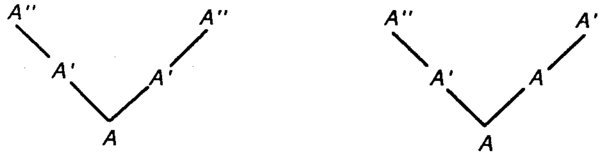
[2] There are schools of taxonomy which are not based on classification by common ancestry. We shall describe the most influential of them in Chapter 3.

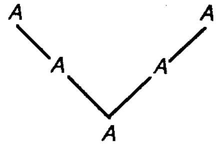
relatives, but frequently they are not. Convergent or parallel evolutionary change (Fig. 1.5) can lead to phenotypic similarities among the members of a guild that are not close relatives.

These two types of comparative biology need to be brought together. We make comparisons because we want to understand organic diversity, and that usually means unravelling the reasons for evolutionary change and stasis. Any difference among organisms, whether the trait is labile over evolutionary time or not, may eventually turn out to have an adaptive basis. Accordingly, it is important to ensure that procedures to incorporate information on phylogenetic relatedness into comparative tests do not rule



Parallel evolution

Convergent evolution



Identity by descent

Fig. 1.5. Three phylogenetic trees showing the evolution of a single character which may occur in any one of three states: *A*, *A'*, and *A''*. If each character state is unique to a particular environment (say *A* with E, *A'* with E', and *A''* with E'') then both parallel evolution (the same phenotypic change occurring in separate lineages: A' to A'' in the figure) and convergent evolution (the same phenotype arising from phenotypically different ancestors: A and A' both changing to A'' in the figure) may suggest evidence for evolution of adaptation by natural selection. If the environment has remained the same, as in the identity by descent case, adaptation still cannot be ruled out (phenotype *A* may be adapted to environment E). Separate evolutionary origins of the same character states, under either convergent or parallel evolution, define them as analogous character states. The single origin of the character state under identity by descent labels it homologous in the two taxa. We shall discuss in Chapter 3 how ancestral character states are reconstructed, but this figure presages one of the problems highlighted in that chapter. If the only information available is the character states of the pairs of extant species, and the most parsimonious phylogenetic trees are sought, then each tree would demonstrate identity by descent: the common ancestor of two species with identical character states would also be deemed to have had that phenotype. The frequency of convergent and parallel evolution would be under-estimated, while the frequency of identity by descent would over-estimated.

out the possibility that identity by descent from a common ancestor is maintained by selection. Evolutionary biologists have demonstrated many instances in which identity by descent is, indeed, maintained by selection (see Cain 1964; Endler 1986). In the next chapter we shall provide an explicitly adaptive scenario for the maintenance of identity by descent (Section 2.3.1).

1.4 The comparative approach for studying diversity

Comparative studies identify evolutionary trends by comparing the values of some variable or variables across a range of taxa. The variables may include descriptions of the environments inhabited by the organisms as well as phenotypic characters. Huey (1987, p. 76) describes these procedures as 'documenting the extent and pattern of organic diversity'.

We have been careful to avoid saying that comparative studies are only concerned with the study of adaptation. As we shall see throughout this book, comparisons do often help us to understand the adaptive significance of phenotypic variation. Stripped to the bone, however, the evidence for adaptive evolution revealed by comparative studies is correlated evolution among characters or between characters and environments. Nevertheless, such evidence can be convincing, and the success of one comparative test can lead to others that produce a better understanding of the reasons for organic diversity. Our goal is to identify the variable or variables responsible for variation in some other variable. For example, taxonomic variation in testes size among mammals may reflect the influence of two such very different variables as the production of testosterone and the production of spermatozoa. We can use variation in testes size as an example of how comparative studies often proceed.

Correlation
not
causation

Primates and other mammals with larger body weights generally have larger testes. This pattern might be expected for at least two reasons. First, larger bodied species need larger endocrine glands to maintain threshold levels of testosterone in the blood. Second, if larger bodied species are to fertilize an egg successfully after mating, they need the capacity to produce more spermatozoa than smaller species if they are to counter the dilution effects of a larger female reproductive tract. However, there are interesting comparisons which provide exceptions to the positive relationship between body weight and testes size. For example, the gorilla *Gorilla gorilla* is four times the body weight of a chimpanzee *Pan troglodytes*, but has testes which are one quarter the mass of a chimpanzee's. In a series of articles, Short (1977, 1979, 1981) developed the idea that the difference in relative testes size between the chimpanzee and the gorilla was a consequence of sperm competition. Female chimps regularly mate with several males during a single oestrus, and males can increase their chances of paternity by producing more sperm (like having more tickets in a lottery), hence the larger testes. Female gorillas mate with only one male, and sperm competition is therefore not important.

The sperm competition idea makes a testable prediction for other primates. Harcourt *et al.* (1981) predicted that those primates with relatively large testes would be the ones living in multi-male groups where females had the opportunity of regularly mating with more than a single male during a given oestrus. The prediction proved to be correct (Fig. 1.3). But the comparative tests did not stop there. Subsequent work on primates shows that those sexually selected traits having to do with competition for access to mates vary in predictable ways with testes size (Harvey and Harcourt 1984), and that rates of sperm production are higher in species with relatively large testes (Møller 1988*a*). Furthermore, analyses both within other orders of mammals (Møller 1989) and among birds (Møller 1988*b*) reveal similar relationships between testes size, sperm production and mating patterns (for a review, see Harvey and May 1989).

In the testes example, the pattern of variation suggested to Short a possible adaptive explanation. The first test of the explanation involved controlling for extraneous influences (in this case body size) while varying the presumed causal influence (the amount of sperm competition). An alternative to using statistical methods (such as regression analysis or partial correlation) to control for the effects of body size would have been to compare many species of the same size (Smith 1980) but, because of the relatively few species involved, that did not prove practical for primate testes. Subsequent tests involved other taxa and finer-grained comparisons which focused on other correlates of testes size, such as sperm production. The example shows how, once patterns and probable causal variables have been identified, comparative studies can begin, cautiously, to make inferences about adaptation. However, because comparative studies seldom have access to the actual selective forces, inferences about adaptation are partly a matter of good comparative methodology. The demonstration that similar relationships evolved in different families of primates, different orders of mammals, and in birds, lends additional credence to Short's explanation because it is unlikely that the same alternative explanation could be responsible for an association between mating system and relative testes size in all those taxa.

Other comparative studies can provide strong evidence against particular adaptive explanations for species differences. One example concerns life history variation among vertebrates. Some vertebrates seem to live faster lives than do others: even after body mass has been factored out by partial correlation, short gestation lengths are associated with early ages at maturity and short reproductive lifespans. It has been suggested that those species which live relatively fast lives are able to do that because they have higher metabolic rates (e.g. Brody 1945; McNab 1980, 1986*a*, *b*). When this idea was tested in both birds and mammals, there were no statistically significant correlations between speed of life and rate of metabolic turnover after controlling for differences in body mass (Harvey *et al.* 1990; Trevelyan *et al.* 1990).

