

Chapter 2. Testing Hypotheses in Behavioural Ecology

TESTING HYPOTHESES/25

A rigorous scientific approach to the function of behaviour will involve four stages: observations, hypotheses, predictions and tests. The first two, observation and hypotheses, often go hand in hand. It may take many years getting to know a particular species before it is possible to ask good questions about its behaviour and ecology. Niko Tinbergen's work (1953) on the herring gull, *Larus argentatus*, was the result of over 20 years' painstaking observations of the bird's behavioural repertoire and the environment in which it lives. Having observed some aspect of the behaviour of an animal that we do not understand, how should we proceed?

Let us assume, for example, that we want to discover why our animal lives in a group as opposed to on its own. We may get a strong hint about the function of this simply from observation. If the animal only lived in a group in the breeding season we might suspect that it gained some advantage in terms of increased mating efficiency, for example, whereas if it only lived in a group in winter we may suspect some advantage concerned with improved feeding efficiency or avoiding predation. We can test our ideas in three main ways.

1 *Comparison between individuals within a species.* Individuals in groups may have greater success at feeding, mating or avoiding predators than solitary individuals. Furthermore, success may vary with group size. The problem is, however, that there may be confounding variables: solitary individuals may be poorer competitors and this, rather than their solitary existence *per se*, may explain their lower success, or individuals in groups may live in better quality habitats, and so on.

2 *Experiments.* It is often better, therefore, to perform an experiment. With an experiment we can vary one factor at a time; for example we could change group size and see how this influenced success under a particular set of conditions. Niko Tinbergen pioneered the method of elegant field experimentation to answer functional questions. For example, to test the hypothesis that spacing out of gull nests functioned to reduce predation he put out experimental plots of eggs with different spacing patterns and found that those with a clumped distribution suffered greater predation than those that were spaced out as in nature [Tinbergen *et al.* 1967].

3 *Comparison among species.* Different species have evolved in relation to different ecological conditions and so comparison among species may help us to understand how differences in

Correlating differences in behaviour with differences in ecology

feeding ecology or predation pressure, for example, influence the tendency to live in groups or to be solitary. Using the comparative method is rather like looking at the result of experiments done by natural selection over evolutionary time. The results of these 'experiments' are the designs of the various species' behaviour which we now observe. For example, group living may occur in species which experience particular feeding conditions. In this chapter we will discuss in detail these last two methods for investigating adaptation.

The comparative approach

The idea of comparison lies at the heart of most hypotheses about adaptation. It is the comparative study of different species which gives us a feel for the range of strategies that animals adopt in nature. When we ask functional questions about the behaviour of particular species we are usually asking why it is different from other species. Why does species A live in groups compared with species B which is solitary? Why do males of species B mate monogamously compared with males of species A which are polygynous, and so on? A powerful method for studying adaptation is to compare groups of related species and attempt to find out exactly how differences in their behaviour reflect differences in ecology. We will first describe two examples which pioneered the comparative approach and inspired workers to use the method with other animal groups. Then we will point out some of the methodological difficulties in formulating and testing hypotheses based on comparison. Finally we will describe some recent examples of the comparative method which have attempted to overcome these problems.

SOCIAL ORGANIZATION IN WEAVER BIRDS

The first person to attempt a systematic analysis of this kind was John Crook (1964) who studied about 90 species of weaver birds (Ploceinae). These are small finches which live throughout Africa and Asia, and although they all look rather alike there are some striking differences in their social organization. Some are solitary, some go around in large flocks. Some build cryptic nests in large defended territories while others cluster their nests together in colonies. Some are monogamous, with male and female forming a permanent pair bond; others are polygamous, the males mating with several females and contributing little to care of the offspring. How can we explain the evolution of this great diversity in behaviour?

Weaver bird social behaviour and mating systems are correlated with diet.

Crook's approach was to search for correlations between these aspects of social organization and the species' ecology. The ecological variables he considered were the type of food, its distribution and abundance, predators and nest sites. His analysis showed that the weaver birds fell into two broad categories.

- 1 Species living in the forest tended to be insectivorous, solitary feeders, defend large territories and build cryptic solitary nests. They were monogamous and males and females had similar plumage.
- 2 Species living in the savannah tended to eat seeds, feed in flocks and nest colonially in bulky conspicuous nests. They were polygamous and there was sexual dimorphism in plumage, the males being brightly coloured and the females rather dull (Fig. 2.1).

Why is the behaviour and morphology of the weaver birds linked to their ecology in such a striking way? Crook invoked predation and food as the main selective pressures that have influenced the evolution of social organization. His argument was as follows.

- 1 In the forest, insect food is dispersed. Therefore it is best for the birds to feed solitarily and defend their scattered food resources as a territory. Because the food is difficult to find, both parents have to feed the young and therefore stay together as a pair throughout the breeding season. With the male and female visiting the nest, both must be dull coloured to avoid attracting predators. Cryptic nests spaced out from those of neighbours decrease their vulnerability to predation.
- 2 In the savannah, seeds are patchy in distribution and locally superabundant. It is more efficient to find patches of seeds by being in a group because groups are able to cover a wider area in their search. Furthermore the patches contain so much food that there is little competition within the flock while the birds are feeding.

In open country the birds cannot hide their nests and so they seek safety in protected sites, such as spiny acacia trees. Nests are bulky to provide thermal insulation against the heat of the sun. Because good breeding sites are few and scattered, many birds nest together in the same tree. Within a colony, males compete for nest sites and those that defend the best sites attract several females while males in the poorer parts of the colony fail to breed. In addition, because food is abundant, the female can feed the young by herself and so the male is emancipated from parental care and can spend most of his time trying to attract more females. This has favoured brighter plumage coloration in males and the evolution of polygamy.

