SPECIAL ISSUE: VERTEBRATE SOCIETIES

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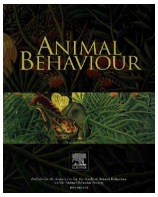

Special Issue: Vertebrate Societies

Clearly membered societies among the nonprimate vertebrate animals

The authors of this special issue present concise descriptions of a selection of vertebrates forming ‘societies’, in the specific sense of long-lasting, clear-cut groups. More specifically, the members must distinguish one another from outsiders, a requirement that prioritizes the animals' capacity to identify others over the patterns of cooperation that can emerge in varied ways within or between the groups, so formed. The authors were asked if the well-defined groups of their species retain ultimate control over a physical space, a possible additional criterion for a society as a territory-holding group that proved problematic for some taxa. Here I reflect on the variability of the societies represented by these essays, including the diverse ways these groups might maintain dominion over an area, as promising subjects for future research.

The colonies of many social insects (notably termites, ants and some bees and wasps) have long been known to fit these criteria. I chose to concentrate on vertebrates given that insect societies are widely recognized and largely well understood; because of limitations in space, I have been selective even there, leaving out primates since the societies (troops or communities) of monkeys and apes have been far more commonly discussed than those of most other vertebrate groups. Indeed, mammals have the best-established examples of vertebrate societies, many of which are known by common names such as the pack, clan, troop or pride (although ‘pride’ is ambiguous for African lions, *Panthera leo*, referring as it can to adult males and females with their cubs, a lion ‘society’ sensu this issue, or to the lionesses exclusively: Packer, 2026, in this Special Issue). Hence I have made it a point to include a fish, a reptile and two birds, taxa for which the ‘closed’ societies conceived of here are less appreciated and generally understudied.

Below, I provide a synopsis of some of the key attributes of societies, focusing on the taxa addressed by these essays.

GROUP IDENTITIES

Framed as described above, membership is generally a consequence of what psychologists call group identity, based on a strict, and in this case enduring, perception of being associated (whether such association is welcome or not, since rivals, like the competitors for alpha status in a hyaena clan, can be co-members; as used here, group identity implies nothing about the cognition underlying membership: ants almost certainly detect nestmates, for example, without categorizing them as part of a ‘colony’). This approach differs from a widespread concern in biology with social systems that emerge from interactions between individuals. The fact is that while group identities have social ramifications, social networks and patterns of cooperation seldom accurately represent societal boundaries, extending as they can within and even between societies, as in the intergroup alliances in species like bonobo, *Pan paniscus* (Samuni et al., 2022), and vulturine guineafowl, *Acryllium vulturinum* (hereafter, guineafowl, whose responses to other ‘stable identity groups’ vary widely from favourable to hostile, suggesting that the birds not only distinguish between but maintain distinct relations with foreign stable identity groups: Farine, 2025, in this Special Issue). Moreover, within societies, cooperation can be minimal, as Blumstein (2025, in this Special Issue) emphasizes for the yellow-bellied marmot, *Marmota flaviventer* (henceforth, marmot) (Fig. 1).

Because this special issue is specifically concerned with societies understood as identity groups, a comprehensive treatment of sociality will not be the goal of the overviews to follow; rather, each will establish that such groups are the norm for their taxon, summarizing the formation and maintenance of membership boundaries and relationships between societies. Most of the authors offer insights as well regarding the adaptive value of societies for their study organism; typical benefits include the possibility of protecting one another from competing societies or predators; cooperation in rearing and safeguarding young; increased efficiency in foraging, most notably in predators like the African lion, grey wolf, *Canis lupus* (hereafter wolf), and spotted hyaena, *Crocuta crocuta* (hereafter hyaena) that hunt game together; enhanced opportunities for social learning and labour specialization; and the potential to nurture intimate relationships within a discrete collection of individuals. Many of these advantages exist to some degree in species forming more temporary, fluid associations, and so the enhanced payoffs of life in more permanent groups will be a worthy focus of future studies.