In the next section we develop further some of these ideas about the methods and products of comparative studies. Immediately below we discuss what can and cannot be concluded from simple comparative relationships. We have in mind here specifically the inference of adaptation from comparative data. We argue that the inference of adaptation is often an explicitly historical one, that depends on being able to say something about the transition from ancestral to derived conditions. Nevertheless, as the testes example showed, it will often be possible to argue that differences are adaptive without knowledge of ancestral conditions.

Not always need reference to phylogeny

The subsequent section (Section 1.4.2) will examine further the difference between comparisons of ancestral and derived conditions (directional comparisons) and comparisons among taxa that do not specify ancestral and derived conditions (non-directional comparisons). Methods appropriate for examining these two different approaches will be discussed in Chapters 4 and 5.

1.4.1 Inferring adaptation from comparative studies

If comparative studies reveal only correlated evolution, how do we go about inferring adaptation from comparative relationships? We shall first explain what we mean by an adaptation, and then examine how the concept can be applied to comparative studies.

What is an adaptation? The answer to this seemingly straightforward question has been and will continue to be debated in the literature (e.g. Mayr 1982). Adaptation is an inherently comparative idea (see also Hinde 1975; Clutton-Brock and Harvey 1979). When we ask how white rabbits are adapted to snowy environments, our answer will inevitably make an implicit or explicit comparison with rabbits that are not white. For example, we might answer that: 'White rabbits are adapted to snowy environments because they are camouflaged against a background of snow, and are thereby protected against predators', by which we mean that, for rabbits living in a snowy environment, white provides better camouflage than other colours. Similarly, when we ask why leaves are an adaptation for flowering plants, we have in mind a comparison with plants that do not have leaves. However, we shall adopt a more restricted meaning of the term: for a character to be regarded as an adaptation, it must be a derived character that evolved in response to a specific selective agent. The rabbit's white coat would be an adaptation for camouflage if it evolved from a brown ancestral condition in response to selection for camouflage in snowy environments. If, however, it evolved from brown because of its improved thermal properties, it would not be an adaptation for camouflage but, perhaps, an exaptation for camouflage (Gould and Vrba 1982). How, does this notion of adaptation fit in the Darwinian scheme of things?

Although evolution by natural selection can produce adaptations, the concept of adaptation is not necessarily inherent in a description of natural selection. For example, Lewontin has often argued that evolution by natural selection occurs when: (1) there is phenotypic variation; (2) that variation is heritable; and (3) some variants leave more reproductive offspring than others (e.g. Lewontin 1978).[3] To introduce the idea of adaptation, several authors (e.g. Williams 1966; Brandon 1978; Dunbar 1982; Krimbas 1984; Coddington 1988) would modify this scenario to the effect that: (3) some variants function better than others and are thereby better adapted; and (4) the better adapted variants leave more offspring. To avoid circularity, we need to explain *why* some variants function better than others, and that accords with our understanding of adaptation. For example, white rabbits may leave more offspring than brown rabbits in snowy environments, and the reason *why* white rabbits leave more offspring is that they live longer than brown rabbits because they are less likely to be detected by predators. The process is specific to a particular environment, so that different variants may be the better adapted in different environments; brown rabbits would be better camouflaged in snow-free woodlands. Evolution by natural selection is also specific to a particular ancestral state: white rabbits must have evolved from something. The natural comparison, then, is between ancestral and derived traits.

Survival of
the fittest
tautology

According to the above perspective, adaptations are produced by natural selection. Coddington (1988, p. 5) comes near to our meaning of an adaptation, which he defines as 'apomorphic [evolutionarily derived] function due to natural selection'. If we were interested in finding out whether aposematic coloration among insects evolved to advertise distastefulness (Harvey *et al.* 1982) we should look for several different instances of the origin of distasteful aposematic insects from cryptic palatable ancestors. If, whenever distastefulness evolved in lineages of cryptic palatable insects, aposematic coloration soon followed, we should see that as useful support for our adaptive generalization.

The methodology that Coddington proposes for studying adaptation comparatively is summarized in Fig. 1.6. Character state 1 is shown here to have evolved in the branch linking the nodes that lead to species *B*

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[3] Heritability of traits will usually differ among environments (Falconer 1981; Lewontin 1974, 1982), and no distinction need necessarily be made between genetic and cultural transmission (Boyd and Richerson 1986).

and *C*. Character state 1 is then lost in the branch leading to species *E*. The adaptive hypothesis is that 1 evolved from 0 due to natural selection, and to perform derived function 1, denoted F_1. Implicit in the hypothesis is the belief that 1 evolved because it conferred an advantage to its possessors for performing F_1, compared to individuals with 0. Adaptation is here defined explicitly with respect to a primitive feature. This rules out the question 'What is 0 in species *A* and *B* an adaptation for?', at least with respect to the phylogeny given in Fig. 1.6. Even though 0 may be derived in these species with respect to some more primitive state, such a state is not represented in the phylogeny of Fig. 1.6.

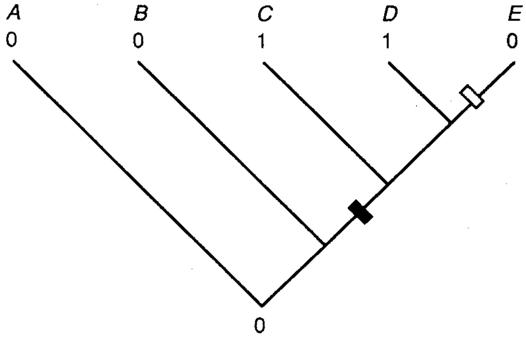

Fig. 1.6. Five species, labelled *A* to *E* are scored for a character which is either in state 0 or state 1. The dark cross bar indicates the acquisition of 1 from 0, and the open cross bar is the reversion of state 1 to 0. The hypothesis is that between the nodes leading to *B* and *C*, character 1 evolves from character 0 in response to natural selection. (After Coddington 1988).

Problem w/ knowing what Selective envir. was like and the genetic assemblage acted upon.

The secondary loss of 1 in species *E* produces a different origin of 0 which may be an adaptation with respect to 1. However, the evolution of 0 in that species follows rather than precedes the evolution of 1, and thus 0 in species *E* is not ancestral to 1. Thus, Coddington's methodology defines which taxa are to be used as 'control' groups for testing the adaptive hypotheses. Species *E* in Fig. 1.6, despite lacking 1, is not appropriate for testing whether 1 is an adaptation with respect to 0.