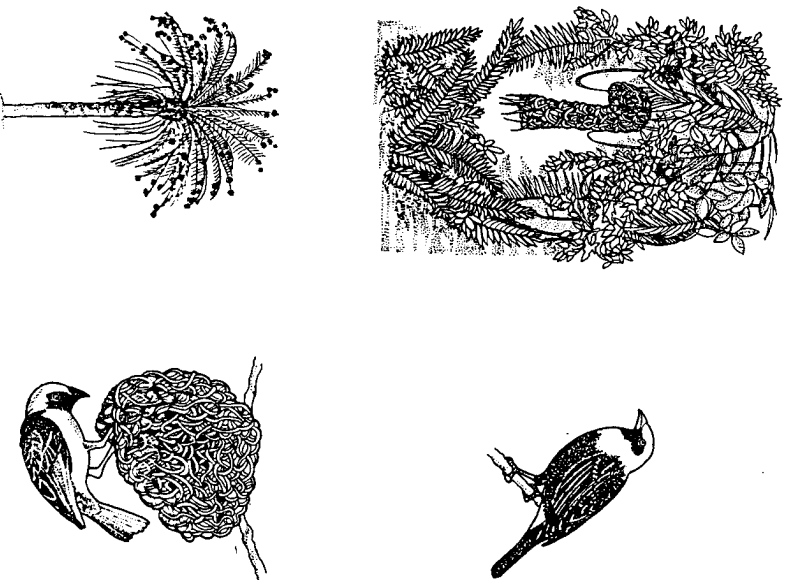


Fig. 2.1 Top: some species of weaver birds, like this one (*Malimbus scutatus*) are insectivorous, building cryptic solitary nests in the forest and feeding alone in large territories. Bottom: other species like this one (*Ploceus cucullatus*) feed on seeds out in the open savannah. They build conspicuous nests in colonies and feed in flocks. The males are often brightly coloured.

Supporting evidence for this interpretation comes from species with intermediate ecology. The grassland seed-eaters have patchy food supplies so group living is favoured for efficient food finding. However, in grassland the nests are vulnerable, so predation favours spacing out. The result is a compromise; these species have an intermediate social organization, nesting in loose colonies and feeding in flocks.

These results show clearly how food and predation may be important in determining social organization. They also reveal how several different traits such as nests, feeding behaviour,

plumage colour and mating system can all be considered together as a result of the same ecological variables. Crook's work with the weaver birds inspired several people to use the comparative method to study social organization in other groups. David Lack (1968) extended the argument to include all bird species and Peter Jarman (1974) used the same approach for the African ungulates.

SOCIAL ORGANIZATION IN AFRICAN UNGULATES

Jarman (1974) considered 74 species of ungulates, all eat plant material but differences in the precise type of food eaten are correlated with differences in movements, mating systems and antipredator behaviour. The species were grouped into five ecological categories (Table 2.1). Just as in the weaver birds, several adaptations seem to go together.

The major correlate of diet and social organization is body size. Small species have a higher metabolic requirement per unit weight and need to select high quality patches of food such as berries and shoots. These tend to occur in the forest and are scattered in distribution, so the small species are forced to live a solitary existence. The best way to avoid predators in the forest is to hide. Because the females are dispersed, the males must also

Table 2.1 The social organization of African ungulates in relation to their ecology. From Jarman (1974)

Exemplary groups	Body weight (kg)	Habitat	Diet	Group size	Reproductive behaviour	
					unit	Antipredator behaviour
Grade I Dikdik Dukker	3-60	Forest	Selective browsing; fruit, buds	1 or 2	Pair	Hide
Grade II Reedbuck Cervuk	20-80	Brush, riverine grassland	Selective browsing or grazing	2 to 12	Male with harem	Hide, flee
Grade III Impala Gazelle Kob	20-250	Riverine woodland, dry grassland	Grazes or browses	2 to 100	Males territorial in breeding season	Flee, hide in herd
Grade IV Wildbeest Hartebeest	90-270	Grassland	Grazes	Up to 150 (thousands on migration)	Defence of females within herd	Hide in herd, flee
Grade V Eland Buffalo	300-900	Grassland	Grazes unselectively	Up to 1000	Male dominance hierarchy in herd	Mass defence against predators

Problems in interpreting comparative data

be dispersed and the commonest mating system is for a pair to occupy a territory together.

At the other extreme, the largest species eat poor quality food in bulk and graze less selectively on the plains. It is not economical to defend such food supplies and these species wander in herds, following the rains and fresh grazing. In these large herds there is potential for the strongest males to monopolize several females by defence of a harem or a dominance hierarchy of mating rights. When predators come along these species cannot hide on the open plains and so either flee or rely on safety in numbers in the herd. Ungulates of intermediate size show aspects of ecology and social organization in between these two extremes (Table 2.1).

Adaptation or story-telling?

This comparative approach to adaptation is persuasive, but there are problems (Clutton-Brock & Harvey 1979, Gould & Lewontin 1979). Many of the following problems are not unique to comparative studies and it is worth bearing them in mind throughout the book.

ALTERNATIVE HYPOTHESES

The explanations for the differences in social organization are plausible, but alternative hypotheses have not been considered in a rigorous manner.