To stand on its own as a worthwhile concept, a society needs to be distinguished from a simple immediate family, that is, one or both parents raising a brood that normally becomes independent on reaching sexual maturity. However, the societies of some vertebrates arise via a multigenerational expansion of such a family (Stahler & Cassidy, 2025, in this Special Issue; Whiting & While, 2026, in this Special Issue). In fact, society existence in yellow-bellied marmots is optional in that some females drive off all their offspring when they are yearlings so that the residents of the territory never expand beyond the nuclear family (Blumstein, 2025, in this Special Issue). At the opposite extreme are species for which genetic relatedness among adults is not a factor. Their societies form when individuals that are unrelated except by chance join together after emigrating from different natal societies. This is true for greater spear-nosed bats, *Phyllostomus hastatus*, which nevertheless defend the offspring of other members of their roosting group (Wilkinson, 2025, in this Special Issue), demonstrating

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Figure 1. Cooperation exists in species-specific patterns both within and between societies. (a) Vulturine guineafowl (image from Mpala Research Centre in Kenya) can establish positive relationships within groups as well as between them; whereas (b) yellow-bellied marmots (image from Rocky Mountain Biological Laboratories in Colorado) are invariably antagonistic toward outsiders and show minimal cooperation toward other members. Photographs © Mark W. Moffett.

that direct benefits suffice to bind them together (bands of horses represent another example: Mills & McDonnell, 2005); indeed, indirect benefits may be effective only in maintaining very small groups (i.e. Lukas et al., 2005). Even when high levels of kinship are guaranteed, as in societies that emerge from the expansion of a family, in some species (Stahler & Cassidy, 2025, in this Special Issue; Whiting & While, 2026, in this Special Issue) immigrants may become integrated as members that are treated no differently from kin (although the existence of social insect societies is often explained in terms of kin selection, some species form distinct colonies where relatedness is low; e.g. Moffett, 2013a; 2013b; Zweden et al., 2012).

Each essay addresses the possibility of such permanent transfers in membership. While societies can be stable over the long haul, that does not mean all individuals stay with their natal society. Immigrants are female in the guineafowl and usually in the pinyon jay, *Gymnorhinus cyanocephalus*, invariably male in the marmot, hyaena, wolf and lion, predominantly male in the two mole-rat species examined (where societal transfer occurs extraordinarily rarely), and of either sex in the bottlenose dolphin, *Tursiops truncatus*, greater spear-nosed bat, certain tiliquin skinks, and the cichlid fish *Neolamprologus multifasciatus* (hereafter 'multi' cichlid; in this species, as in the wolf, a new male can be admitted if the dominant male dies). While we need to learn more about how transfers are negotiated in many species, we know that the male bats, lions, and sometimes wolves integrate by force, and that the dominant male cichlid can intervene to stop the resident females from driving off a female newcomer (Jordan et al., 2026, in this Special Issue). Integration seems to be a matter of persistence for the guineafowl and hyaena, with some would-be immigrants suffering repeated attacks before giving up and returning to their natal group, only to attempt to make the transfer again later (Farine, 2025, in this Special Issue; Holekamp, 2025, in this Special Issue).

Sex plays a role in society membership. Species differ as to whether adults of both sexes or just the females distinguish one another as part of the society. Male marmots may not be recognized as society members in that the females appear indifferent as to which adult males are present (D. Blumstein, personal communication). Males may retain their connection to a society for a far shorter term than females: in greater spear-nosed bats, the single male attached to each roosting group drives away competitors until he is overthrown himself; in lions, a fresh coalition of males is periodically incorporated into a pride when they push out their predecessors (the females having little say in the matter other than to show a lower fertility for several months, 'apparently [to] 'test' the new males' ability to maintain tenure': Packer, 2026, p. 3, in this Special Issue). Males of both these species that fail to become part of a society must get by on their own or in shifting clusters of bachelors. In lions and, at least for short periods, hyaenas, males can 'play the field' by integrating themselves into adjacent groups, a manoeuvre that is easily accomplished given that the members of a pride or clan move around by fission—fusion and therefore are often on their own; Packer relates how this 'duplicity' can lead to interpride conflicts. Social dominance is commonplace in societies, with the males at the apex in most species, although female hyaenas have the upper hand (Holekamp, 2025, in this Special Issue).