Coddington's strict cladistic approach to studying adaptation may seem restrictive to those used to studying adaptation by comparing the character states of groups of species or higher taxa that inhabit different environments or which differ in other ways thought to be responsible for variation in the trait of interest. Put another way, what is wrong with studying adaptation by assessing the fit or current utility of characters to their environments? The answer to this question hinges on a subtle but important distinction. If we believe that character variation is largely due to the effects of natural selection, then it is reasonable to suppose that variation in complex characters across current environments does represent *adaptive* variation in the sense that the character states associated with particular environments serve a function. We do not usually have an alternative theory to explain recurrent similar fits between a trait and the environment. However, analyses of current utility do not necessarily inform us of the origin of trait variation. That is, the associations of traits with environments does not necessarily imply that those traits are *adaptations* to perform particular functions in those environments, where by an 'adaptation to perform function X' we mean a character that arose by natural selection to perform function X.

adaptive
vs
adaptation

Some examples may help make these points. Suppose we were interested in whether long necks in mammals had evolved to help them browse from the leaves of trees because grass was in short supply. If we sought a correlation between leaf eating and long necks across mammals, it is perfectly possible that no significant relationship would be found. This is largely because the lack of long necks need not indicate the lack of selection pressure to feed on leaves: many mammals climb up trees to feed on leaves. Use of the climbing species as controls to test for long necks as an adaptation for leaf eating makes the same error as using species E in Fig. 1.6 as a control for species C and D. Species E may lack the character for reasons that are different from those in the ancestral condition of species A and B.

The proper comparative test in this instance would be to compare long-necked mammals with their short-necked ancestral forms. If it were also possible to argue that the short-necked ancestors of long-necked forms, such as the giraffe, lived in treeless environments whereas the long-necked forms always fed from trees, then long necks in the descendants would constitute evidence for adaptation.

Surely, though, if we actually find a relationship between character and environmental variation among contemporary forms we can give it an adaptive explanation? Here the argument has both semantic and plausibility components. Suppose, for example, that we find longer canine teeth in the adult males of primates species with intense male–male competition, and that the males of species lacking such competition also lack long canines. It seems reasonable to argue that long canines are an adaptation to male–male competition, which they probably are (Harvey *et al.* 1978). The criticism of such a conclusion, however, is that nothing in the 'current utility' methodology guarantees that long canines are the derived form. It seems very likely that they are, but if they are not it makes no sense to talk of long canines as an adaptation, with respect to short canines, for use in male–male competition. This may seem a mere semantic point but consider our position if males with long canines predated the origin of intense male–male competition among primates, we would have to give a somewhat different explanation for their present day association with mating systems.

This latter point brings up the plausibility argument. It is implausible that a costly character like long canine teeth could be *maintained* without having some function. The argument goes that if long canines had no function they would be lost by natural selection over evolutionary time. So, if we find them repeatedly in species with male-male competition, and if it can be shown that similar levels of male-male competition are not found in primates in which the males lack long canine teeth, some selective explanation is called for. The argument is slightly different from that which links the *origin* of a character to a particular selective force. Here, even if the origin of a character cannot be attributed to a particular selective force, it is ~~suggested that it is~~ maintained by it. Regardless of their origin, the adult males' long canines have a function. In this sense, *variation* in canine length among species is adaptive even if the long canines are not adaptations in Coddington's sense of the term. Gould and Vrba (1982) would label long canine teeth in this context an exaptation. This is a useful term in so far as it calls our attention to the fact that the particular solution to an environmental problem may depend on what selection has to work with. The following (unlikely) scenario illustrates the point. Long canines evolved in the adult males of ancestral primates as a result of selection to defend their mates and young against predators (DeVore and Hall 1965). The primates subsequently have evolved societies with intense male-male competition and the long canines were used in combat between males. The long canines are exaptations. (We should point out, however, that if canines became even longer in response to selection for fighting than they were to ward off predators, the difference is an adaptation.) The original predators now went extinct and, as the primates radiated, those lineages in which male-male competition became less intense evolved shorter canines because males with long canines were less fit. The short canines are the adaptation.

Coddington (1988) provides a nice example that reinforces the points we are making about the current utility of a character. An accepted dogma in arachnology was that the orb web evolved from a primitive cob web as an adaptation for catching flies more effectively. However, careful cladistic analysis indicates that orb webs were ancestral to cob webs (Coddington 1986*a*, *b*), so the proper question is what were cob webs an adaptation for? If an analysis of current utility shows that, indeed, orb webs are more efficient than cob webs at catching flies, how should the variation be interpreted? Originally, we might have supposed that the correct mutants to allow the evolution of orb webs from cob webs had not occurred but that if they had then orb webs would have evolved in cob web lineages. The cladistic analysis argues against that interpretation.

Causal relationship btwn. env. & char. not make char adaptitive

We have already mentioned the problem that environmental correlates of phenotypic variation may result from the confounding effects of some third variable which does not have a direct effect on (nor is directly affected by) the character state or trait in which we are interested. But, even when there is a causal relationship between the environmental variable and character state, does the relationship have to be adaptive? The answer to this question is no.

One reason why adaptive traits have apparently failed to evolve in some situations is because of genetic constraints. For example, toxic compounds are frequently sequestered by caterpillars from their food plants, thus rendering those species feeding on poisonous food plants unpalatable. Caterpillars do not synthesize such toxins, which means that caterpillar species living on palatable food plants have not evolved to become distasteful (see Rothschild 1972). If ancestral caterpillars lived on toxic food plants and were unpalatable, but we could identify several instances of the evolution of palatability associated with a switch to host plants that are not toxic, the evolutionary association might well not be adaptive. If caterpillars living on palatable food plants could have evolved to become toxic to their predators, they probably would have done.

Adaptive story telling

There have been many useful criticisms of the so-called 'adaptationist program' (e.g. Lewontin 1978, 1979; Gould and Lewontin 1979). The comparative method might seem to fit nicely into the mould defined by the adaptationist program, which was caricatured by Lewontin (1979): (1) find phenotypic variation; (2) ascribe genetic causation to that difference; and (3) produce an adaptive explanation for the difference by, for example, 'imaginative post-hoc reconstruction'. That procedure is, indeed, adaptive story telling, and the trap is all too easy to fall in to. Our procedure runs differently: (1) find phenotypic variation among taxa; (2) produce one or more adaptive explanations for that variation which may include assumptions about heritability and ancestry; and (3) test the explanation(s) by predicting particular environmental or constitutional correlates of the variation and by comparing ancestral and derived character states wherever possible.

To summarize this section. Comparisons between contemporary forms, unsupported by attempts to reconstruct ancestral character states, often reveal correlations between character states or between character states and environments that can readily be given an adaptive interpretation. Not all such differences are, however, adaptive and we must be careful to examine alternative explanations. The proper inference of an adaptation *per se* depends critically on understanding which features are primitive, and which derived. Many characters have different functions from those for which they evolved. As a consequence, we should not too readily label characters as adaptations to their current function, even though they may confer current selective advantage. Nevertheless, changes in such characters from their original state can be thought of as adaptive changes.