The ecological variables, such as predator pressure and patchy environment, have also been used in rather a vague way. Indeed, in the weaver birds we invoked a patchy food distribution as responsible for the evolution of flocking while in the ungulates we said that high quality patchy foods favour a solitary existence. There is the obvious danger here of explaining things too easily without any rigorous quantification of the ecological factors concerned.

CAUSE AND EFFECT

Consider the observation that weaver birds with a diet of seeds go about in flocks. Our explanation was that seed eating selects for flocking because this is the best way to find a patchy food supply. However we could equally well have suggested that predation selects for flocking and, as a consequence, the birds are forced to select locally abundant food so all the flock can get enough to eat. In this case a diet of seeds is a consequence, or

effect, of flocking, not a cause. Maybe predation also selects for flocking in the forest insectivores but because their diet is incompatible with flocking they have to forage singly.

CONFOUNDING VARIABLES

With the comparative approach there are often confounding variables. For example, we observe the giraffe with its long neck feeding at the tops of trees and the buffalo with its short neck feeding on the ground. We then say that a long neck is an adaptation for feeding high up in the trees. But a long neck could equally well aid predator detection. How can we control for such confounding variables and decide which selective pressure has favoured the trait? Perhaps it is both!

A particularly important confounding variable in comparative studies is body size. Jarman controlled for this in his analysis of the ungulates by dividing the species up into categories of different body weight (Table 2.1). Most biological traits do not increase in a 1:1 relationship with body size; their relation to body size is said to be allometric (Gould 1966). For example, the brain mass of different bird species increases at about the two-thirds power of body weight. In this case, before we can examine the ecological correlates of brain size we first have to remove the effects of body size. This can be done by calculating the appropriate line of best fit when brain mass is plotted against body weight and then measuring deviations from the line to see whether the size of the trait is greater or less than expected from body weight.

ALTERNATIVE ADAPTIVE PEAKS OR NON-ADAPTIVE DIFFERENCES

It is tempting when comparing between species to assume that differences are always adaptive but some differences may simply be alternative solutions to the same ecological pressures. An ecologist from Mars who visited the Earth would observe that in the United States people drive their cars on the right hand side of the road while in Britain they drive on the left. He would then perhaps make lots of measurements in an attempt to find ecological correlates to explain the adaptive significance of the difference. In fact driving on the right and driving on the left may just be equally good alternatives for preventing accidents (Dawkins 1980).

Some differences between animals may be like this. Sheep use horns for fighting and deer use antlers. Horns are derived from skin while antlers are derived from bone (Modell 1969). The

Some differences between species may reflect different solutions to the same problem

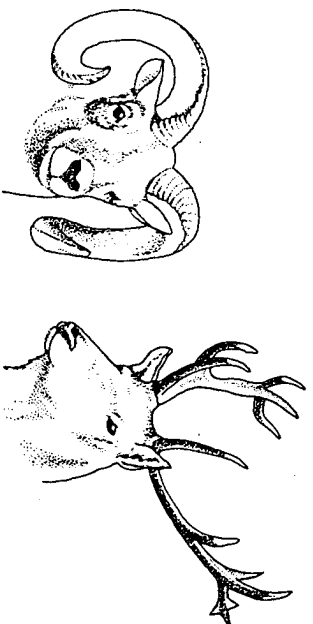


Fig. 2.2 The horns of the sheep (left) and antlers of the deer (right) are both used in fighting. Horns are derived from skin and antlers from bone.

differences between horns and antlers need not necessarily reflect ecological differences; it may simply be a case of evolution working with different raw materials to produce the same functional end (Fig. 2.2). The problem with non-adaptive explanations is that they are hypotheses of the last resort. Further scientific enquiry is stifled. Maybe there is an adaptive explanation for the difference but we just haven't discovered it yet. For example, antlers are dropped and then renewed each year whereas horns are not. Perhaps this difference is related to the extent of seasonal variation in mating competition and food supply?

These criticisms are important, but they certainly do not mean that the comparative method is a failure. On the contrary, the approach is impressive in the way it brings together such a wide diversity of behavioural and morphological traits within the same ecological framework. Crook's study of the weaver birds and Jarman's work on the antelopes have served as models for ecological work on other groups of species. However the most recent comparative studies have attempted to control for these various problems, and we will now discuss another example, bearing the criticisms in mind, to illustrate how changes in methodology have made comparison between species a more rigorous exercise.

Primate social organization

Early knowledge of primate behaviour came mainly from studies in zoos. In 1932 Lord Zuckerman suggested that primates tend to be social animals because they have continuous sexual activity. It should be clear from the last chapter that this is a causal explanation and leaves the functional significance of sociality

