

Review

Multilevel Organisation of Animal Sociality

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Multilevel societies (MLSs), stable nuclear social units within a larger collective encompassing multiple nested social levels, occur in several mammalian lineages. Their architectural complexity and size impose specific demands on their members requiring adaptive solutions in multiple domains. The functional significance of MLSs lies in their members being equipped to reap the benefits of multiple group sizes. Here, we propose a unifying terminology and operational definition of MLS. To identify new avenues for integrative research, we synthesise current literature on the selective pressures underlying the evolution of MLSs and their implications for cognition, intersexual conflict, and sexual selection. Mapping the drivers and consequences of MLS provides a reference point for the social evolution of many taxa, including our own species.

Multilevel Sociality in Nature

Animal sociality reflects the interplay between attractive and repulsive forces: opportunities for reproduction, cooperation, protection, and information acquisition are counterbalanced by competition and vulnerability to predators and pathogens [1]. One outcome of this interplay is a **social system** (see [Glossary](#)) with multiple levels, a **multilevel society (MLS)**, comprising **core units** organised into increasingly inclusive entities. Understanding how these social constituents interact and coexist, and how dispersal shapes the resulting kinship structure across multiple levels, is fundamental to a holistic understanding of the evolution of these systems.

MLSs are best known from primates but have recently been reported in a range of animals [2–7]. Here, we synthesise current knowledge on MLSs, critically evaluate their causes and consequences, and offer prospects for future research. We build from socioecological principles emphasising ecological (resource distribution, and predation threat) and social (kin selection and sexual conflict) factors in organising individuals and relationships in space and time [1]. We focus on Mammalia, given the predominance of MLSs in this class. Given that this very system also characterises our own species, mapping the causes and consequences of MLSs provides a valuable reference point for tracing human social evolution.

Defining Multilevel Societies

MLSs are social systems characterised by nested social entities comprising a minimum of two discernible, consistent levels of social integration between the individual and the population ([Figure 1](#)). The terms describing these nested social levels are inconsistent across species; thus, to facilitate comparison, we propose a standardised terminology: ‘core units’ and ‘upper levels’ for these two mandatory levels, and ‘intermediate levels’ and ‘apex levels’ for the facultative levels described below ([Table 1](#)).

In non-human primates, the primary entities of MLSs are usually small core units comprising one reproductive male and multiple females, called one-male units or OMUs [8]. In other mammals,

Highlights

There has been growing recognition of the multilevel nature of many animal social systems but little effort to operationalise it by integrating findings across species.

How members of social units in MLSs interact and how dispersal shapes the kinship structure across multiple levels of society is of paramount importance for a holistic understanding of the evolution of sociality.

MLSs may offer a flexible solution to a set of socioecological challenges at multiple levels.

Whether the structural complexity of MLSs has knock-on consequences for sexual selection, cognition, cultural transmission, and disease dynamics remain important avenues for future research.

Understanding the evolution and functional significance of animal MLSs will prove valuable for reconstructing the pillars of human sociality.

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there is greater variability: in African elephants (*Loxodonta africana*) and sperm whales (*Physeter macrocephalus*), core units comprise closely associated breeding females and their calves, with occasional male visitors [9,10]. Core units are usually highly cohesive and stable: individuals show strong fidelity to their units, and sociopositive interactions are more frequent within than between units [2,11]. In terrestrial MLSs, core units are usually spatially discrete, defined by spatial and social proximity among members [12]. Closely associated core units may form a secondary, less consistent level of organisation with various names [11,13,14], herein called an intermediate level.

For a system to be an MLS, in addition to core units there needs to be an upper level that is stable enough to be recognisable, despite variability in spatiotemporal cohesiveness [8]. Membership in an upper level can be consistent [15] or more probabilistic [13]. In primates, the upper level is often called 'band'. In some cases, upper levels coalesce to form even higher levels, herein called apex levels, which are distinctively larger and number several hundred to over a thousand individuals. Apex levels can be induced by habitat features rather than social attraction; thus, they do not always represent genuine social units.

The organisational complexity of MLSs is best exemplified by hamadryas baboons (*Papio hamadryas*), which exhibit four distinct social levels [14,16,17]. At the heart of their society are core units, called OMUs or 'harems', comprising a 'leader' male, multiple breeding females, and occasional follower males. Their intermediate level is the clan, consisting of two or more closely associated OMUs and solitary (unaffiliated) males. Clans are nested within bands (upper levels), the most visibly apparent, spatially cohesive level. Finally, troops (apex level) represent temporary associations of bands at sleeping cliffs. Other primate MLSs show a superficially similar **social organisation**, but the number and cohesion of nested levels vary.