1.4.2 Directional and non-directional comparisons

Two different but complementary trends have recently emerged in comparative studies (Huey 1987; Pagel and Harvey 1988*a*). What we shall call 'directional' studies make use of ancestral character states to infer the direction and rates of evolutionary change between ancestors and descendants. Not surprisingly, in the absence of a good fossil record, this branch of comparative studies draws on developments in the reconstruction of phylogenies and ancestral character states. In contrast, 'non-directional' studies analyse evolutionary trends across either contemporary species, or across higher nodes which are usually at a similar taxonomic or phylogenetic level. In the past, non-directional studies did not make much use of phylogenetic information. However, the picture is changing rapidly as new developments in the analysis of contemporary forms which do rely on phylogenetic information have become available.

directional /

non directi

Stated more simply, the two different approaches to comparative analysis can be thought of as looking down lineages over time versus looking across different lineages (Fig. 1.7). The distinction between the directional and non-directional approaches is more than just conceptual. Each approach has given rise to one or more comparative techniques, some appropriate to discrete variables, some appropriate to continuous variables. These techniques are the topics of Chapters 4 and 5.

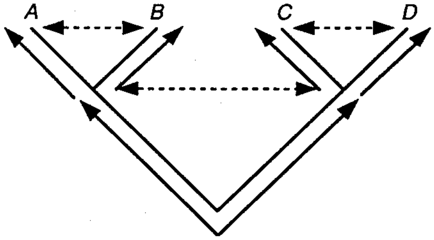

Fig. 1.7. The difference between directional and non-directional comparisons. The phylogenetic tree shows the relationships among the four extant species *A*, *B*, *C* and *D*. Species A and B are in one genus, with species *C* and *D* in another. The solid arrowed lines represent directional comparisons between ancestors and descendants, while the dotted arrowed lines represent non-directional comparisons between taxa that each have part of their ancestry independent of the other.

Huey (1987) and Huey and Bennett (1987) report an example of a directional analysis of changes in preferred body temperature and optimal running temperatures in lizards. These authors were interested in the idea that changes in optimal running temperatures over evolutionary time have kept pace with changes in preferred body temperatures. If they have, then the differences between ancestors and descendants, measured over many different branches of a phylogeny, should covary with a slope of 1.0. In fact, they found that this slope was significantly less than 1.0, indicating that changes in optimal running temperatures have not kept up with changes in preferred body temperatures in these lizards. Because directional analyses rely on explicit reconstruction of ancestral states, these authors were also able to describe the direction of evolutionary change. Over time lizards have evolved to run at lower preferred temperatures. We shall describe in more detail in Chapter 5 the method that Huey and Bennett (1987) used.

Directional tests are also available for discrete characters. Some studies have simply asked whether particular evolutionary sequences among states of a single character are more likely than others. For example, Gittleman (1981) tested the suggestion that the only types of transition likely between patterns of parental care in bony fish would be between: (i) no care and paternal care; (ii) no care and maternal care; (iii) paternal care and biparental care; and (iv) maternal care and biparental care (Fig. 1.8). Of 21 transitions, all were of the predicted type and none were between: (v) biparental care and no care; or (vi) paternal care and maternal care. Similarly, Carpenter (1989) tested West Eberhard's (1978) rather complex model for the evolution of patterns of social behaviour in the vespid wasps. Some transitions did not accord with prediction, although others did.

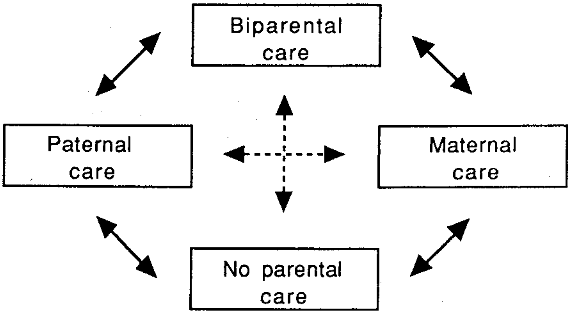

Fig. 1.8. Directional tests of parental care in fishes. Four states are possible. Solid arrowed lines are hypothesized transitional routes, whereas dotted lines do not accord with the hypothesis. All 21 transitions detected by Gittleman (1981) were in accord with the hypothesis.

Other directional tests are available to examine the correlated evolution of two or more characters. Donoghue (1989), using a method developed by Maddison (1990), tested whether the evolution of dioecy in plants was more likely to occur in plants with fleshy or with dry propagules. There was only partial support for the hypothesis. Donoghue's results, and Madison's method are described in Chapter 4.

The more traditional approach to comparative studies involves non-directional analysis of contemporary forms. As will be seen in Chapters 4 and 5, a variety of methods have been developed for this kind of analysis. Many of the now classic studies of allometric scaling are examples of this approach. More recently, several new techniques have been developed that measure pairwise differences between sister taxa at all levels of a phylogeny. These techniques, described primarily in Chapter 5, offer much hope for extracting from a comparative data set a group of independent comparisons with desirable statistical properties, each of which bears on the comparative idea being tested.

Superficially, non-directional analyses would seem not to make as much use of phylogenetic information as do directional analyses. This has been true in the past. However, non-directional analyses now rely to the same extent as directional methods on patterns of phylogenetic branching, and on the reconstruction of ancestral characters. Where directional analyses make use of this information to examine directions and rates of evolutionary change, non-directional analyses examine the nature of covariation among different phylogenetically defined groups. Sometimes such relationships vary depending upon the taxonomic or phylogenetic level. Huey (1987), for example, summarizes several studies on the relationship between 'performance breadth' (the range of body temperatures at which lizards can exceed some level of performance), and the range of body temperatures at which they are commonly found in nature. Across genera these two traits are negatively correlated. However, among more closely related taxa, the expected positive relationship holds.

The choice between the two sorts of methods, then, is a choice between the kinds of ideas one wants to test. Directional tests offer much promise as techniques for phylogeny and ancestral character state reconstruction improve. Furthermore, they test directly the transition from primitive to derived forms, and so are more immediately responsive to the criteria outlined in the previous section for studying adaptation. Directional tests may prove to be very useful for detecting instances of parallel and convergent evolutionary change (Fig. 1.5). In some instances parallel change may be masked if non-directional analyses are used (Fig. 1.9). Non-directional analyses of contemporary forms are particularly useful for detecting and describing the nature of the current utility or fit between characters and environments across taxa. Coupled with careful biological

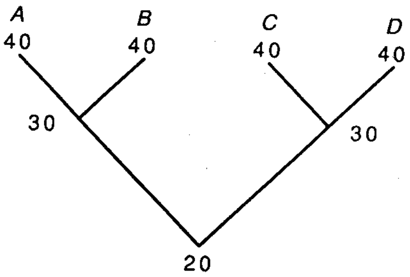

Fig. 1.9. The same phylogeny as Fig. 1.7 but with the state of a particular character, such as body weight, given for each species and node. Directional analysis would reveal parallel evolutionary change, or Cope's Law (Cope 1885; Newell 1949), but non-directional analysis would detect no differences among the character states of taxa being compared. An accurate directional analysis would depend on an accurate reconstruction of ancestral character states. For example, if higher level nodes were estimated as the average of daughter taxon values, directional analyses would reveal no differences between primitive and derived forms.