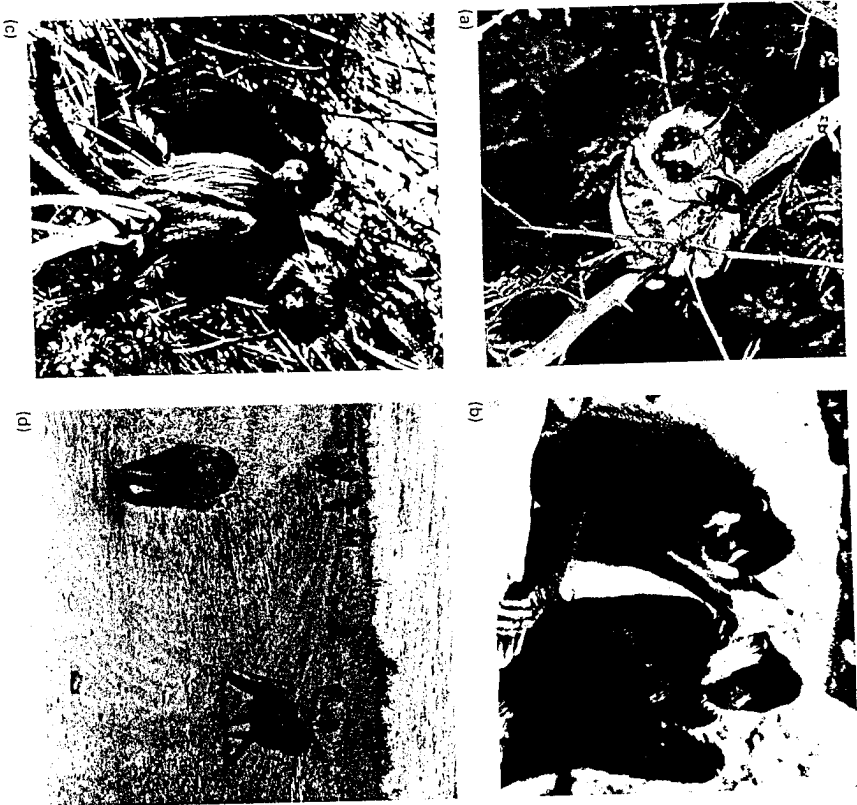


Fig. 2.3 Four photographs illustrating the variety of primate social organization. (a) Table 2.2, Grade I: A solitary insectivorous prosimian, the lesser bushbaby (*Galago senegalensis*) (photo by Caroline Harcourt). (b) Table 2.2, Grade II: A monogamous pair of folivorous, arboreal, black gibbons (*Hylobates concolor*). The male is on the left. © Ron Tilson/BPS. (c) Table 2.2, Grade IV: Part of a troop of folivorous, arboreal, dusky langurs (*Presbytis obscurus*). © Ron Tilson/BPS. (d) Table 2.2, Grade V: A troop of savannah-dwelling olive baboons (*Papio anubis*). There are two subordinate males in the foreground and the dominant males are in the background near the females and young. Photo by Iven De Vore (Anthro-Photo).

unexplained. In the 1950s, the first studies of primates in the field (e.g. Carpenter 1954) revealed that sexual activity was not in fact continuous. It also became clear that different species have very different social organizations (Fig. 2.3). Tiny farsiers and

lemurs hunt solitarily in the tree tops for insects at night. Some monkeys go around in small groups in the trees by day, feeding on leaves or fruit. Others are terrestrial and live in large troops. Among the apes, the orang-utan is solitary, the gibbon lives in pairs and small family groups while the chimpanzee may live in bands of up to 50.

How can we explain the evolution of this bewildering array of social organizations? It soon became apparent that ecological factors were important. For example, De Vore (1965) noticed that, compared with other species of primates, anubis baboons live in large groups, the males are large and they have big teeth. He suggested these may all be adaptations to predator defence in a terrestrial environment. By 1966, there were sufficient field data for John Crook and Stephen Cartlan to apply the first comparative approach to a large number of primates.

Like the weaver bird and antelope work, they categorized the species into several groups based on ecology and behaviour. Table 2.2 shows that at one extreme, insectivorous primates are nocturnal, forest animals which are solitary, then there is a variety of fruit and leaf eating species which are diurnal and live in small to large groups; finally, at the other extreme, are the vegetarian browsers of the open country which live in large groups and

Table 2.2 Crook and Cartlan's (1966) division of the primates into five 'adaptive grades'

Exemplary species	Habitat	Diet	Activity	Group size unit	Reproductive unit	Sexual dimorphism
Grade I <i>Galago</i> <i>Lepilemur</i> <i>Microcebus</i>	Forest	Insects	Nocturnal	Solitary	Pairs	Slight
Grade II <i>Indri</i> <i>Lemur</i> <i>Hylobates</i>	Forest	Fruit or leaves	Crepuscular or diurnal	Very small groups	Single male with family	Slight
Grade III <i>Colobus</i> <i>Saimiri</i> <i>Gorilla</i>	Forest or forest edge	Fruit or fruit and leaves	Diurnal	Small groups	Multi-male groups	Slight to fairly marked
Grade IV <i>Macaca</i> <i>Cercopithecus</i> <i>aethiops</i> <i>Pan</i>	Forest edge to savannah	Vegetation	Diurnal	Medium to large groups	Multi-male groups	Marked
Grade V <i>Erythrocebus</i> <i>patas</i> <i>Papio</i> <i>hamadryas</i> <i>Theropithecus</i> <i>relata</i>	Grassland or arid savannah	Vegetation /omnivore	Diurnal	Medium to large groups	One-male groups	Marked

Food and predation seem to be the main selective pressures

show intensive competition between males for females and marked sexual dimorphism.

Once again, food and predation were suggested as the main selective pressures responsible for this link between social organization and habitat. Insects are dispersed and difficult to find, so just like the insectivorous weaver birds, these primates are solitary. In open country, predation favours grouping for safety and food is locally abundant so this allows many individuals to congregate at a food source; like the open-country weaver birds, these primates live in groups. In a large group, males compete with each other for mating rights and hence large male body size has been selected for.