To identify the boundaries of each social level, researchers rely on long-term empirical data and clustering or community detection methods (Box 1). While there are boundaries between core units, these are not impermeable, and some individuals are socially connected across units. Occasionally, members of different units interact socially [18,19], engage in joint patrolling [20], mingle [21], or copulate [22].

Shared space use can set the stage for the emergence of MLSs [3,23,24]. However, **aggregations** of social units without active social preferences (e.g., attracted to the same localised resource or co-occurring due to constraints of habitat structure) cannot be considered MLSs; neither can social units that occasionally encounter and mingle nonagonistically [25] be MLSs, because these encounters are infrequent and transient.

The term 'multilevel society' is sometimes used interchangeably with '**fission–fusion**', but this is a conceptual error. Fission–fusion is not a type of social system, but instead describes how social units cleave and coalesce over time to form subunits with variable size and composition [26]. Fission–fusion dynamics unfold over various timescales, from hours to months, and are generally found in MLSs [10,12,17] as well as in unilevel societies [27]. In non-MLSs, fission–fusion is individualistic and subunits vary widely in composition ('atomistic' fission–fusion), whereas, in MLSs, fission–fusion usually happens along the boundaries of the core units or intermediate levels without compromising the integrity of those units ('molecular' fission–fusion) [8,28].

Taxonomic Distribution

MLSs are relatively uncommon and patchily distributed on the mammal phylogenetic tree (Figure 2). First described for hamadryas baboons in the pioneering study by Hans Kummer during the 1960s [17], they have subsequently been documented in other primates (papionins,

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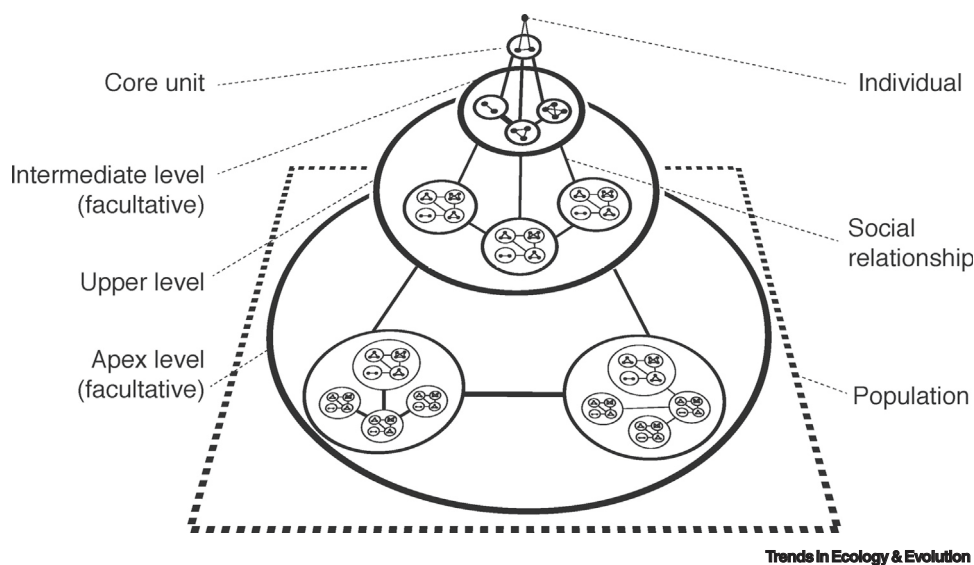


Figure 1. Multilevel Society (MLS) as a Nested Assemblage of at least Two Discernible Social Levels between Individual and Population. Individuals represented by nodes are connected by links representing social interactions and/or relationships. The core units and upper level are the two mandatory social levels, while (one or more) intermediate levels and the apex level are facultative levels. Core units are more cohesive than the higher social levels, which vary in stability and cohesiveness.

colobines, and humans), cetaceans, elephants, and equids [2,10,13,29–31] (for a full list, see Figure 2). Some taxa show MLSs in only some ecological contexts (e.g., [2,32]). For example, bottlenose dolphins (*Tursiops* sp.) are generally characterised by atomistic fission–fusion dynamics [33]. However, some populations exhibit **multilevel alliances** among males embedded in an open fission–fusion network, with up to three levels of social integration between the individual and the population. In Shark Bay, Western Australia, males form stable second-order alliances of 6–14 adult males. Nested within these second-order alliances, two to three males form first-order alliances with varying composition for the purpose of coercing females in reproductive condition. To this end, Shark Bay dolphins deviate from our MLS definition in that the highly cohesive and stable units in these dolphins occur on a higher level. Second-order alliance members may cooperate in attacking, or defending against, other second-order alliances, sometimes even cooperating on a third level [34].

