

The ecology of carnivore social behaviour

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Diverse selective pressures have contributed to the evolution of the varied social groups of carnivores: the benefits of strength of numbers for defence of kills and territory, and in the hunting and killing of large prey; the ability to intimidate predators and to be vigilant against their approaches; the potential for information transfer and social learning, and a suite of alloparental behaviour patterns. Each of these may operate within the constraints upon group size and home range size set by patterns of resource dispersion. Between and within species, the magnitudes of costs and benefits attendant upon group life vary with circumstances and between individuals.

TRADITIONALLY, two selective pressures have been invoked to explain why some of the Carnivora live in groups: the need for assistance in hunting and killing large prey, and the need for defence against attacks by other predators¹⁻⁴. Wolves, for example, hunt cooperatively to capture their large, and sometimes dangerous, quarry while, in contrast, red foxes, *Vulpes vulpes*, kill small rodents by stealth and do better to hunt alone^{5,6}. Representatives of at least four genera of mongooses benefit from living in packs through the increased vigilance provided against marauding predators, and through the potential for intimidating predators^{1,2,7} by their group defiance.

Neither of the above selective pressures explains, however, why some species live in groups but travel and hunt alone. Clans of European badger, *Meles meles*, living in communal setts^{8,9}, parties of giant otter, *Pteronura brasiliensis*¹⁰, groups of red foxes¹¹, colonies of 'feral' cats (refs 12, 13 and D.W.M., P. J. Apps and G. M. Carr, in preparation), groups of palm civets, *Nandinia binotata*¹⁴, and groups of brown hyaena, *Hyaena brunnea*¹⁵, serve as examples from five families where other reasons must be sought to explain social grouping. Study of these carnivores indicates that selective pressures previously thought of as rather incidental, have given rise to complex social groupings. Benefits, which vary according to the species or population, come not only from cooperative hunting, defence of territory and prey, and defence against predators but also from the opportunities to learn from other group members' experiences, division of labour, care of the sick and several advantages associated with alloparental behaviour, that is, the care of the offspring of others. However, all the many benefits of group living must operate within a framework of constraints determined largely by the dispersion and abundance of available resources, especially food. Considering the great diversity of carnivore social systems, both inter- and intraspecific variation in the ecological costs of sociality is as relevant as is variation in the behavioural benefits. Here I shall argue that there are ecological circumstances in which the benefits of 'spatial groups' (and equally perhaps the evolutionary origins of contemporary highly social groups) may have little or nothing to do with advantages directly consequent on sociality. Rather, resource (particularly food) dispersion is fundamental to the spacing and structure of carnivore society in that it may set the limits to the group and territory sizes within which other combinations of selective pressures operate.

Resource dispersion hypothesis

The idea that certain patterns in the availability of food (and other resources) may allow group living, originates largely from work on birds¹⁶⁻²⁰. The general principle applies to all social systems, and has been applied in particular to several mammalian societies (bats²¹, primates²²⁻²⁴, antelope²⁵), several carnivores^{8,9,11,26-30}, and generally to mammalian mating systems^{20,31} and, very convincingly, to the social organization of badgers³⁰.

Two extreme examples show how the pattern of food availability influences the way in which carnivore groupings develop. In Portsmouth, female dockyard cats live in groups (mean 5.4 individuals) sharing large areas of their individual home ranges (mean 1.8 hectares)¹³. Each colony's range is centred on a 'skip' of refuse containing edible offal and from which other female cats are debarred. Similarly, golden jackals, *Canis aureus*, observed in Israel form stable social groups of as many as 25 adults around a feeding site³². These jackals ring their territory with communal latrines, patrol the borders as a cohesive group, share food and repel intruders collaboratively—behaviour very different from that found in other ecological circumstances. These cats and jackals fed largely from one or a few sites whose existence provided the possibility of group formation and whose collaborative defence provided one obvious advantage of group living.