Crook and Gartlan's approach was to categorize the primates into a small number of discrete groups. This raises two main problems. First of all, variation in features such as home range size and group size is continuous and so division into hard and fast groups is a bit arbitrary. Because the groups are subjectively defined, it is difficult for subsequent workers to categorize new species in the scheme. Second, different aspects of social organization such as breeding system and group size do not necessarily vary together in the same way. For example, two species of primate could have the same breeding system but live in different sized groups.

Comparative analyses should be based on independent evolutionary events . . .

Tim Clutton-Brock and Paul Harvey tried to avoid these problems, firstly by measuring the various aspects of social behaviour and morphology on a continuous scale. Secondly, they used multivariate statistics to tease out the effects of several different ecological variables on the same traits, and to analyse the influence of ecological factors on each aspect of social organization independently. Their third improvement in approach was a careful consideration about which taxonomic level should be used for analysis, e.g. species, genus, subfamily or family.

This last problem is one about the independence of data points. Imagine plotting all the species of primates on a graph in order to investigate the relationship between body weight and some interesting variable such as home range size, brain size or mating system (e.g. females per male in a breeding group). On our graph we would find that within a genus all the species will be clumped together in a cluster of points. For example, all six species of gibbons are of similar body weight, all are monogamous, arboreal and eat fruit. Our problem is whether we should treat these as six independent points or just one point in any statistical analysis. If we treated them as six independent points our analysis may be biased because it would reflect phylogeny, rather than ecology; all six gibbons may be descended from a single ancestor which

. . . which can be identified from a phylogenetic tree

was monogamous, arboreal and ate fruit. Because species within a genus tend to have similar characteristics due to phylogenetic constraints, analysis of species data will be statistically biased by those genera containing large numbers of species.

A number of different solutions to the problem of taxonomic independence have been proposed. One conservative option is to base comparative analyses on higher taxonomic levels such as genera, or even families, taking one average value for, say, all species within a genus or genera within a family. This method might succeed in eliminating problems of non-independence, but it is also likely to throw away useful data, for example where evolutionary divergence between species within a genus represents genuinely independent evolutionary events.

Evolutionary biologists now agree that the ideal way to carry out a comparative analysis is to reconstruct a phylogenetic tree of the group under study and to use this tree to make comparisons between data points that can be clearly defined as independent evolutionary events (Harvey & Pagel 1991, Harvey & Purvis 1991, Box 2.1). In practice, such phylogenetic trees are not always available, in which case either they can be approximated (Box 2.1) or the comparative biologist can revert to the approximate, conservative approach of using higher taxonomic levels for statistical comparisons, as do the examples in the following sections.

We shall now consider some examples of the comparative approach to primate social organization and morphology, treating different genera as independent points for analysis, to illustrate how comparison has become a more rigorous and objective exercise.

HOME RANGE SIZE

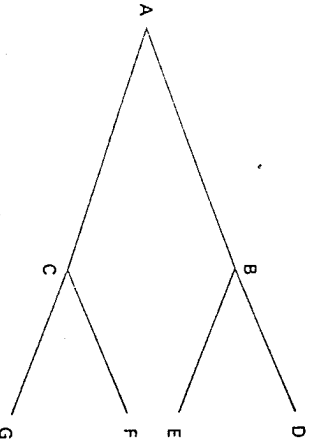
Larger animals need to eat more food and so, in general, we would expect them to have larger home ranges. Therefore, if we want to examine the influence of an ecological variable, such as diet, on home range size, we have to control for body weight as a confounding variable. When home range size is plotted against the total weight of the group that inhabits it, as expected the larger the group weight the larger the home range (Fig. 2.4).

The influence of diet on home range size can be seen when the specialist feeders (insectivores, frugivores) are separated from the leaf eaters (folivores); the specialist feeders have larger home ranges for a given group weight. The probable explanation is that fruit and insects are more widely dispersed than leaves and so specialist feeders need a larger foraging area in which to find enough food.

Specialist feeders have larger home ranges than generalists

Box 2.1 *The comparative method of independent comparisons.*

- 1 In carrying out a comparative analysis, it is essential to base the statistical analysis on independent evolutionary events. For example, Höglund (1989) found a strong association between lekking behaviour and sexual dimorphism in birds when he used species as the units of comparison, but the relationship disappeared when he did the correct comparison of independent points. Be wary of species as data points!
- 2 The ideal method is to construct a phylogenetic tree, as illustrated below:

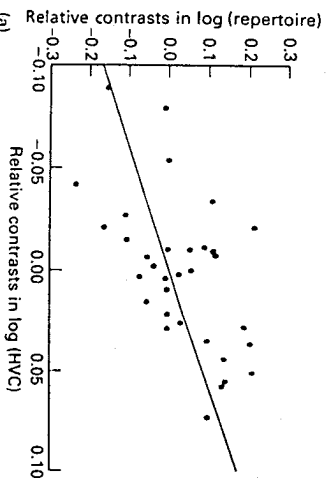


In this tree A gave rise to two descendants, B and C, each of which gave rise to two more, D, E, F and G.

3 If the phylogeny and the 'character states' (values of the relevant variables) are fully known, comparisons can be made between each ancestor-descendant pair as independent events (A and B, B and D, B and E, A and C, C and F, C and G). Thus one would have six comparisons of, say, sexual dimorphism and home range size.

4 Most often the ancestral character states are not known. The living species D, E, F and G can be studied directly, but the behaviour of A, B and C can only be guessed. In this case comparisons can be made between D and E and between F and G on the basis of measured values, and between B and C on the basis of an estimated value (e.g. half-way between the two descendant species). There is considerable debate about how best to estimate the ancestral values B and C (Harvey & Purvis 1991). In order to avoid such debates, some authors prefer just to analyse differences between pairs of extant species (Møller & Birkhead 1992).

