

review article

Mammals, resources and reproductive strategies

T. H. Clutton-Brock* & Paul H. Harvey†

The breeding systems of mammalian species are strongly influenced by the density and dispersion of their populations. These in turn are affected by variations in the distribution of resources. Through quantitative comparisons, it is possible to trace evolutionary relationships between feeding behaviour, population dispersion, breeding systems and morphology.

FUNCTIONAL explanations of species differences among vertebrates have been bedevilled by the absurd and the fantastic. Thayer's classic suggestion that the pinkness of flamingoes may serve to camouflage them against red sunsets is a well known example, but many hypotheses on a similar level of improbability can be found in the recent literature. The problem is not principally that of armchair theorists getting progressively out of touch with ecological reality. On the contrary, unlikely explanations frequently arise when a scientist explains the occurrence of a trait in a particular species (or of a difference between two species) with which he is closely familiar, without considering the broader distribution of the trait. A good example is provided by the recent finding that sexual dimorphism in size is greater among the larger australopithecines than among the smaller ones^{2,3}. Several explanations of this difference have been advanced, but all ignore the fact that there is a widespread tendency among mammals (and among primates in particular) for larger species to show increased size dimorphism⁴. A reasonable explanation of the difference between australopithecines would clearly need to take cognisance of the broader trend.

Functional explanations of species differences are most likely to be reliable when the adaptive significance of a trait is reasonably well understood and accords with its distribution across species. For this reason, we believe that an early step in understanding adaptive variation among mammals should be to investigate distributions of interspecific differences. By this, we do not intend to argue that such studies should supersede attempts to investigate in more detail differences within or between related species. Examination of the precise interrelationships between behaviour and ecology in particular species and broad interspecific comparisons are clearly complementary. Nor do we wish to disguise the problems of investigating the distributions of traits across species: not only may similar traits have different functions⁵, but it is often difficult to interpret relationships between particular traits and ecological variables⁶. As a result, attempts to explain distributions can themselves lead to spurious relationships and absurd explanations.

In this review, we consider four aspects of mammalian biology (population density, group size, breeding system and sexual dimorphism) where it has proved possible to demonstrate systematic associations between species differences and environmental variables. All four are interrelated: the thesis which we shall advance is that variation in the distribution, density and quality of food supplies is largely

responsible for species differences in the density and distribution of mammalian populations; that differences in population density and distribution play an important part in determining differences in breeding systems and that these affect a wide variety of morphological and physiological traits. The recognition of these trends is nothing new: it is clear that sociobiology was well advanced in ancient Greece—"For it is differences in feeding habits that make some animals live in herds and others scattered about; some are carnivorous, some vegetarian, others will eat anything. So, in order to make it easier for them to get these nutrients, nature has given them different ways of life. Again, since animals do not all like the same food but have different tastes according to their nature, so the ways of living of carnivorous animals differ among their different kinds, as do also those of the vegetarian."⁷

In the past, functional approaches to interspecific differences among mammals have been hampered by the lack of relevant theory on which to base predictions, as well as by the paucity of field studies to test them. Over the last half decade the situation has changed. Developments in ecological and evolutionary theory⁸⁻¹⁰ make it increasingly possible to predict distributions, while the growing number of species which have been studied in their natural environment allows us to examine the fit between theory and practice. In some cases, relationships are surprisingly close: we have been able to show that over 75% of the variance of average home range size among primate species can be accounted for by two variables, group weight and the proportion of foliage eaten⁶.

Another factor which has hindered functional explanations has been the failure to combine genetic and energetic theory: in our experience it is almost always necessary to consider both when seeking to understand species differences.