The factors permitting and promoting group formation are less clear for some other species, such as red foxes. In rural suburbia outside Oxford¹¹, groups of red foxes consist of one male and up to five adult vixens (mean 3.4 females, $n = 5$). Each individual is in physical contact with another for as little as 4 min each night³³, yet they are social units in that members have clearcut, amicable relationships and share a fairly well defined group territory (mean 45.2 hectares, $n = 7$). Their most important foods are earthworms, scraps scavenged from human settlements and fruits^{11,28}. These foods vary in their spatial and temporal availability. Worms are caught on the surface³⁴ and only emerge when the microclimate is appropriate. Local microclimates vary independently, and thus from night to night, and even within one night, patches of higher availability of worms occur in different parts of each fox's territory. Similarly, a garden may be rich in household scraps one night but devoid of them the next, and fruits are seasonal. The minimum territory size required to sustain a pair of foxes, and the territory's configuration, may thus be determined by the dispersion of transient patches of available prey (ephemeral from night to night, or shifting from one season to the next), and constrained by the costs of defence of irregularly shaped areas. In contrast, group sizes are limited by the availability of prey in these patches. In this context, the resource dispersion hypothesis (see refs 11, 15, 29, 30) suggests that the smallest home range with an economically defensible³⁵ configuration which will reliably support a pair of red foxes (on a bad night or a bad year) may sometimes support additional foxes. These other foxes are tolerated in numbers and at times when any costs (to the basic pair) due to their presence are outweighed by the overall benefits. If the costs are small then of course the advantages need not be great; thus, for example, a minimal advantage of group membership might be no more than the avoidance of dispersal³⁶ (the surrounding habitat may be saturated or dangerous) or guaranteed access to a den site, water hole or familiar hunting ground. Such benefits have little (or even nothing) to do with social behaviour *per se* but need not result

in groups that are merely structureless aggregations. Just as territories can usefully be defined as ranges which overlap less than expected by chance³⁷, so members of 'spatial groups' can be defined as individuals whose ranges overlap more than expected by chance. Members of spatial groups are likely to meet frequently and would be readily available as beneficiaries of advantages derived more directly from sociality. In the case of red foxes these social advantages include alloparental behaviour^{36,38}, increased boundary surveillance and occasional corporate attack of trespassers²⁸.

Resources, group size and territory size

From the resource dispersion hypothesis one would not necessarily expect (even in broadly similar habitats) any relationship between group size and territory area, as the two are argued to be affected, largely independently, by the abundance and dispersion of available food respectively. However, for a given patch-richness one would expect minimum sized territories to be larger where patches were more dispersed (Fig. 1). The resource dispersion hypothesis neither discounts nor precludes the possibility that animals may strive to maintain territories and/or groups that are larger than the minimum^{38,39}, rather it provides an ecological explanation of how, at minimum costs to themselves, members of a pair could incorporate additional group members into even the smallest economically defensible territory which will sustain them. The absolutely greater (but proportionately less) costs of border defence for the territorial expansion required to support larger groups might be offset by greater benefits. On the other hand, advantages to a carnivore of knowing its home range extremely well may favour ranges which are as large as necessary but as small as possible.

To measure the availability of resources, such as prey, is notoriously difficult. However, to the extent that habitat types are an index of prey abundance (for example, a ploughed field supports fewer mice than does mature grassland), the geometry of the habitats within a territory may be reflected in the pattern of prey availability. In this case, the sizes and configurations of territories will be such as to encompass at least a minimum total area of key habitats, representing rich prey-patches scattered in otherwise barren areas. Studies of three species of carnivore illustrate the argument. The European badger, *Meles meles*, specializes on one prey, the earthworm^{8,9}, whose abundance is readily measured and whose availability in given habitats can be estimated. This enabled Kruuk and Parish³⁰ to show that variations in badger society reflect resource dispersion. Badgers forage in patches of short grass pasture which have high earthworm availability, 4–5 areas of which are found per territory. If the patches are widely dispersed, territories are correspondingly larger, but there is no correlation between territory size and group size. In contrast, mean 'patch quality' (that is, abundance of earthworms) in each territory did correlate with group size. Thus, patch dispersion influences territory size, whereas patch quality independently influences group size. The problem remains of what social mechanism adjusts group sizes to patch quality.

In one study of red foxes¹¹, adjacent territories varied in size between 18.6 and 72.0 hectares and groups consisted of 3–6 adults, but larger groups did not occupy larger territories. Radio tracking, diet analysis and prey sampling indicated that residential habitats (houses, gardens and orchards) were intensively used and rich in food. In adjacent arable farmland prey was scarce. Analysis of seven adjacent territories showed a comparable area of residential habitat in each [mean = 10.4 ± 3.5 hectares (±s.d.)] and territory configurations clearly designed to encompass these key patches. The most constant component in each territory was the number of houses (mean = 23.7 ± 4.8) (probably an indicator of the availability of scraps).