5 An example of using the method of independent comparisons: De Voogd *et al.* (1992) [Fig. a] measured the volume of a brain nucleus (the higher vocal centre, HVC) involved in song learning in 45 species of passerine birds. They examined the relationship between the size of the brain nucleus relative to the rest of the brain and an estimate of song learning — the size of song repertoire. The phylogenetic tree of birds constructed from genetic divergence by Sibley and Monroe (1990) was used to apply the technique described in paragraph 3. A significant relationship between the size of song repertoire and the brain nucleus was observed. The results are expressed as differences ('contrasts') in the two measures between pairs of taxa that have been identified as independent divergences.



These general trends are confirmed by more detailed studies of particular species. The red colobus monkey (*Colobus badius*) is a specialist feeder, eating shoots, fruit and flowers. The food occurs in scattered clumps and this species wanders over a large home range of about 70 ha. The black and white colobus (*C. guereza*) is a generalist, eating leaves of all ages. Its food supply is dense and evenly distributed and its home range is only 15 ha (Clutton-Brock 1975).

SEXUAL DIMORPHISM IN BODY WEIGHT

In primates, males are often larger than females. Two hypotheses could explain this observation. Sexual dimorphism could enable males and females to exploit different food niches and thus avoid competition (Selander 1972). If this was true, then we might

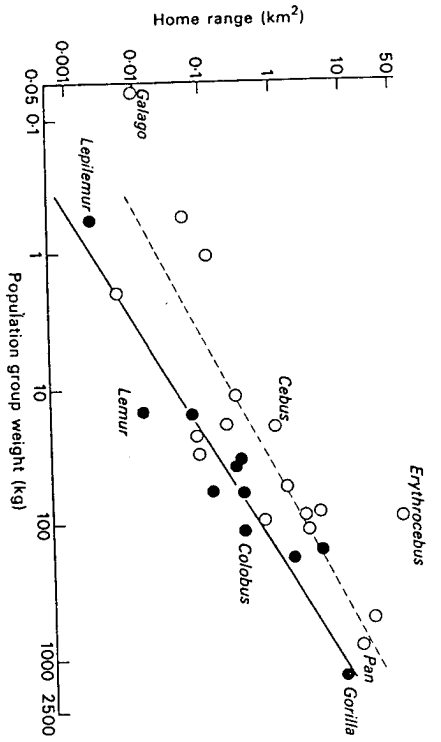


Fig. 2.4 Home range size plotted against the weight of the group that inhabits the home range for different genera of primates. The solid circles (●) are the home range for different genera of primates. The open circles (○) are the population group weight for different genera of primates. The solid line is a regression line for the population group weight data, and the dashed line is a regression line for the home range data. Some of the genera are indicated by name. From Clutton-Brock and Harvey (1977).

Sexual dimorphism in body size results from sexual competition

predict that dimorphism would be greatest in monogamous species where male and female usually associate together and feed in the same areas. Alternatively it could have evolved through sexual selection, large body size in males being favoured because this increases success when competing for females (Darwin 1871). If sexual competition is important then we would predict that dimorphism should be greater in polygamous species, where large male size would be especially advantageous because a male could potentially monopolize several females.

The comparative data show no sign of the trend predicted by the niche separation hypothesis but do support the sexual competition hypothesis; the more females per male in the breeding group, the larger the male is in relation to the female (Fig. 2.5).

SEXUAL DIMORPHISM IN TOOTH SIZE

Males often have larger teeth than females. Again, two hypotheses can be suggested (Harvey *et al.* 1978). Large teeth may have evolved in males for defence of the group against predators. Alternatively males may have larger teeth for competition with other males over access to females. There is the problem here of body weight as a confounding variable; males are larger than

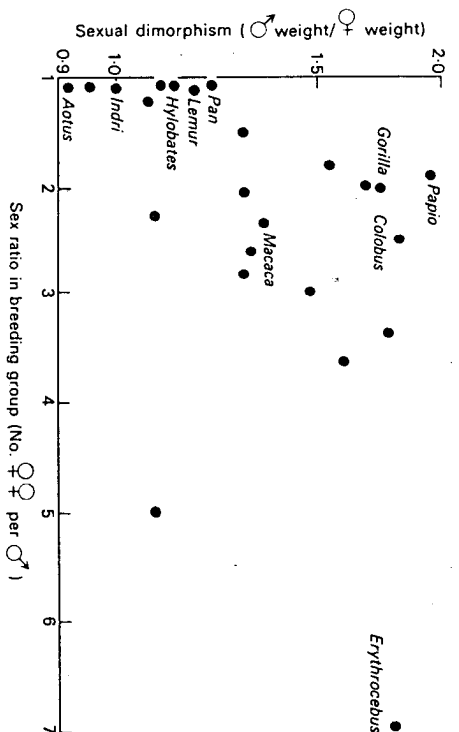


Fig. 2.5 The degree of sexual dimorphism increases with the number of females per male in the breeding group. Each point is a different genus, some of which are indicated by name. From Clutton-Brock and Harvey (1977).

females and so a difference between the sexes in tooth size could just reflect a difference in body size.