Population density, biomass and home range size

Two energetic principles—truisms, almost—help to explain much about interspecific differences in population distribution among mammals. First, the gross nutritional requirements of an individual increase with body weight but do not do so proportionately. Owing to decreasing heat loss per unit weight in larger mammals, the basal metabolic rate rises as the ~0.75 power of body weight^{11,12}. The relative costs of most forms of locomotion also decrease with body size^{13,14}. Total energetic requirements may vary widely between phyla, but it is usually safe to assume that absolute energetic requirements increase with body size while relative requirements (that is per unit body weight) decline¹⁵. Second,

*King's College Research Centre, Cambridge, UK.

†School of Biological Sciences, University of Sussex, Brighton, UK.

gross interspecific differences in population density and biomass are usually related to differences in the availability of food. It is generally more useful to consider variations in biomass since this takes account of interspecific size differences. Since standing crop of the non-reproductive parts of wild plants (leaf, stem) available to herbivores generally far exceeds that of reproductive parts (flowers and fruit)¹⁶, we can expect to find the highest biomasses among relatively unselective grazers and the lowest among specialised frugivores. Similarly, because the biomass and energy available from plant matter almost always greatly exceeds that of animal prey, we can expect insectivores and carnivores to show lower biomasses than folivores and frugivores.

As might be expected, total herbivore biomass is closely related to variation in primary production: it is greater in the tropics or subtropics than in temperate or arctic regions¹⁷. In the tropics and subtropics both biomass and primary production are closely related to annual precipitation and evapotranspiration¹⁸, although other factors including soils^{19,20}, altitude^{21,22} and human interference²³ may also be important.

In addition, species differences in population density and biomass are related to food availability. Since large-bodied species require absolutely more energy than small ones, their population densities should usually be lower: this can be shown to be the case among ungulates and primates⁶, although the relationship is complicated by an association between small body size and highly selective feeding²⁴. Species feeding on relatively abundant foods show higher population density and biomass than those feeding on less common ones: biomasses of folivorous primates are higher than those of frugivores⁶, while among African ungulates, grazers show higher biomasses than browsers. The biomasses of carnivores are generally far lower than those of herbivores or frugivores²⁵⁻²⁷.

Translated into behavioural terms, this means that large-bodied species (or those living in large groups) have absolutely larger home ranges or territories than smaller species (or those living in small groups) and that home range size is related to diet type. Relationships between home range size, diet and body weight have been demonstrated in small mammals²⁸, primates^{29,30}, carnivores³¹ and ungulates (T.H.C.-B. and P.H.H., in preparation). Home range size does not always increase in proportion to body weight. Among herbivorous and omnivorous small mammals, larger species have relatively small (per unit body weight) home ranges, and home range size increases with body weight to about the 0.65 power. In contrast, among carnivores, relative home range size increases with body weight (power of 1.41; ref. 31), and a similar trend is found among predatory birds³¹. The difference between carnivores and other dietetic groups may arise because increasing body size in carnivores restricts the size range of prey that are economical to hunt, leading to a decrease in the biomass of available prey as body size increases^{30,31}. The relative decrease in home range size with increased body weight among small mammals has been explained as a result of the decline in relative metabolic costs with increased body weight²⁸.

The dispersion of resources also affects home range size. Where food supplies are strongly clumped, widely dispersed or unpredictable in abundance, mammals occupy large home ranges^{32,33}. In contrast, where supplies are evenly dispersed and predictable, small home range size results and the defence of feeding territories becomes practicable if food density is high enough³⁴.

Group size and patterns of population dispersion

The abundance and distribution of food supplies affect population dispersion. While grouping can serve many dif-

ferent functions in mammals³⁰, species differences in group size seem to be best predicted by variation in the disadvantages (rather than the advantages) of grouping³⁰. Group feeding is likely to lead to feeding interference and a decline in the rate of food intake^{24,35,36}. Feeding interference will be most pronounced where individuals eat out (or defend) whole food sources, forcing latecomers to search elsewhere, and where the distance between food items is large²⁴. In contrast, it will be least important where individuals only take a proportion of the food available at each source (as in many grazing species) and where the distance between food items is small. Among the African ungulates, highly selective grazers and browsers (duicker, klipspringer, oribi, gerenuk, kudu) generally live alone or in small groups, whereas less selective grazers (wildebeest, zebra, topi, buffalo) often feed in large herds^{24,37}. Similar trends occur among pachyderms³⁸, cervids (T.H.C.-B. and P.H.H., in preparation) and herbivorous marsupials^{39,40}.