HOW INDIVIDUALS DIFFERENTIATE MEMBERS FROM NONMEMBERS

How do animals identify those who belong to their society? Many of the authors describe how their study animals tell one another apart on the basis of sound, scent or physical features. Probably all vertebrates have a capacity to distinguish conspecifics, if only their mate, offspring, and, in some cases, allies or competitors (potentially creating a dear enemy effect: Tumulty, 2022). Many society dwellers use this skill to detect fellow members, a strategy yielding what I call individual recognition societies (some species may also come to recognize certain individuals belonging to other societies, e.g. bonobos: Samuni et al., 2022; bottlenose dolphins: Wells & McHugh, 2025, in this Special Issue). Schaller (1972, p. 46) describes how lions convey this recognition: 'A pride member joins others unhesitatingly, often running toward them, whereas a stranger typically crouches, advances a few steps, then turns as if to flee, and in general behaves as if uncertain of its reception'.

Whether or not they individually distinguish fellow members, certain species produce and detect 'markers' of identity that are unique to their society, such as the socially learned vocalizations of a pinyon jay flock (which, in this jay, is a specific group of individuals: Marzluff, 2025, in this Special Issue) or the colony scent of naked mole-rats, *Heterocephalus glaber* (Hart et al., 2026, in this Special Issue). These may be used as signals to coordinate groups, like the pastings hyaenas leave on vegetation that have a scent distinctive to each clan, signalling territory ownership, or the roost group-specific screech made by greater spear-nosed bats as they travel and forage together. But for some species at least, these markers are alternatively, or additionally (as Wilkinson, 2025, in

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this Special Issue, argues for the bats and Holekamp, 2025, in this Special Issue, for hyaenas), shared advertisements of identity that allow everyone to assess the memberships of others, thereby creating what I call 'anonymous societies' (for a just-discovered example, see Perrier et al., 2025). Holekamp (2025, in this Special Issue) intriguingly submits that the slow pace of integration for hyaenas into a new clan may have to do with the need for a male to attain, over time, the correct scent: the 'national flag' of the clan. After driving another colony from its nest, naked mole-rats often assimilate its resident pups, perhaps because they were not old enough to have acquired the scent of their birth colony.

Unlike animals without such group-specific markers, those in anonymous societies can categorize individuals without constantly confirming the identity of each familiar animal, thus reducing identification errors while allowing for co-membership of strangers. This gives their populations the potential to grow beyond the point where each member can distinguish all the others individually. This may well be true for naked mole-rats, whose societies reach many hundreds, and likewise for pinyon jays, which 'recognize important individuals' (Marzluff, 2025, in this Special Issue) and use transitive inference to work out their social position relative to unknown others (Paz-y-Miño et al., 2004). The mole-rats could prove valuable for studying this distinction, as Damaraland mole-rat, *Fukomys damarensis*, colonies are apparently based on individual recognition while those that independently evolved in the naked mole-rat are anonymous (Hart et al., 2026, in this Special Issue).

SOCIETIES AS ENDURING GROUPS

The second criterion put forward for a society is longevity, with generations of individuals remaining together into adulthood when conditions are favourable. A couple of the species discussed here have relatively fragile, short-lived societies, namely the tiliquin skink *Liopholis whitii*, whose incipient societies often disband after the breeding individuals die (Whiting & While, 2026, in this Special Issue), and the marmot, where female expulsion of older young can reduce the society to a nuclear family, as described above. By contrast, under suitable conditions many vertebrate societies endure for decades if not centuries (e.g. those of chimpanzees, *Pan troglodytes*: Langergraber et al., 2014) with multiple generations likely present at any time. Even though all these authors have studied their species for lengthy periods (e.g. the dolphin community that Wells & McHugh investigate has been going strong for over a half century), this longevity means that critical events that might be a regular part in the unfolding histories of animal societies (their society 'life cycles') may nevertheless remain undocumented, notably how societies emerge or replicate, which is so far unknown for the pinyon jay and tiliquins and has only been inferred for the guineafowl. In short, given the longevity of societies, we should be cautious about assuming that our understanding of any species is complete. Furthermore, nothing concerning societies should be dismissed out of hand as insignificant, or ignored, because it occurs rarely.