Three groups of Arctic foxes, *Alopex lagopus*, studied in the fjords of north-west Iceland lived in units of one male and two adult vixens²⁹. The groups occupied territories varying between 8.6 and 18.5 km², and gained 60–80% of their food by beach-

combing. Carrion could be found only in those 'productive' bays favoured by the drift of the current. Despite their different areas and total lengths of coastline, each territory encompassed rather constant lengths of 'productive' coastline. More strikingly, each territory's coast yielded annually a comparable bulk of driftwood to local farmers (mean = 1,900 ± 44 fence posts), and so presumably also a comparable availability of carrion to foxes.

Territory sizes in contrasting habitats

Even within broadly similar habitats there is considerable intraspecific variation in the basic parameters of carnivore social organization—that is, group size and home range size (equivalent to territory for most species mentioned here). Between populations in contrasting habitats the variation can be enormous: in the uniform and sparse habitats of the North American prairies, red foxes live in pairs within large (500–2,000 hectares) territories⁴⁰; in the diverse, rich habitats on the outskirts of Oxford they form groups within small (10–100 hectares) territories¹¹, while in the taiga forests of Sweden where prey abundance cycles from year to year, territory sizes of 700 hectares remain unchanged in area (perhaps adjusted to the worst years) while group sizes vary with vole abundance³⁹. Like those between adjacent territories, these variations between dramatically different habitats seem explicable in terms of variation in the constraints imposed by food dispersion on group formation: where prey are more homogeneously distributed, as in intensive arable land of the prairies, then the smallest territory that will support a pair may not support another adult. Where there are cycles of prey availability between years, as in the taiga, then the smallest territory which supports a pair during troughs of vole abundance can incorporate additional adults during the peaks of vole numbers. During bottleneck years or seasons, groups shrink, but territories do not necessarily contract³⁹. The regulation of group size involves social status: there is evidence that amongst wolves^{41,98} and foxes²⁸ low ranking animals are expelled as aggression mounts with diminishing food availability. These observations are compatible with Bertram's²⁷ view of lion pride and range sizes—in the long term, pride ranges probably respond to changes in food availability, but in the shorter term they remain constant, adapted perhaps to the worst of recent conditions, but with the option of altering pride size through recruitment of sub-adult females. That social factors affect the regulation of group size among many carnivores^{42–44} is of fundamental importance to their population dynamics^{16,45}.

Females as a resource

Female, rather than food, dispersion may underline spacing of males in those species where several exclusive female territories are encompassed within that of one male³¹ (for example, bobcat, *Felis rufous*⁴⁶, stoat, *Mustela erminea*⁴⁷, and wolverine, *Gulo gulo* (refs 48, 49 and A. Magoun, personal communication)). Amongst both Mustelidae and Ursidae there is a spectrum from male monopoly of several female territories and greatest sexual dimorphism (100%) and carnivory, to species where the sexes are equally sized, frugivores or omnivores inclined to more amicable social ties involving monogamy or group formation, such as in Tayra, *Tayra barbarosa* or sloth bears, *Melursus ursinus*, and sun bears, *Helarctos malayensis* (10–25% dimorphism) (ref. 50 and F. Bunnell, personal communication). As work on supposedly less sociable carnivore species continues⁵¹, the pattern in which the spatial organization of females is determined by the distribution of food resources, and that of males is determined by the distribution of females, may turn out to be widespread.

Group size and hunting success

Cooperative hunting has only been documented for members of the Hyaenidae, Canidae and Felidae of the seven families of carnivores (although some members of all families forage in bands). Among the canids, the hunting dogs, *Lycaon pictus*,

almost invariably hunt cooperatively⁵², as do dholes, *Cuon alpinus*⁵³, but most other pack hunters are only facultatively cooperative in their pursuit of prey. For example, wolves⁵⁴, coyotes, *Canis latrans*⁵⁵, dingos, *Canis dingo* (L. C. Corbett, personal communication), jackals, *C. aureus* and *Canis mesomelas*^{44,56}, and probably also bush dogs, *Speothos venaticus*, regularly, but not invariably, hunt together for large prey, whereas other species do so infrequently. Bat-eared foxes, *Otocyon megalotis*, are unusual among canids in foraging in small family parties but for invertebrate prey^{57,58}.