The dispersion of food sources can also influence population dispersion. Species which depend on food sources occurring in large, evanescent clumps often feed in big groups and rarely defend territories^{8,24,32}. In contrast, where the distribution of food supplies is regular enough and food density high enough to permit territory defence³⁴, group size may be constrained by the inevitable decline in the efficiency with which other animals can be excluded as group weight (and hence territory size) increases^{33,41}.

Many other environmental factors apparently affect group size. Among primates², nocturnal species usually feed alone, irrespective of their diet type: one possible explanation is that most small nocturnal primates rely on crypsis for defence^{30,43} and that this precludes social feeding. And among carnivores, social feeding is often an adaptation to large prey size and tends to occur among species which feed primarily on prey whose body size is larger than their own^{26,44}.

Breeding systems and constraints on polygyny

Because the abundance and distribution of food resources affect population density and dispersion, they also have profound effects on the breeding systems which different animals adopt⁴⁵. Two recent developments in evolutionary theory are of particular importance in understanding the functional significance of breeding systems. The first is the extension of the concept of 'Darwinian fitness' (the number of direct descendants that an individual leaves in subsequent generations) to that of 'inclusive fitness' (the amount of an individual's genotype which is passed on to subsequent generations), a development due largely to W. D. Hamilton⁴⁶ and often referred to as 'kin selection'. The second is the reinterpretation of the Darwinian theory of intra-sexual selection^{47,48}. The first has been successfully used to explain a wide variety of examples of cooperative breeding by related animals, from communal suckling in lions⁴⁹ to the evolution of sterile casts in the social hymenoptera⁴⁶. The second is of particular importance in understanding mammalian breeding systems. Trivers⁴⁸ envisages individuals of each sex as having limited resource budgets which they can invest in their offspring (or other relatives). One sex generally invests more than the other: in mammals this is usually the female since she suffers the costs of gestation and lactation (the reasons for this initial asymmetry in investment have been discussed elsewhere^{48,50}, but are not directly relevant to the present argument). As a result, female mammals cannot produce and rear offspring at the rate at which males can father them. Consequently, while the reproductive success of females will usually be limited by the number of young they can produce and raise, that of males will often be limited by factors affecting the number of females they can fertilise.

The theory explains why, among mammals, polygyny is common and polyandry rare or nonexistent: the advantages

to a female of maintaining mating access to several males will, in almost all circumstances, be less than the advantages to a male of maintaining mating access to several females^{48,50}. Through its effect on the distribution of females, the distribution and density of resources plays an important part in limiting the degree of polygyny which can evolve. Early interpretations of mating systems⁵¹⁻⁵³ suggested that the occurrence and extent of polygyny is limited by female choice, and that unmated females will only breed polygynously when they improve their fitness by doing so (for example, where a successful male defends access to resources adequate for several females and their young). In a recent review, Emlen and Oring⁵⁴ extend this hypothesis, suggesting that polygyny will occur either where males can monopolise resources sufficient to attract several females ("resource defence polygyny") or where they can defend groups of females ("female defence polygyny"). The feasibility of defending either resources or females will be affected by their distribution in time and space as well as by the amount of time and energy which the male can afford to devote to defence of mating access.

The argument successfully merges evolutionary and ecological theory. An individual male may be able to defend access to resources adequate for several females either where resources are evenly dispersed and their density is high, or where resources show some degree of clumping but are concentrated and predictable enough to permit several females to depend on them throughout the year. Examples of this first situation are the harem groups monopolised by territorial males in many South-East Asian langurs³⁰. An example of the second is the yellow-bellied marmot, where males defend areas of rock outcroppings used as wintering sites by several females and are thus able partially to control breeding access⁵⁵⁻⁵⁹.