(2

and phylogenetic arguments these analyses can also make inferences about adaptations. Many of the newer techniques for non-directional analysis work at the level of making pairwise comparisons between closely related taxa as a way of assessing the number of times that some evolutionary relationship has evolved.

1.5 The comparative method and other ways of studying evolution

Evolutionary biologists use a variety of different methods for studying their subject. The results of comparative studies are often used to complement those from observations and experiments. The interpretation of results from comparative studies depends on the statistical test used, which is itself based on an implicit or explicit model of evolutionary change. In this section we examine briefly the relationship of comparative studies to other methods for solving problems in evolutionary biology. We start by distinguishing between two ways of modelling evolution (kinematic and optimality), both of which have their use in comparative studies. We then examine two case studies where the optimality class of model has taken a central role for integrating observational, comparative and experimental results.

kinematic
optimality

There are two fundamentally ~~different~~ approaches which are in common use for studying evolutionary change and evolutionary equilibria. The first is the kinematic approach used by population geneticists (e.g. Lewontin 1974; Crow and Kimura 1970). Genotypes (or phenotypes) are specified with set frequencies, selective coefficients, migration rates, and mutation rates; and, perhaps, population sizes are specified in a spatially structured population. The model is then set to run for a specified number of generations, or equilibrium gene frequencies are sought. We shall use a kinematic model as our null model for independent character evolution in Chapter 4.

The second approach, favoured particularly by those studying behavioural ecology and animal mechanics, is optimality modelling (Maynard Smith 1978; Oster and Wilson 1978; Alexander 1982; Krebs and McCleery 1984; Stephens and Krebs 1986). Much of the rest of this chapter will be devoted to explaining what optimality models are, and how they are used in comparative tests. We stress from the outset that we are not advocating the unbridled use of optimality models, but pointing to their value as an aid for understanding many naturally complex systems, not least because of their ability to generate testable predictions.

The procedure for an optimality test is to specify an optimality criterion, ① ② to define alternative strategy sets, and to estimate the pay-offs for each ③ strategy thus determining which is optimal under the conditions specified. The optimal strategy is the one predicted to occur. For example, foraging birds may have been selected to maximize the weight of food brought back to nestlings per unit time (optimality criterion). If there are alternative prey types consisting of large and small worms, birds might adopt one of three foraging strategies: gather all worms encountered, gather large worms only, or gather small worms only (alternative strategy sets). Different foraging strategies will result in different weights of worm brought back to the nestlings per unit time (different pay-offs), depending perhaps on the handling time for each type of prey, the weight of large versus small worms, and the time taken to travel between food patches and the nest. Birds will be expected to adopt that foraging strategy with the highest pay-off.

The reason for using optimality theory in evolution is that, subject to certain constraints, natural selection is expected to maximize Darwinian (or, more properly, inclusive) fitness, which is therefore the appropriate optimization criterion. A bird's beak might be engineered so that it provides an optimal tool for catching worms, and efficiency at catching worms in the short term may be a suitable optimization criterion as far as foraging is concerned. Birds which catch more worms leave more offspring. Optimal foraging theory considers a number of short-term optimization criteria, any one of which might ultimately maximize Darwinian fitness in a particular case. According to circumstance, maximizing the mass of worms provided per unit time, minimizing the amount of time taken to produce a set mass of worms, or minimizing the energy utilized while catching a fixed mass of worms might be an appropriate optimization criterion. For example, if foraging entails an increased risk of predation for either the adults or for the nestlings while the adults are away from the nest, time minimization might be more suitable than energy maximization. On the other hand, if predation is unimportant, a parent's Darwinian fitness might be limited by the rate at which it can feed its offspring.

One of the valuable facets of optimality modelling is that specified constraints are built into the system. We assumed above that a foraging bird was constrained to eat worms but not nuts, and that it took a set amount of time to handle a prey item or to travel from the nest to the foraging patch. Optimality models force us to make our constraints and our assumptions clear. In fact, one model's optimality solution may be another model's constraints. We can illustrate this point using the feeding bird example. One of the constraints concerned travel time. If larger birds could travel faster but need to use more energy for both maintenance and movement, we might reasonably seek the optimal body size for a bird that used a particular foraging strategy. Because the extra energy that a larger bird uses must be provided by food, our optimality criterion might be that body size which maximized the net rate of return of energy to the nest.

1.5.1 Implicit and explicit optimality models

Many of the best comparative tests, particularly those in animal mechanics, are based on *explicit* optimality models (Alexander 1968, 1982). However, preliminary comparative tests of adaptationist ideas are often based on *implicit* optimality models. We do not see this as a problem, but as a reasonable first step in a scientific investigation. For example, some years ago it was unclear to many primatologists whether sexual dimorphism in body mass among monkeys and apes resulted from selection for feeding niche differences between the sexes, as seemed likely for some birds (Selander 1972), or from sexual selection. If sexual selection is important, sexual dimorphism should be more pronounced among the more polygynous species, where one or a few males denies other males access to a group of breeding females. Polygyny places a premium on larger male body size because larger males are more likely to win fights. On the other hand, if feeding niche differentiation is more important, monogamous pairs living in a shared territory should be the most dimorphic. As it turned out, the sexual selection explanation made the correct prediction not only for primates (Clutton-Brock and Harvey 1977; Clutton-Brock *et al.* 1977) but also for several other groups of vertebrates including other orders of mammals, as well as some reptiles and amphibians (Alexander *et al.* 1979; Gittleman 1983; Shine 1978, 1979; Berry and Shine 1980). It took several years before more explicit optimality models were developed to predict or explain the degree of dimorphism for particular species. Sandell's (1989) optimality model for the evolution of sexual dimorphism in stoats (*Mustela erminea*) is a fine example. This, we believe, is an appropriate role for comparative studies of adaptation. They can usually demonstrate the generality of adaptive trends but, in the absence of suitable data, often they cannot test the fine details. We need to describe and explain both general trends and fine details if we are to achieve the real synthesis in evolutionary biology, which is to understand organic diversity. We shall return to this point later. Before doing that, we shall show that optimality models ~~in comparative studies are often less~~ explicit than ~~may appear~~ at first sight.