Members of a clan of spotted hyaena, *Crocuta crocuta*, may assemble into temporary hunting parties, of which larger parties (mean = 10.8 members) hunt zebra, *Equus burchelli*, smaller ones (mean = 2.5) hunt adult wildebeest, *Connochaetes taurinus*, and yet smaller ones (mean = 1.2) hunt the fawns of gazelle, *Gazella thomsoni*⁶. Parties of a given size search for 'their' prey species, ignoring others and thus indicate a remarkable corporate decision about which prey to hunt, even before sensing their victims. However, although there is a positive correlation between prey size and social group size across the Carnivora⁵⁹, the variance in hunting party membership is only partly explained by the increased difficulty of killing larger, fleet prey. Also, jackals cooperate to hunt small prey⁵⁶, whereas kit foxes, *Vulpes macrotis*, hunt alone for rabbits twice their weight⁶⁰. The question thus arises of whether hunting together functions solely to increase efficiency of hunting and killing large prey.

Clearly, cooperative hunting is not the sole benefit of group living for, in at least some cooperative hunters, groups may be much larger than hunting parties (for example, spotted hyaenas⁶ and lions⁶¹). Even the size of hunting parties is probably not primarily governed by the requirements of cooperative killing^{62,63}. Nevertheless, in some circumstances cooperative hunting is more efficient than foraging alone: two silver-backed jackals, *Canis mesomelas*, can thwart a mother gazelle's defence of her fawn whereas a single jackal can rarely do so⁵⁶. Similarly spotted hyaenas hunting in pairs can invariably separate a wildebeest calf from its mother⁶. Larger packs of coyotes may kill relatively more larger prey such as deer⁵⁵, and van Orsdol⁶¹ reports that hunting efficiency increases with the size of lion hunting parties up to a maximum of four or five members. The defence of kills from conspecifics and scavengers⁶⁴ may also encourage group hunting and this selective pressure may affect different species differently: for example Lamprecht⁶⁴ has argued that jackals do not hunt in larger groups for bigger prey because even their corporate power would be insufficient to repel large scavengers. He also argued⁶² that other (larger) species hunt in larger groups primarily to secure the collective strength to defend their spoils.

I suggest that all the possible advantages of group hunting act within the fundamental framework of constraints set by the dispersal of resources, such that an imaginary, smaller group will require a territory just as large as that occupied by the observed larger group. As a speculative example, lions often ambush their prey around water holes⁶⁵. An ancestral lion might have required several water holes to ensure access to prey across seasons and through ungulate migrations. However, each waterhole, when productive at all, might easily support several lions and some or all of the combined advantages of increased hunting success, nursing coalitions, defence of kills, the need to avoid interference with each other's hunting, could then favour cooperative hunting as well as group living. I therefore argue that the evolutionary catalyst for group living (that is, prey dispersion) could have been the same for, say, red fox and wolf and that the contemporary nature of the groups (for example, solitary or collaborative hunting) differs partly due to the prey's size and ability to defend itself.

That several hunting units of variable composition operate within lion prides (and spotted hyaena clans⁶) and that any advantage of cooperative hunting only applies to hunting parties of 4–5 lions⁵⁹ whereas prides may number up to 37, and even hunting parties may number over 4–5, indicates that factors