Where resources are evenly distributed but sparse, females will be widely dispersed and males may be unable to monopolise access to more than one female: probably for this reason, extreme polygyny is rare among the smaller carnivores and insectivores⁵⁰. An association between low density food supplies and monogamy has been suggested both in birds⁵³ and primates³⁰. In the latter group, Clutton-Brock and Harvey³⁰ suggest that monogamy occurs where males cannot defend resources adequate for several females either because female size (and hence nutritional requirements) is large or where the biomass of available food supplies is low. In some monogamous species (as in the gibbons and siamangs) the mated pair and their dependent offspring travel and feed together while in others (including many monogamous ungulates), the male and female spend most of their time apart. The latter seems to apply either in species where feeding interference is intense because of the nature of food sources⁶² or where individuals rely on crypsis to avoid predators.

Finally, where resources are heavily clumped and clumps are unpredictable or widely dispersed, males will be unable to defend resources adequate for several females. In this situation they may either defend groups of females (as in patas monkeys or hamadryas baboons) or, where the size of female groups is large and they are difficult to defend, accept the presence of other males and attempt to maintain priority of access to receptive females (as among most baboons and macaques). In these cases, the numbers of females which a male can monopolise will be affected by the density of resources as well as by the extent of reproductive synchrony among females: where conceptions are highly synchronised and the duration of courtship is long, males will be less likely to monopolise access to several females successfully⁵⁴. For example, almost all strongly polygynous pinniped species copulate and give birth on land, where females are closely spaced and easily defended⁶³⁻⁶⁵. In contrast, among species which copulate primarily in the water (such as the common seal, *Phoca vitulina*, and the

monk seals) extreme polygyny has not evolved, probably because aquatic territories are difficult to defend⁶⁵. While most pinnipeds have well defined breeding seasons, synchrony is most marked among species which breed on pack ice where most matings occur within a 10-day period. Extreme polygyny is also absent in this group, perhaps both because females are dispersed and because breeding is highly synchronised^{64,65}.

Even where the distribution of females or resources provides the potential for polygyny, males will not always be able to take advantage of it⁵⁴. This will be the case where successful rearing of offspring requires paternal as well as maternal care, when the number of females they breed with may be limited by the number of offspring they can look after^{48,50}. While paternal care is closely associated with monogamy among mammals^{66,65,30}, it may take a number of different forms. In the majority of monogamous species, males help to defend food reserves used by their mates and offspring⁶⁶. In some arboreal or volant mammals, males also help carry the young. For example, among primates, male marmosets, tamarins, night monkeys, titis and siamangs carry the infant(s) for much of the day⁶⁷. All these species usually breed monogamously and similar behaviour is not recorded among polygynous primates, though males may carry infants and frequently protect them⁶⁸. Not all monogamous primate fathers regularly carry their young, but they tend to do so where the weight of the young is large relative to female weight⁶⁶. Finally, in some mammals (as in many birds) the male helps the female to bring food to the young and/or mother. This tends to occur where food is energetically costly to collect and where litter size is large: for example, it is common among monogamous canids^{69,66}. Monogamy developing for this reason alone is most likely to be found in relatively stable environments where intraspecific competition is intense^{9,10}.

The difficulty with explaining monogamy as the consequence of the need for paternal care is that paternal care is likely to evolve in circumstances in which polygyny is prevented by other factors. In an evolutionary timespan, it is as possible that the presence of extensive paternal care (and even of increased neonatal weights and larger litter sizes) in the monogamous primates we have listed is a product of the fact that males breed monogamously for other reasons as that the need for paternal care requires monogamous breeding. There is no obvious way out of this problem.