This can be controlled for by calculating the line of best fit when female tooth size is plotted against body weight. If the tooth size of a male is now plotted on the same graph, it can be seen whether its size is greater than expected for a female of the same body weight. The results show that in monogamous species male tooth size is as expected for a female of equivalent body weight. However it is larger than expected in harem-forming species. These data support the sexual competition hypothesis for the evolution of larger teeth in males. However we cannot exclude the predator defence hypothesis because maybe the harem-forming species are the ones most vulnerable to predation.

The analysis can be taken a step further by considering species where several males live together in a group (multi-male troops). It is found that, within this type of social organization, the males of terrestrial species have larger teeth for their body size than arboreal species. Therefore even within the same mating system there is a difference in tooth size in different habitats. The terrestrial environment is usually thought to present greater risks of predation and so predation pressure may have been responsible for the evolution of larger teeth in terrestrial species.

Our conclusion is that both sexual competition and predation may have influenced the evolution of sexual dimorphism in tooth

Sexual dimorphism in tooth size is related to sexual competition and defence against predators

size. There is also the further possibility that differences in tooth size are important in reducing diet overlap between the sexes and so preventing competition for food. This example shows that, even with careful analysis, it may be difficult to tease out the effect of several variables on the evolution of a trait.

TESTIS SIZE AND BREEDING SYSTEM

The heaviest primates, the gorilla (*Gorilla gorilla*) and orang-utan (*Pongo pygmaeus*) have breeding systems that involve one male monopolizing mating with several females, and have testes that weigh 30 g and 35 g respectively (average weight of both testes). The smaller chimpanzee (*Pan troglodytes*), by contrast, has a breeding system where several males copulate with each oestrus female and this species has testes weighing 120 g! It seems likely that the marked differences in testes weights are related to differences in breeding system. In single-male breeding systems (gorilla and orang-utan) each male need ejaculate only enough sperm to ensure fertilization. In multi-male systems (chimpanzee), however, a male's sperm has to compete with sperm from other males. Selection should, therefore, favour increased sperm production and hence larger testes.

Harcourt *et al.* (1981) tested this hypothesis by comparing 20 genera of primates, varying in body size from the 320-g marmoset (*Callithrix*) to the 170-kg gorilla. Figure 2.6 shows that, as ex-

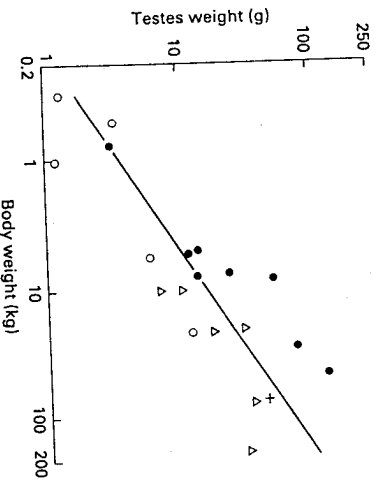


Fig. 2.6 Log combined testes weight (g) versus log body weight (kg) for different primate genera. ●, Multi-male breeding system; ○, monogamous; Δ, single-male; +, *Homo*. From Harcourt *et al.* (1981).

pected, testes weight increases with body weight. For a given body weight, however, it is clear that genera with multi-male breeding systems have heavier testes than genera with single-male or monogamous breeding systems. The data points for the former group lie above the line, and those for the latter lie below ('single-male' indicates that there is only one breeding male although, as in the gorilla, there may be more than one male in the social group; 'monogamous' indicates that there is just one male and one female in a group). These data therefore support the sperm competition hypothesis.

The comparative approach reviewed

The statistical approach we have described for the primates is certainly a major improvement on the first applications of the comparative method. To summarize, the main improvements are as follows.

- 1 Different aspects of social organization are treated independently and as continuous variables.
- 2 Confounding variables are dealt with in a rigorous manner.
- 3 Care is taken to choose the most appropriate taxonomic level for analysis.
- 4 The data are used wherever possible to discriminate between alternative hypotheses such as predation or sexual competition.

The end result of many of the analyses is a plausible interpretation which may be treated as a hypothesis for further testing. In conclusion, the comparative approach is very useful for looking at broad trends in evolution and the general relationship between social organization and ecology. It generates hypotheses which can be used as predictions for other groups of animals. It can also be used to test hypotheses which are not amenable to experimentation, such as the effect of polygamy on sexual dimorphism. Furthermore, it is impressive in the way it shows how diet, predation, social behaviour and body size, for example, can all be interrelated.

However, we need a different approach to understand in detail why animals adopt particular strategies in relation to their ecology. Can we actually measure patch structure and predation risk and then come up with precise predictions as to how an animal will behave? Can we explain why a monkey goes round in a group of 20 rather than one of 16 or 25, why its home range is 10 ha rather than 8 or 12 ha, and why it spends 1 hour in a patch of fruit? Indeed we can attempt to answer precise questions like these. No one has yet attempted this for anything as complicated as primate social behaviour. However a start has been made for simpler

The comparative method can be used for testing hypotheses not amenable to experimentation

kinds of behaviour using optimality theory and an experimental approach.

Experimental studies of adaptation

We now turn to a different, and complementary, way of looking at how selection moulds behaviour. Instead of broad scale comparisons between species, the emphasis will be on the behaviour of individuals of the same species and analysing their behaviour in terms of costs and benefits.