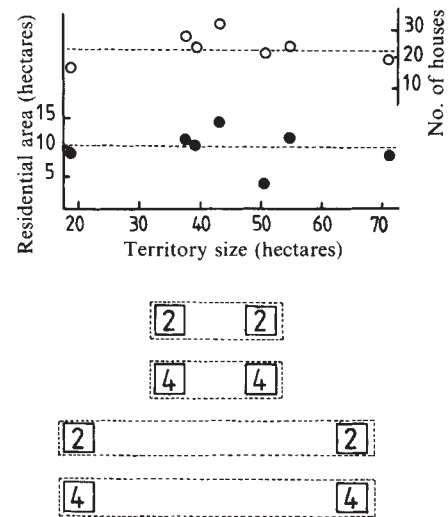


Fig. 1 A simplified case of the resource dispersion hypothesis: temporal variation in the availability of prey means that even a pair of animals require two patches (symbolized as squares) and the dispersion of these patches determines the minimum necessary economically defensible area, whereas patch richness (for example, values of 2 versus 4 indicate patches which support either two or four animals) determines the maximum group size that can be supported in that minimum area. In a habitat where dispersal was disadvantageous it could thus be advantageous for these four animals to form a spatial group purely because of the availability of resources and irrespective of any direct benefits of sociability *per se*. These schematic patches may be thought of as gardens with nightly variations in the availability of scraps for foxes¹¹, or pastures that are more or less bountiful for foxes and badgers foraging for earthworms depending on prevailing wind direction^{8,9,30,34}, or they could be asynchronously fruiting trees upon which frugivores feed^{22,23}. The graph shows that red fox territories of widely differing sizes embrace similar areas of 'residential' habitat (which is prime foraging habitat) and roughly the same number of human residences from which food was scavenged from bird tables and compost heaps, and on whose lawns earthworms were caught. Territorial configurations were clearly adapted to embrace clumps of houses and gardens¹¹.

other than the collaborative hunting of even the largest prey underlie group living and hunting by cooperative hunters today. Schaller's⁶⁵ lions only doubled their success by hunting in pairs but two or more lions were better able to repel scavenging hyaenas after making a kill. Packs of hunting dogs contain 1–18 members; some packs learn, from pack tradition, to kill zebra using a restraining nose-hold and a pack of four and one of eight seemed equally adept at this^{66–69}. Similarly, two or three dholes can overpower a 60 kg deer apparently as well as a pack of the average (8.3 adults) or maximum (16–20) size⁵³.

Population differences in cooperative hunting

In Texas, coyotes feed mainly on rodents⁷⁰, but they nevertheless live in groups, whereas on a similar diet, coyotes in the Rocky Mountains⁷¹ live in pairs. Elsewhere, coyotes live in packs and feed almost exclusively on ungulate carrion⁷² which larger packs are more successful at defending from rival packs than are pairs^{55,71}. Also, larger packs appear to be more effective hunters of deer than are smaller ones⁵⁵. Thus, a diet of large prey may favour (but not necessitate) the formation of large hunting parties, and the fact that groups and hunting parties are often apparently supra-optimal for hunting presumably means that their membership is in response to other selective pressures. In coyotes, hunting by man may depress group sizes both directly and by creating vacant territories and so reducing the costs of dispersal.

Territory size versus group size

Considering adjacent territories in broadly similar habitats, no correlation between group size and territory size has been found