Functional interpretations of breeding systems still present many difficulties. Partly because many different ecological variables are involved and partly because several of these cannot be measured accurately (in particular, the extent to which food supplies are clumped) it is seldom possible to make useful quantitative comparisons. As a result, arguments inevitably rely on selected examples rather than systematic analyses. Finally, there are many unanswered questions: while, in outline we can account for the distribution of monogamy versus polygyny, it is often difficult to explain species differences in the degree of polygyny³⁰. Nor do we understand why, in some species, breeding males tolerate the presence of peers whereas in others they do not³⁰.

Breeding competition and sexual dimorphism

The breeding system adopted is known to affect the degree of intrasexual competition for mating access⁷⁰: in strongly polygynous species, we should expect competition between males for access to females to be intense, while in monogamous species it should be reduced or absent^{10,70}. Consequently, we might expect traits affecting competitive ability to be better developed in males of species which usually breed polygynously than in those that usually breed monogamously⁴⁸.

Systematic investigation of sexual dimorphism among primates confirms this prediction. In polygynous species, males are larger, relative to female size, than in monogamous ones¹, show greater development of pelage used in defence or display⁷¹ and have relatively larger canine teeth for their body weight⁷². A similar trend occurs among ungulates where males of polygynous species typically have bigger horns or antlers than males of monogamous species⁷⁴.

While the gross distribution of sexual dimorphism conforms with the pattern predicted by sexual selection theory, it is clear that the trait has also been moulded by many other evolutionary and ecological pressures. In a number of bird species, selection has apparently favoured sex differences in body size or feeding apparatus which allows the sexes to diverge in food choice and thus to utilise food supplies more efficiently^{73,74}. Such a process may also help to explain the presence of marked sexual dimorphism in some mammals which are not strongly polygynous⁷⁵. Similarly, since increased body size permits a larger feeding radius from some fixed point such as a burrow or nest, selection may favour increased body size in the sex which is responsible for feeding the young⁷⁶. Both mechanisms would be most likely to be found in species whose searching or pursuit costs are high⁷⁷ and should, for this reason, be most likely to occur among predators.

Ecological factors may also constrain sexual dimorphism. The most extreme cases of sexual dimorphism among mammals far exceed birds⁷⁸, presumably because the restrictions on increased weight are reduced in ground dwelling species. Similarly, among primates, dimorphism in body weight is greater in terrestrial than arboreal species, probably because increased weight does not restrict the male's access to food resources growing on fine branches or terminal twigs⁴.

Selection pressures acting on females can also have profound effects on sexual dimorphism. Since body size is positively related to maturation age in many species, selection for early maturation in females (perhaps associated with fluctuating environments) may lead to a decrease in female body size, while large male body size may be maintained by intra-sexual selection^{58,79,80} thus producing marked sexual dimorphism in species that are only slightly polygynous. Conversely, selection for increased litter size or neonatal weight may lead to increased female size⁸¹: large mothers can produce bigger litters (or offspring). The breeding system can affect the breeding access of females to males and this, too, may effect selection pressures operating on sexual dimorphism. In some primate species, females show pronounced swelling of the perineal or para-callosal areas which signal their sexual state⁸². The distribution of swellings is not obviously associated with either environmental or taxonomic differences and has puzzled primatologists since Darwin: "In my *Descent of Man*" he wrote "no case interested me and perplexed me so much as the brightly coloured hinder ends and adjoining parts of certain monkeys". Recent studies show that, with one exception (the hamadryas baboon), the trait occurs in species where females have mating access to several males (although only a proportion of such species have sexual swellings) and suggests that swellings may have developed to attract the attention of males and increase a female's chance of being mated by a high-ranking male⁶⁷. On a similar line of argument, Cox and LeBoeuf⁸⁴ suggest that the vociferous complaints of female elephant seals which are mated by subordinate males may serve to increase the chance that they will be mated by a dominant animal.