trends & details

Explanations of comparative associations based on quantitatively defined functional relationships can mask unstated (and possibly unrealized) assumptions. Armstrong (1983), for example, claimed that the 0.75 exponent linking adult brain (A) to adult body mass (B) among mammals of different species ($A \propto B^{0.75}$) was a consequence of metabolic turnover constraining adult brain size: brains are energetically costly structures, and mammals have the largest brain mass that their metabolic turnover can maintain. Martin (1981, 1983) had both pre-empted Armstrong's explanation and cast doubt on it when he pointed out that the brain mass of birds and reptiles increases with the 0.56 power of adult body mass. Martin suggested that metabolic rate did indeed limit the evolution of brain mass, but through a different route: neonatal brain mass in mammals (N) was limited by the rate at which mothers could provide nutrition for their offspring. Maternal basal metabolic turnover (M) scales with the 0.75 power of body mass across species ($M \propto B^{0.75}$), and adult brain mass scales in direct proportion to neonatal brain mass ($A \propto N$). Martin argued, correctly, that the exponent linking the neonatal brain mass to the mother's body mass in mammals should be 0.75 ($N \propto B^{0.75}$). He also suggested that the 0.56 exponent in birds and reptiles was a consequence of their laying eggs. Mother's body mass constrains egg mass, and egg mass constrains neonatal brain mass, both according to a 0.75 exponent. As a consequence, neonatal brain mass should scale on mother's body mass to the $(0.75)^2$, which is about 0.56.

Martin's explanation is based on tests that involve juggling exponents, but that is no bad thing in itself because it may give biological insight. But why should the particular exponential relationships hold? If we take the relationship of metabolic rate to adult body mass as given, even if we do not yet know the cause, what are the supposed costs and benefits to a mother of providing more or fewer calories to her offspring's brain? Why should mothers belonging to related species of different sizes be able always to provide the same fixed proportion of their metabolic turnover to their offspring? Furthermore, even if it is plausible that mothers should supply a constant proportion of their metabolic turnover to their eggs, why should neonatal brain mass scale on egg mass with an exponent of 0.75? The egg must provide nutrient to nurture the young and its growing brain. It is therefore necessary to know the curves of neonatal mass and neonatal brain mass against time of incubation, and to compare these across eggs of different sizes, as a first step towards estimating how neonatal brain mass or neonatal mass might be expected to scale on egg mass.

As it happened, there was no need to develop Martin's argument because mothers belonging to species with high basal metabolic rates for their body size do not produce young with relatively large brains, as Martin's theory would predict (Pagel and Harvey 1988*b*, 1990). In other words, there are species deviations from the allometric relationship linking maternal body weight to metabolic turnover which do not correspond to deviations from the relationship linking maternal body weight to neonatal brain weight. If Martin's prediction had held, the next investigative step might have been to develop an explicitly formulated model, the assumptions of which could be tested, possibly using comparative data.

1.5.2 Symmorphosis as an explanation for scaling laws

Perhaps the most ambitious claim for optimality in evolution is symmorphosis. The idea is that each of the components of a physiological system should match the maximal requirements of the overall system. The system must perform at maximum capacity, but components are not likely to be over-designed because 'maintaining biological structures with their high turnover rates is costly' (Taylor and Weibel 1981, p. 3). Although Taylor and Weibel argued that symmorphosis may serve as a unifying principle for anatomy, Calder (1984) went further and suggested that it may provide a theoretical basis for scaling relationships. Weibel and Taylor (1981) predicted that the interspecific scaling of respiratory structures across animals of different size should match the scaling of maximal oxygen consumption. On the whole, the data went against their prediction. Garland and Huey (1987) took a slightly different approach and asked if species with high or low rates of maximal oxygen consumption for their size were those with high and low structural capacities to match (e.g. pulmonary diffusing capacity, mitochondrial volume densities, and capillaries per cross-sectional area of muscle). Again, the results tended to go against the idea of symmorphosis. Various explanations for the results are possible. One is that the components of the respiratory system have not been selected to function independently of other physiological and biochemical systems. Over-design for one system may constitute adequacy for another (Garland and Huey 1987). One of the heuristic contributions of the idea is that comparative results may reveal excess capacity for one function, and a legitimate question is now to seek the cause. For example, why are there more mitochondria in some species than appear to be needed by their respiratory systems working at maximum rate?

1.6 Testing adaptationist ideas using experiment, observation, and comparison

We have seen that comparative relationships can suggest adaptive scenarios which can then be tested and often falsified using other comparative relationships. What, then, can experiments achieve that comparisons cannot? One answer is that comparisons can provide an internally consistent story but, unlike experiments, they usually cannot distinguish cause from effect. (If ancestral character states were accurately recorded, prior evolution of one character state invariably followed by the evolution of a second character state may in fact distinguish cause and effect, as we saw in Section 1.4.2). Another advantage of experiments is that only one variable (the test variable) need differ among the various treatments, whereas with comparisons it is likely that many uncontrolled variables differ among taxa in addition to the variable of interest.

The complementarity of experimental and comparative approaches developed within the framework of optimality theory is nicely illustrated by work on sex ratio variation in the Hymenoptera and on foraging models and territory size among birds. These examples also demonstrate how optimality models can sometimes be used to provide quantitative predictions about comparative relationships.

1.6.1 The sex ratio

Fisher's (1930) argument for the equality of sex ratios was an early application of optimality theory to evolution. The optimality criterion is to leave the greatest number of grandchildren, and the strategy set is defined by the range of probabilities (zero to one) that any offspring produced will be female. Fisher assumed that male and female offspring cost different amounts, so that the total number of offspring produced by a female depended on the sex ratio, and he concluded that the evolutionarily stable investment strategy was to invest the same into both sexes. If two males cost the same to produce as one female, the evolutionarily stable sex ratio would be two males to one female. Several assumptions were built into Fisher's model and, as they are changed, so does the optimal investment strategy (Hamilton 1967; Charnov 1982).

Hamilton (1967) suggested that producing sons can often result in diminishing returns. For example, if a mother's male offspring competed among only themselves for exclusive mating access to females (Hamilton termed this 'local mate competition'), then one son would produce as many grandchildren for her as would any number of additional sons. The mother would leave more grandchildren if she produced one son and invested the other resources in daughters. Furthermore, if mating between sibs is common in the population, there is a second advantage for a mother producing more daughters: they provide additional mating opportunities for her sons (Taylor 1981). Several models predict the equilibrium sex ratio under different degrees of local mate competition and inbreeding (see Harvey 1985).

Hymenoptera provide good material to test these ideas because of the mother's ability to determine the sex of each offspring by deciding whether or not to fertilize an egg (Hamilton 1967): fertilized eggs become daughters and unfertilized (haploid) eggs develop into sons. Differences in population structure among species, associated with differences in local mate competition and degree of inbreeding, have provided useful material for comparative tests.