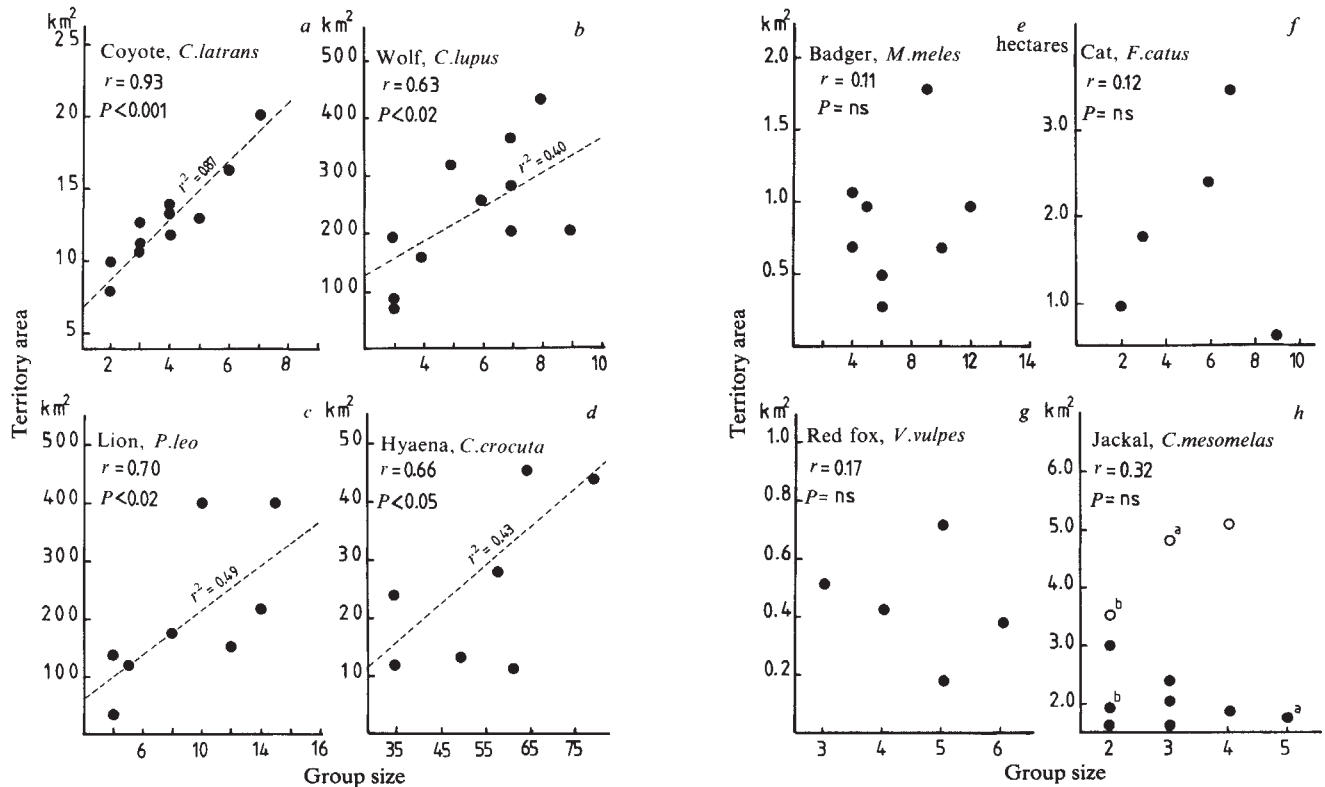


Fig. 2 Two patterns emerge from plotting group sizes against territory areas for eight species of carnivore, representing four families. In *a-d* there are variously precise correlations between the two parameters, whereas there is no such relationship for the species in *e-h*. NS, not significant. Each graph concerns more or less adjacent ranges from broadly similar habitats (which minimizes the effect of confounding variables, such as any inter-population variation in body size which might affect range sizes). Territory sizes were measured from maps, using a planimeter, and combined with data from tables in refs 6, 8, 9, 11, 13, 44, 55, 65, 94 and personal communications from the same authors. (In each of these, and many other carnivore species, home range is the same as territory.) The resource dispersion hypothesis can explain, but does not necessitate, the absence of correlation between territory and group sizes. In *b*, group sizes refer to adult wolves in spring. In *h*, open circles represent jackal territory and group sizes in 1 yr of prey scarcity; these were excluded from the analysis (a and b were jackal territories studied in 2 yr)⁴⁴. These varying relationships within populations do not detract from (and are actually incorporated in) the broader interspecific correlation which Gittleman and Harvey⁹⁷ found between home range sizes and metabolic needs (a measure which includes group sizes) across the carnivores. Presumably, the selective pressures which give rise to interspecific variation are the same as those causing intraspecific variation.

among several group-living but solitarily hunting species (Fig. 2*b*). In contrast, membership of packs of several cooperatively hunting species does increase with territory size (Fig. 2*a*). Pack size accounts for 87% of the variance in home range size amongst one coyote population, and in two cases range sizes were reduced after the death of pack members⁵⁵. Bygott *et al.*⁷³ report how a large coalition of male lions may successively gain control of two or even three formerly independent territories and hence prides of lionesses. Male cheetah, *Acinonyx jubatus*, form similar coalitions of 2-4 members⁶⁹, and tigers, *Panthera tigris*, expand their territories into that of a sick neighbour⁷⁴. In some areas, red fox territories may expand after the death of a neighbour⁷⁵, and elsewhere³⁹ territory sizes remain the same in years of widely different food abundance. Thus carnivores sometimes defend a larger area than the minimum necessary for a pair, and sometimes they thus incorporate additional group members. The advantages of expansionism to members of male felid coalitions include procuring more matings and surviving serious fights^{69,73}, whereas the coyotes probably found and retained more moose carcasses⁵⁵.

The differences between cooperative and solitary hunters in Fig. 2 are puzzling: one would expect that by travelling together, larger parties of cooperative hunters were better placed to overwhelm their neighbours and hence to secure larger territories. However, packs of banded mongoose travel together, forage individually and show no correlation between group and pack sizes, although larger groups do win fights (ref. 7 and J. Rood, personal communication). The situation is complicated as although all four species in Fig. 2*b* are cooperative hunters, they differ with regard to the relationship between their social

and foraging units. Each may enjoy a wide range of benefits from group living, but there is little evidence of their comparative importance. Some benefits to group living are mentioned below.