Other practical difficulties exist in gathering data on the societies of many species, for instance in monitoring the interactions in nature between fossorial mole-rats from our aboveground vantage point, or in observing bottlenose dolphin behaviours from over the water surface at night or in murky estuarine sites, such as their initial contacts with either casual visitors or potential immigrants (although the general lack of injuries suggests the interchanges do not turn violent: Wells & McHugh, 2025, in this Special Issue).

What can cause a society to fizzle out, or fragment, and new groups to arise? While societies as conceived of here are long-lasting, environmental stresses or competing societies can bring them down. Yet societies may not persist indefinitely even under ideal conditions: a hyaena clan, a lion pride, the colonies of both mole-rat species, and most likely a guineafowl stable identity group will split in two on occasion (Farine, 2025, in this Special Issue; Hart et al., 2026, in this Special Issue; Holekamp, 2025, in this Special Issue; Packer, 2026, in this Special Issue). In the multi cichlid, both mole-rat species (but most commonly *F. damarensis*), and the grey wolf, male and female emigrants join up to start a society after generations of their young have accumulated (with wolf packs occasionally multiplying by dividing as well). Yet the possibility remains that in some cases (perhaps in the Sarasota Bay dolphin community mentioned above), a society has the potential, barring catastrophe, to carry on indefinitely as a single unit.

ULTIMATE CONTROL OVER ACCESS TO A PHYSICAL SPACE

How is occupancy of a physical area expressed in each species? Even animals that are consistently aggressive towards neighbours, such as the wolf with its expansive territories (but see the discussion of the 'deer yard' in Theberge & Theberge, 2004), cannot be vigilant against every intruder. Some incursions, often in the periphery, will go unnoticed. Indeed, the home ranges of some animals extend beyond a central territory into regions open to visits by multiple groups; during the seasons when hyaenas and wolves travel far in pursuit of migrating herds, clans and packs pass through foreign territories with little harassment. Each roosting group of greater spear-nosed bat defends a distinct domain on the cave ceiling, and apparently at least in some populations they forage in areas that may be largely, if not entirely, exclusive, yet multiple roosting groups will converge at exceptionally rich feeding sites (Wilkinson, 2025, in this Special Issue). Who carries out the defence of a group-held space depends on the species: males collectively do the job in the guineafowl, while the dominant male exerts most of the effort for the multi cichlid. Multi cichlids are remarkable in that each adult has a private domain within their joint territory: an empty mollusc shell that the fish defends as a home (which a female shares, for a time, with her fry).

In my view biologists too often look at territoriality in an overly restrictive manner, excluding interesting 'shades of grey' phenomena (e.g. Kamath & Wesner, 2020; Maher & Lott, 1995; Moffett, 2025). An important dimension of group-held territories, for example, is stability: are they truly static, or can they shift daily, yearly, or hardly ever? The territory of a lion pride can drift over the years to an entirely new location (C. Packer, personal communication). What if we take this to the logical extreme to consider as a territory the ever-shifting space that is collectively occupied and defended, for example, by a wandering baboon troop (Moffett, 2025a)? While Farine (2025, p. 2, in this Special Issue) accurately portrays 'nomadic' guineafowl as not having territories in the traditional sense, their stable identity groups (SIGs) can be treated as having 'mobile territories' on this basis, given his description: 'Agonistic responses typically involve males from each SIG forming into a tight cluster that then 'patrols' the area currently used by the other members of their SIG'.

Could useful insights be gained from conceiving of territoriality not in terms of compulsory expulsion of outsiders but rather as the drive to maintain ultimate control, when push comes to shove, over a physical space? In some species this description would allow for visits between members of amicable groups under favourable conditions. Greater spear-nosed bats are generally hostile towards other roosting groups, but a female will at times stay with a neighbouring roost for a few days, perhaps to test the waters for a membership switch (how she overcomes or avoids attacks is not known: Wilkinson, 2025, in this Special Issue).

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Certain societies of guineafowl intermix while resting in the same tree night after night with no sign of aggression and can travel and feed together as well (Farine, 2025, in this Special Issue). Lion pride fission–fusion groups draw together to repel intruders, but (Packer, 2026, in this Special Issue) reports that lionesses at a kill will allow a female from another pride onto their territory to share the meal if she can find an unoccupied corner of the carcass at which to feed (one wonders if the visitor may have been born into this pride, with its members retaining some openness to her temporary return). The practice of visiting other societies is well developed in pinyon jays (Marzluff, 2025, in this Special Issue), where, notably in autumn, a bird can reside for weeks in a neighbour flock (in contrast to birds that permanently immigrate, which tend to make their move in the spring).