Sex ratios might be expected to be biased towards females when the brood mates before dispersing, because in such species both local mate competition and inbreeding are likely to be common. Scolytid bark beetles are of particular interest here (Charnov 1982) because some species mate before and others after dispersal. As theory predicts, those species which mate before dispersal have female-biased sex ratios, whereas those which mate after dispersal have sex ratios near equality. Similarly, the presence of winged males in fig wasps is an indicator of how much mating takes place after dispersal, and there is a positive relationship between the absence of winged males and the proportion of females (Hamilton 1979). In another notable comparative study, Waage (1982) examined sex ratio variation among species of Scelionid wasps which parasitize the eggs of other insects. One parasitoid egg is laid per host egg. Waage argued that those host species which laid small clutches would be exploited by a single parasitoid at most, but when host clutch size was large several Scelionid females might parasitize a single host clutch. Local mate competition should, therefore, be more intense when host clutches are small, and we should expect a positive correlation between the proportion of males per parasitoid clutch and host clutch size. Waage's data demonstrate the predicted correlation (Fig. 1.10), with the exception that when host species laid single eggs the parasitoids did not produce a heavily female-biased sex ratio, which was to be expected because the singletons produced would have to disperse in order to find a mate.

Although the cross-species comparative data can be nicely explained by the models, it is always possible that some other component of the biology of the species in the sample is responsible for the sex ratio differences. Experimental studies performed *within* species can control for such variables. For example, laboratory experiments on the wasp *Nasonia*

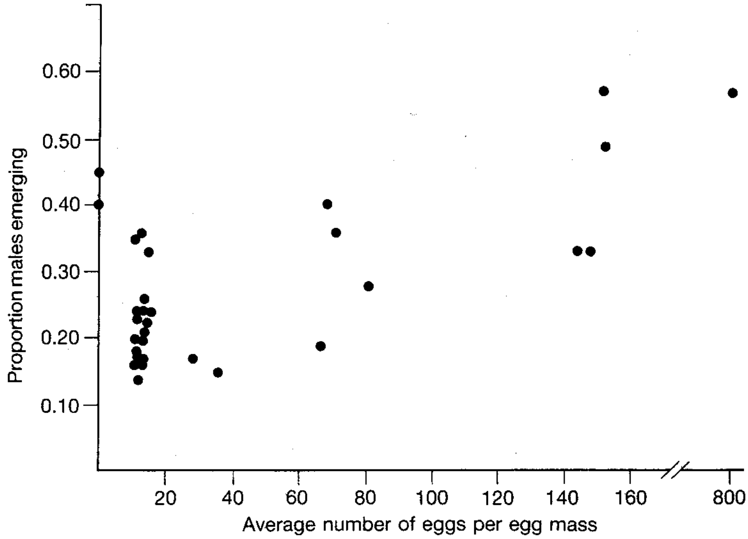

Fig. 1.10. The proportion of males emerging from Scelionid wasp clutches plotted against host egg mass size. Each point is a different species. Sex ratio theory, invoking local mate competition, predicts both the overall positive correlation and the observed exception that host species laying single-egg clutches have parasitoids with a sex ratio near 50:50. (After Waage 1982).

vitripennis showed that the sex ratio of emerging adults shifted from a strong female bias towards equality as more parasites were given the opportunity to lay their eggs on groups of host pupae (Walker 1967). This is to be expected because both local mate competition and inbreeding should be reduced when more broods are laid per host and when wasps are emerging simultaneously from nearby hosts. Subsequent work by Werren (1980, 1983) demonstrated that super-parasitism and host clumping resulted in sex ratio shifts, but that sex-specific mortality among parasites was not involved. Furthermore, the sex ratios in the smaller brood laid by super-parasitic second females accorded with theoretical predictions based on brood sizes and the proportion of males laid by the first female (see Fig. 1.11). (Orzack's (1986) experimental results from the same species found a poor fit with theory which, he suggests, is due to constraints on the wasps' ability to detect previous oviposition and to produce an exact sex ratio.) Other experimental studies also provide excellent tests of the theory (e.g. Herre 1985, 1987).

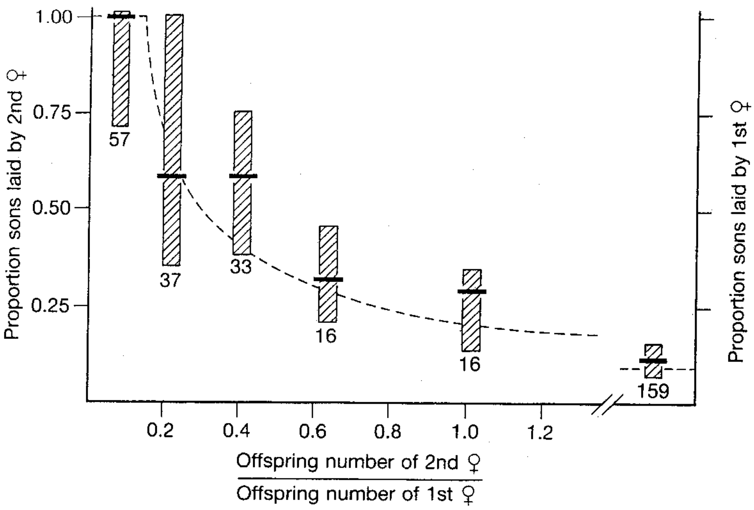

Fig. 1.11. Super-parasitic female wasps of the species *Nasonia vitripennis* lay clutches with higher proportions of male eggs. Data from 159 super-parasitized hosts show that, as predicted by sex ratio theory (dotted line), the super-parasitic female decreases the proportion of sons laid as a function of her brood size relative to that of the first female. (After Charnov 1982).

1.6.2 Home range and and territory size

A similar but less complete story can be told for the development of our understanding of the determinants of variation in territory and home range sizes among vertebrates. Preliminary comparative studies in the 1950s, 1960s, and 1970s examined the ways in which species' territory and home range sizes change with body size and diet (Hutchinson and MacArthur 1959; McNab 1963; Schoener 1968; Milton and May 1976). A reasonable question to ask at that time was whether larger animals need larger territories to satisfy their larger metabolic needs. As predicted, territory size did increase with body size and, furthermore, species living on more sparsely distributed food resources also had larger territories.

The next step was to ask whether territory size increased with body size in a quantitatively sensible way. Because, as we have seen, metabolic rate increases with body weight raised to the 0.75 power, presumably the minimum size, continuously productive territory (energy produced per unit time) for animals with similar diets living in similar habitats would also be expected to increase with the 0.75 power of body mass (*contra* Lindstedt *et al.* 1986). The data did not accord with that expectation: territory size in a variety of taxa increased with body size with an exponent appreciably greater than the metabolic exponent (e.g. Harvey and Clutton-Brock 1981; Gittleman and Harvey 1982; Mace and Harvey 1983; Lindstedt *et al.* 1986).