Anti-predator behaviour

Rood⁷ found that baby-sitting by adults reduced predation on young dwarf mongooses by slender and banded mongooses; he also described (personal communication) a dramatic rescue from an eagle's talons of a captured banded mongoose by the alpha male of the pack. Predators are more likely to be spotted and/or intimidated by larger groups of prey⁷⁶, and this advantage has been ascribed especially to social viverrids^{1,2}. Vigilance for predators may be an important benefit of cohesive group travel, and, as Rasa¹ argues, where life in open terrain puts small carnivores at particular risk (indeed, across the order group living is associated with open habitat⁵⁹).

Kinship

It is axiomatic that groups may be expected to develop where the costs of the resident's fitness of evicting an interloper exceed those of tolerating it. At worst, an extra 'group member' could thus be a harmless but stubborn sitting tenant. However, to an extent which depends on their degree of relationship⁷⁷, the net cost of tolerance to the occupier's fitness is diminished in proportion to the benefit accruing to the interloper, if they are related. In most carnivore species for which there is evidence, groups consist at least largely of relatives^{78,82} (for example, lions⁷⁹, wolves^{41,43,98}, hunting dogs^{66,67}, spotted and brown

hyaena^{6,15}, two species of jackal^{32,44}, two species of fox^{29,36}, two of mongoose⁷, coyotes (refs 55, 72), dingo⁵⁶ and dholes⁵⁴; coatis, *Nasua narica*, provide the only documented exception where female group membership (and alloparental behaviour) is not largely restricted to kin⁸⁰. Male lions increase their chances of procuring and retaining a pride if they form coalitions^{73,79} and 58% of coalitions comprise related males⁸¹. All else being equal, kin selection should favour joining forces with a relative⁷⁹, but the benefit of kinship is merely a bonus to the overwhelming advantage of any coalition. An effective unrelated companion is presumably preferable to an ineffective related one. Irrespective of relatedness, male lions squabble within a coalition⁸¹, the winners securing more key matings, emphasizing that while it may be better to lose to a relative, it is best not to lose at all.

Alloparental behaviour

In carnivore societies, the guarding and defence of and provision for young other than one's own is common⁷⁸. Among feral cats, immature males baby-sit kittens^{12,13}, and breeding females guard, nurse and feed each other's offspring, as do lionesses⁷⁹. Similar collaborative rearing is found among many canids, among which it is also common for non-breeding animals to participate as alloparents^{29,36,44,53,54,72,83}. (Among dwarf mongooses, collaboration extends to care of sick adults⁸⁴.) Information is less complete for other families, but one interesting case is the brown hyaena, among whose groups only dominant females breed, and non-breeders of both sexes provide for the young. The young are sired by nomadic males which have only fleeting associations with the groups whose females they fertilize⁸⁵ and whose cuckolded males act as helpers. Of the Viverridae, *Mungos mungo* and *Helogale parvula* both show communal care of young, but several females breed in *Mungos* packs, whereas only one does in those of *Helogale*⁷. Subordinate members of some carnivore groups (especially canids) endure at least temporary reproductive suppression. When a subordinate does give birth her offspring may be neglected³⁶, killed⁸⁶, or stolen⁶⁹, although on other occasions females may den communally^{36,72,83} and cooperate.

Are 'helpers' helpful?

Although the term 'helper' is often used as a synonym for a non-breeding group member, proof of their helpfulness is scant. Alloparents increase the survivorship of silver-backed and, probably, golden jackals⁴⁴; they probably sometimes contribute to the survival of red fox cubs³⁶, and may adopt orphans³⁸. One would expect the role of potential helpers to be tempered by prevailing ecological circumstances⁷⁸ and this may explain why yearling hunting dogs^{66,67} help feed pups when food is plentiful, but steal from them when food is scarce. Similarly, pup survival for Minnesotan wolves was slightly reduced among bigger packs (with more potential alloparents) during years when the wolves were known to be under mounting population pressure⁸⁷. As most social groups consist of relatives, most alloparents may benefit from kinship⁷⁷, mutualism and reciprocity^{88,89} amongst other possibilities. However, unrelated immigrants occur in dwarf mongoose packs, and one newcomer was a more assiduous helper than were some original pack members⁷. These immigrant helpers benefited by breeding earlier than their counterparts who stayed at home.