The idea of trying to measure costs and benefits grew out of Niko Tinbergen's experimental approach to studying the survival value of behaviour. For example, Tinbergen observed that in a colony of black-headed gulls (*Larus ridibundus*) nesting on sand dunes in north-western England, incubating parents always pick up the broken eggshell after a chick has hatched and carry it away from the nest (Fig. 2.7). Although carrying the shell takes only a few minutes each year it is crucial for the survival of the young. The eggs and young of the black-headed gull are well camouflaged against the grass, sand and twigs around the nest. The inside of the broken shell, however, is white and highly conspicuous. Tinbergen carried out an experiment to test the hypothesis that the conspicuous white broken shell reduces the camouflage of the nest. He painted hens' eggs to resemble cryptic gull eggs and laid them out at regular intervals in the gull colony. Next to some he placed a broken shell. The results confirmed his prediction that the cryptic eggs were much more likely to be discovered and eaten by predators such as crows if they were close to a broken shell. So it is easy to visualize why the parent benefits by removing the conspicuous empty shell soon after the chick has hatched: the camouflage of the brood is preserved and the likelihood of the parent perpetuating its genes is increased.

But there is more to the story than this. The parent does not remove the eggshell immediately; it stays with the newly hatched chick for an hour or more and then goes off with the shell. In order to explain the delay in removing the shell we have to introduce the idea of a trade-off between costs and benefits. If the parent flies off with the shell at once, it has to leave the newly hatched chick unattended (the second parent is away at the feeding grounds fueling up for its next stint at the nest). Tinbergen observed that the new chick, with its plumage still wet and matted, is easily swallowed and therefore makes a tempting meal for a cannibalistic neighbouring adult. However, when the chick's



Fig. 2.7 A black-headed gull removing an eggshell from its nest. Photo by N. Tinbergen.

down has dried out and become fluffy it is much harder for a gull to swallow, and is therefore less vulnerable to attacks from neighbours. The parent's delay before removing the shell therefore probably reflects a balance between the benefits of maintaining the camouflage of the brood and the costs associated with leaving a newly hatched chick at its most vulnerable moment.

When the balance between costs and benefits is changed, the length of the parent's delay might also be expected to change. This is borne out by observations of the oystercatcher, another ground nesting bird with camouflaged eggs and young. The oystercatcher (*Haematopus ostralegus*) is a solitary nester and cannibalism by neighbours is therefore not a risk associated with leaving the newly hatched chicks. The parents benefit by restoring camouflage of the nest as soon as possible after hatching and as expected the parent removes broken eggshells more or less as soon as a chick has hatched and before its down is dry.

Costs and benefits involved experimentally—eggshell removal in gulls

A different balance of selective pressures in oystercatchers

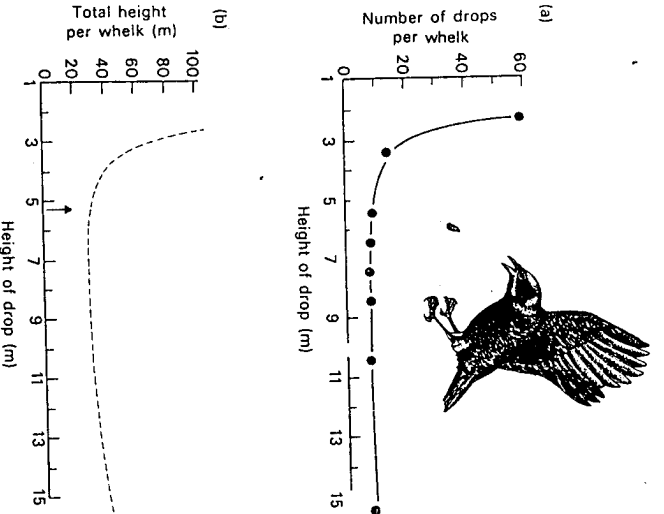


Fig. 2.8 Results obtained by dropping whelk shells from different heights. (a) Fewer drops are needed to break the shell if it is dropped from a greater height. (b) The total upward flight needed to break a shell (no. of drops \times height of each drop) is close to its minimum at the height most commonly used by the crows (shown by arrow). From Zach (1979).

comparative method involves comparing different species to see whether differences in behaviour are correlated with differences in ecology. In weaver birds, antelopes and primates the main factors determining the evolution of social behaviour are the distribution and abundance of food, predators and mates. These have been shown to influence group size, home range size, mating behaviour and sexual dimorphism. Two of the main problems in comparative studies are those of confounding variables and the choice of taxonomic level for comparison.

The experimental approach involves a detailed study of the costs and benefits of a behaviour pattern to an individual of a particular species. Behaviour can be viewed as having costs and benefits and animals should be designed by natural selection

to maximize net benefit. Ultimately the net benefit must be measured in terms of gene contribution to future generations. This will depend on various shorter-term goals such as foraging efficiency, mating efficiency and efficiency of avoiding predators. Optimality models can be used to predict which particular trade-off between costs and benefits gives maximum net benefit.

Further reading

Harvey and Pagel (1991) provide a good discussion of some of the problems in using the comparative approach. David Lack's (1968) book applies the comparative method to the breeding biology of birds. Mark Ridley (1983) discusses the methodology of the comparative approach, particularly the problem of what to use as independent data points. Niko Tinbergen's book on gulls (1953) and his book *Curious Naturalists* (1974) give a marvellous sense of the excitement of observing animals in the field and show the power of performing simple field experiments to help us understand why animals behave the way they do.

Topics for discussion

- 1 What are the relative merits of the comparative method and the experimental approach for studying the adaptive significance of behaviour?
- 2 How can we decide what are the independent units of observation in comparative studies?
- 3 How could Jarman's (1974) analysis of ungulate social organization be improved by applying Harvey and Pagel's (1991) methods?