Several possible causes for this discrepancy seemed likely. First, suitable habitat is not continuous, and larger-bodied species must take in a disproportionate area of unsuitable habitat. Second, the acceptable food spectrum may change with body size (Schoener 1983). For example, individuals supplying food to a nest in the centre of a territory might have evolved an optimal foraging strategy resulting in the selection of only the larger food items at an increased foraging distance from their nest. Larger bodied species might become increasingly selective at greater distances from the nest, possibly because of intruder pressure at the nest. It is both unnecessary and impractical to perform detailed field observations and food manipulation studies on more than a few species in order to determine the likely reasons for the comparative relationship. A series of optimality models has been developed, based on a variety of optimization criteria, which predict different relationships between territory size and body size (Schoener 1983). Also, the likely optimization criteria are becoming better known as a consequence of carefully controlled field and laboratory experiments (Davies and Houston 1984; Stephens and Krebs 1986). The integration of foraging theory with comparative studies has been a long time coming, in part because it has proved difficult to paramaterize simply the cost and benefit curves for foraging animals.

1.7 Defining characters and environments

We have described the comparative biology that concerns us here as belonging to the 'the guild school'. That may have seemed an unfortunate denomination because ecological guilds are rather fuzzy objects (but see Adams 1985). Originally, Root (1967, p. 335) defined a guild as 'a group of species that exploit the same class of environmental resources in a similar way'. Just as Root's concept has been of enormous heuristic value in ecology, so a catholic interpretation of his definition captures the essence of character states and environments that are used in comparative analyses. For example, winged animals exploit air for flight and animals with eyes use light for vision. Both wings and eyes have evolved on separate occasions in different lineages. If we were interested in adaptations for flight, we should compare the guild of flying animals (which would contain most birds, bats, and beetles) with each other and with the guild of their flightless relatives (such as crocodiles, cetaceans, and collembola). However, if our interest was adaptations for a carnivorous diet, our guild structures would naturally change.

Character states or environments may need to be redefined as we learn more about the problem we are tackling, particularly about how our study organisms interact with their environments. After all, if we were interested in coloration among insects as an adaptation to avoid predation by reptiles and we found that reptiles do not have colour vision, we should translate our colour scores to a monochromatic scale. To illustrate the major problems associated with the definition of character states and environments, we shall take two further examples in a little more detail. The first is beak morphology in birds and the second is rates of genetic recombination in mammals.

Our first example concerns the need for careful definition of environments. Hawks, shrikes and Australian shrike-tits have very similar beaks. A comparative analysis suggests that long curved beaks have evolved independently in each taxonomic group. Beaks are used for feeding, so we might assume that the three groups have similar diets. We should be wrong. Hawks and shrikes are predators of small vertebrates and large insects, whereas shrike-tits feed on small insects. However, to get at the small insects, shrike-tits need to rip the bark from trees. Although their diets are not the same (Simpson 1978, p. 218), 'in all three groups the function of the beak is to seize and rend and the fact that different things are seized and rent is irrelevant. The functions are the same in all three, and an inference from comparison of similar selection pressure and similar featural response is valid'.

The procedure we have described for the investigation of factors influencing beak shapes has been labelled 'progressive ad hoc optimization' by Lewontin (1979). If theory does not explain the data (diet is not correlated with beak shape), then adjust the theory a little until it does (feeding mode is correlated with beak shape). Lewontin thinks that this is an unsatisfactory way to do science. We see it as a useful way of establishing the truth.

Your (considered) opinion?

Our second example illustrates how characters may need to be reassessed in the light of comparative evidence. Why do rates of genetic recombination vary among mammals? Interspecific comparisons reveal fairly poor relationships between recombination rates and factors that might be expected to influence them (Burt and Bell 1987). For example, higher host recombination rates may be favoured when parasites have several generations per host generation to evolve pathogenic strains. Other things being equal, higher recombination rates might then be expected in host species with longer generation times. Only about 22 per cent of the interspecific variance in recombination rates is accounted for by generation length, estimated by age at maturity. But recombination rates depend on both chromosome number and chiasma frequency. The percentage of variance in chromosome number and in a measure of chiasma frequency accounted for by age at maturity are about 1 and 77 per cent respectively.

In fact, it has proved very difficult to find any good correlates of chromosome number, despite years of effort (Williams 1966; Bell 1982); perhaps the number of chromosomes is a character that does not respond readily to selection? In any event, the constituents of recombination rate should be treated separately in comparative analyses. Biologists were not to know this in advance. The most appropriate atomization of characters is not always obvious (Thompson 1917, p. 713; Gould and Lewontin 1979). The recombination rate example also illustrates how in our search for the adaptive significance of character states, we often seek associations between pairs of characters rather than between characters and environments.

Just as we take a liberal interpretation with the word character, so we do with the concept of phenotype. For the purposes of this book both character and phenotype can refer to any ~~morphological or behavioural~~ trait that differs among species. Very often we do not know the extent to which interspecific differences are caused by environmental or genetic differences, and we usually have little information about their ontogeny. Most comparisons are among adults, although from time to time we shall refer to differences among juveniles. Our approach is pragmatic. We want to reveal new patterns and to test interpretations of old ones. Such studies heighten our appreciation of the importance of both development and genetics in the study of evolution. Comparative studies reveal crucial unexpected differences or lack of differences among taxa that point to the importance of developmental systems and genetic constraints (by which we mean lack of suitable genetic variance on which selection can be effective). We have no doubt that, as they have in the past, comparative studies in the future will reveal new cases of heterochrony and neoteny (Gould 1977). As we shall discuss in Chapter 2, the absence of some comparative trends in some taxa is undoubtedly a result of insufficient suitable genetic variance on which selection can act—and differences in comparative trends between taxa are often the result of different phenotypic responses to similar selective pressures. The extent to which those different responses might be viewed in terms of proximity to alternative adaptive peaks in the sense of Sewall Wright (1932) is open to both question and test (Ridley 1983*a*).

Take it
even
further

1.8 Summary

When similar character states evolve independently in similar environments, it is natural to ask how they adapt their bearers to survive and reproduce in those environments. However, similarity among closely related species provides evidence for identity by descent from common ancestors. Modern comparative methods attempt to distinguish independent evolutionary origins of character states from cases of identity by descent, even though both may have an adaptive basis: similarity among closely related species may be selectively maintained. When attempting to interpret comparative evidence, it is also important to distinguish the selective forces responsible for the origin of character states from those responsible for their maintenance in contemporary populations. Many comparative tests are based on optimality models, and complement the testing of adaptationist ideas by experimentation, which is often impractical.