An intriguing behaviour of pinyon jay flocks is that they can be completely nonterritorial yet occupy distinct but overlapping home ranges, with adjacent flocks merging with no sign of aggression. Staying within their boundaries allows the jays to become familiar with a physical space and develop cooperative relationships with other residents there, but of course that can be true as well for social species without societal boundaries (e.g. Öst et al., 2005); the question becomes what advantage accrues from a shared preference among so many individuals for the identical area. Social learning could be a factor, as Wells and McHugh (2025, in this Special Issue) suggest for their bottlenose dolphins, which likewise show no signs of territoriality in that individuals on occasion move without incident through the spaces occupied by adjacent communities (aside from some male aggression along the borders, likely over females). The dolphins socially acquire foraging techniques, some of which may be especially effective on their particular 'terrain' (e.g. snatching fish together after driving them onto shore works along suitable parts of the coast). Still, I remain curious as to why the dolphins form communities given that, for example, such customs are not shared exclusively among all the dolphins of a specific community. It seems plausible that the dolphins could adopt such mutually advantageous behaviours even if they did not belong to clearly defined groups, in some cases benefiting from them much as birds do by joining an 'open' flock in which they can easily capture insects stirred up by the crowd.

Curiously, in the pinyon jay, flocks overlap with their neighbours only at the periphery of their home ranges; per Marzluff (2025, p. 2, in this Special Issue), 'Prolonged incursion of an entire flock into another flock's range, including its caching and breeding grounds, has not been observed'. Could such a seemingly benevolent spacing be achieved with no enforcement, or is this spatial separation prima facie evidence of territoriality, the dear enemy effect an outcome of waning aggression, which is at its greatest intensity when territories are founded (Tumulty, 2022)? Perhaps conflicts do occur in pinyon jays, but almost entirely in the thus far undocumented period when a flock first establishes its presence, with the jays staying clear of their neighbours' core areas thereafter (as could be true as well for generally affable bonobo communities, which are described as being similarly distributed in space: Moffett, 2025b; Sumani et al., 2022).

Home ranges, defended areas within them included, need to be learned, and maintained, across the society membership, another promising topic for future studies. In the bottlenose dolphin (Wells & McHugh, 2025, in this Special Issue) and the lion (Packer, 2026, in this Special Issue), the borders can correspond to conspicuous natural features. Wolves and hyaenas lay claim to their land with scent posts or pastings, while the multi cichlid raises a perimeter wall of sand that the fish collectively toss up during the excavation of their shell retreats.

SOCIAL TIERS

Some species display other social groupings or strata, such as fission–fusion 'parties' and matrilines that exist within their societies, but as Holekamp (2025, p. 1, in this Special Issue) points out for hyaenas, 'matrilineal family units are secondary in importance to clans as the enduring social units'. In species for which multiple social strata are recognized, which of those tiers can be characterized as societies, in the sense of having multigenerational memberships (i.e. clear group identities)? The greater spear-nosed bat fascinates because of the possibility that groups conforming to this definition exist not just at the level of the small, stable 'roosting groups' scattered throughout a cave but also at the level of the bat population occupying each cave in aggregate. By describing the bats as potentially having cave-specific traditions in diet and foraging, Wilkinson (2025, in this Special Issue) suggests that the differences between cave populations in those preferences could be due to more than the distribution of resources around each cave. But even if the aggregate of all the roosting groups in a cave can be construed as a separate social tier, for its population to represent a second level matching our concept of society, the unanswered question is whether the bats are distinguishing cavemates from bats in other caves, perhaps by discriminating the subtle vocal differences Wilkinson mentions.

Taken together these essays provide a multifaceted, although by necessity preliminary and incomplete, look at how a diversity of vertebrate species other than the primates maintain clearly bounded, and enduring, group memberships. Many of the concepts mentioned here are addressed in further detail by Moffett (2025a, 2025b).

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