Flexible social behaviour

The great flexibility of carnivore societies is perhaps most conspicuous regarding territory and group sizes—wolf territories vary between 50 and 1,000 km² and contain packs of 2–20 members^{54,90}, and red fox territories vary 70-fold in area¹¹ and can vary 600-fold from those of otherwise similar Arctic foxes²⁹. Similarly, raccoon territories vary from 0.5 to 50 km² (D. R. Voigt, personal communication) and those of grizzly bear from 24 to 1,054 km² (F. Bunnell, personal communication). The average size of groups of European badgers varies between habitats, from 3.0 to 7.6 members and average terri-

tory sizes span 22 to over 200 hectares^{30,91}. Interspecifically, the wolverine is less than twice the weight of the American badger⁹², *Taxidea taxus*, yet its home range can be 400-fold larger (both are mustelids). Doubtless there is similarly extensive, but less conspicuous, flexibility in the dynamics of social behaviour (for example, patterns of scent marking differ between populations⁹³ of spotted hyaenas^{6,94}, golden jackal³² and otters⁹⁵). Spotted hyaena clans vary between habitats from large, stable matriarchies to small transient associations, and almost every aspect of their social behaviour changes also^{6,94}.

Carnivore societies are the products of varied effects on different individuals of very many selective pressures⁷⁹. There are contemporary carnivore societies, such as those of red and Arctic foxes, badgers, brown hyaenas and farm cats in which stable, well defined relationships exist and yet where the benefits of social ties often appear infrequent or small. These societies share the characteristic that resource dispersion creates conditions in which the smallest range which will support a pair may also support a group. These ecological conditions, which diminish the restraints on group formation, may originally have facilitated the evolution of other types of carnivore society where the contemporary benefits of sociality are conspicuously great, and hence where bigger groups, and thus perhaps ranges larger than the minimum, are advantageous. Species which originally colonized niches in which the ecological constraints upon group formation were lower could expand their niches and hence give rise to new benefits to group living which, in turn, could modify further their social organization. From this viewpoint, the differences in sociality between species are a consequence of interspecific variation in these subsequent benefits of group living. For each society the balance of these contemporary benefits is not necessarily the same as that which originally selected for group living; the origins of the quite different societies of fox and wolf or farm cat and lion may all lie in patterns of prey dispersion which diminished the need to disperse and hence permitted family ties to persist into adulthood and so provided candidates for subsequent and varied selection directed at sociality *per se*. Similarly, the balance of the contemporary benefits to group membership also varies between populations of the same species in accordance with their ecological circumstances and as carnivores are typified by their opportunism, many species have broad niches and hence highly flexible social systems. Elucidating the contemporary selective pressures that promote such social groups requires exploration of the limits to the flexibility of each species' society, and also the processes whereby individuals develop⁹⁶ into quite different social beings depending on the ecological (and social) circumstances into which they are born.

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ARTICLES

Variations in magnetization intensity and low-temperature titanomagnetite oxidation of ocean floor basalts

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The remanent magnetization of the oceanic crust exhibits a systematic long-term variation which correlates with the amplitudes of marine magnetic anomalies. After a sharp initial decrease of natural remanent magnetization intensity, a minimum is reached at ~20 Myr, followed by a gradual increase up to ages of 120 Myr. The progressive sea floor alteration of the magnetic minerals carrying the crustal magnetism is proposed as a cause for this behaviour.

THE central anomaly over the spreading axis of active oceanic ridges is by far the most prominent in the pattern of marine magnetic anomalies. The flanking anomalies gradually decrease in amplitude for some distance away from the crest¹. Another characteristic of the amplitude variation in linear marine magnetic anomalies seems to have been overlooked or, where noticed, not explained. This is the increase in amplitude of magnetic anomalies older than ~20 Myr (refs 2–6). Worldwide most of the amplitudes show a pronounced minimum over the age range of 10–30 Myr beyond which, on average, they pro-

gressively increase again to another maximum near the end of the Cretaceous magnetic quiet zone (Fig. 1). This tendency seems to be independent of their geographical location or the spreading rate of a ridge.

At the onset of the Mesozoic M-series magnetic anomalies at ~108 Myr the amplitudes are again high in most cases. Longer profiles of the M-series show a steady diminution with age in the amplitudes of the anomalies, leading to a gradual rather than an abrupt transition into the Jurassic magnetic quiet zone^{7,8}.