In yet other cases, competition with males may lead to selection for improved competitive ability among females and thus to reduced dimorphism⁸⁵. Among the Cervidae, female reindeer and caribou are unique in possessing a large pair of antlers and in forming big bisexual herds including large numbers of males⁸⁶. It seems likely that large herd

size may intensify feeding competition between males and females, and that females have developed antlers to allow them to compete successfully with males. In a number of primates which live in large, mixed-sex groups, females may suffer regular feeding interference from males (Packer and Pusey, in preparation). Perhaps because of this, females possess relatively large canines (for their body size) in primate species which form multi-male groups than in those which live in harem groups where the adult sex ratio is strongly biased against males (P.H.H., M. Kavanagh and T.H.C.-B., in preparation).

We have concentrated, in this section, on sexual dimorphism in body size partly because enough data are available for quantitative comparisons and partly because it provides a good example of the interaction of genetic and energetic influences. It is clear that interspecific variation in breeding systems will also prove to be associated with a wide variety of other morphological and physiological differences, including variation in social relationships⁸⁷ and maturational processes^{79,80}.

We must end with two caveats. When explaining interspecific differences, it is almost always impossible to test functional arguments by experiment and we rely on correlations and associations. As we have argued, causes are often difficult to distinguish from effects. In some cases it is not of critical importance to distinguish the direction of causality. For example, large sacculated stomachs equipped with microbial symbionts permit herbivores to use forage with a high cellulose fraction¹⁵. It is not usually important to decide whether, in an evolutionary perspective, forage quality controls digestive anatomy or vice versa. In others, our understanding of causality will have a profound effect on the explanations of distributions. In some of these, the reasons for an association are fairly obvious: it is, for example, more likely that differences in sexual dimorphism are caused (in part) by differences in breeding systems than vice versa. In yet other cases, such as the relationship between monogamy and paternal investment, no such assumption can be made. It is impossible to generalise about relationships of this kind and each case needs to be considered separately. The usual assumption made by evolutionary ecologists (albeit tacitly) is that the feeding niche occupied by a species (and the morphological, physiological and behavioural adaptations which affect food exploitation directly) is most likely to constrain evolutionary changes in other variables⁶.

Second, while we have concentrated throughout this review on generalisations, there are many exceptions to every generalisation that we have cited. We do not believe that their existence reduces the value of attempting to generalise. On the contrary, only when we understand the ground rules of mammalian adaptation shall we be able to ask sensible questions about the exceptions.

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articles

Equivalent circuit analysis of neutral wind effects on equatorial electrojet

C. A. Reddy & C. V. Devasia

Space Physics Division, Vikram Sarabhai Space Centre, Trivandrum 695022, India

The generation of electric fields and currents by local winds in the equatorial electrojet is treated by an equivalent electric circuit method. Apart from its mathematical simplicity, the method provides a full and clear view of the physical processes involved in the generation of currents and electric fields by shearing winds, and thus permits a straightforward interpretation of the main effects of winds. The method is valuable for the theoretical analysis of the wind-related electrostatics of the equatorial electrojet.

THE effects of local winds on the ionospheric dynamo-region currents at or near the magnetic dip equator have previously been considered negligible because the effect of the wind is normally cancelled out by the polarisation electric field set up by the wind. Recently, the local wind effects on the equatorial electrojet have

received increasing attention^{1–6}, as it was realised that height-varying winds, in contrast to the steady winds considered earlier, could have significant electrodynamic effects in the equatorial electrojet region. Kato¹ pointed out that the polarisation electric field set up by wind motion at the magnetic equator would be partially short-circuited by the currents flowing across the curved magnetic field lines in the dynamo region away from the equator. He showed this effect using an equivalent circuit representation of the dynamo region at the magnetic equator and its coupling, through the highly conducting magnetic field lines, to the conducting region away from the equator. His treatment of the problem was incomplete, however, to the extent that the contribution of the wind-induced dynamo fields in the same dynamo region where the short-circuiting currents flow was not taken into account. On the other hand, Forbes and Lindzen³ considered a three-dimensional model of the equatorial electrojet in which the effects of shearing neutral winds were included. They concluded that even a two-dimensional model of the electrojet would