MLSs have been proposed for other mammal species, but some were based on vague definitions. For example, reticulated giraffe (*Giraffa camelopardalis*) are found in social cliques embedded in larger subcommunities and communities, and show partner preferences; however, the composition of core units (cliques) is variable [3]. Observations of members of different social units of western gorillas (*Gorilla gorilla gorilla*) interacting nonaggressively and covisiting forest clearings have been used as evidence for MLSs [7,35], but whether associations are durable across contexts remains poorly known.

Social Dynamics within Multilevel Societies

The proximate mechanisms underlying MLSs can vary widely. For example, geladas and hamadryas baboons differ considerably in their microlevel **social structure**. In geladas, core units are shaped by kin bonds among closely related females [36], whereas, in hamadryas baboons, the pair bonds between a leader male and his females underpins core unit stability, with male–male bonds linking the higher social levels [17,37]. Females are philopatric in geladas,

Glossary

Aggregation: temporary gathering of individuals and units that is usually the result of some nonsocial forcing factor (e.g., localised resources).

Core unit: set of individuals in (nearly) permanent mutual association; in MLSs, 'core unit' is used for the first grouping level; core units in MLSs are to a certain degree behaviourally self-contained over all relevant timescales, so that most interactions and associations occur within, rather than between, units.

Fission–fusion (dynamics): spatiotemporal variation in cohesion of group members and subgroup size and composition.

Multilevel alliance: alliances are temporally stable coalitions of two or more individuals acting cooperatively against a third party; in a multilevel alliance system, context-dependent competitive interactions between alliances are found on several hierarchical, more inclusive levels.

Multilevel society (MLS): social system comprising nested social entities of a minimum of two discernible levels of social integration between the individual and the population (core units and upper level). The primary entities are small core units that are usually stable over time; through proximity maintenance and activity coordination with other core units, they form (at least one more) successively higher levels of grouping.

Social complexity: number of differentiated relationships as well as the extent of relationship differentiation that exists within a society.

Social organisation: size and demographic composition of a social group.

Social structure: content, quality, and patterning of social relationships emerging from repeated interactions between pairs of individuals belonging to a social group.

Social system: social organisation, social structure, care, and mating system of and among the social units of a given population or species.

Table 1. Names and Approximate Sizes of the Various Levels in the MLS of a Representative Sample of Mammals^a

Taxon	Core unit		Intermediate level		Upper level		Apex level	
	Designation	Size	Designation	Size	Designation	Size	Designation	Size
Gelada (<i>Theropithecus gelada</i>)	Unit	2–30	Team	10–50	Band	50–400	Community	50–1500
Hamadryas baboon (<i>Papio hamadryas</i>)	OMU ^b	2–10	Clan	10–75	Band	30–400	Troop	100–800
Guinea baboon (<i>Papio papio</i>)	Unit	2–10	Party	10–51	Gang	>80	Community	375
Rwenzori colobus (<i>Colobus angolensis ruwenzorii</i>)	Core unit	4–23	Clan	37–88	Band	135–512		
Snub-nosed monkeys (<i>Rhinopithecus</i> spp.)	OMU	9			Band	22–480	(Troop)	
Hunter-gatherer humans (<i>Homo sapiens</i>)	Family	5	Extended family	15	Band	50	Community, mega-band, tribe	150–1500
Plains zebra (<i>Equus quagga</i>)	‘Harem’	5			Herd	42		
African elephant (<i>Loxodonta africana</i>)	Family	8			Bond group	16	Clan	34
Sperm whale (<i>Physeter macrocephalus</i>)	Social unit	6–12	Group	7–32	Clan	>1000		

^aRanges are given where there is dramatic variation in level sizes.

^bOMU, one-male unit.

whereas males are philopatric in hamadryas [11,36,38]. Guinea baboon MLSs are similar to those of hamadryas and geladas, but differ from hamadryas in the greater social freedom of females, and from geladas in the presence of male–male bonds across units [39].

MLSs can also shape the typically antagonistic social dynamics between breeding and bachelor males. In geladas, the presence and proximity of bachelors can exert a predator-like effect and cause spatial clumping of breeding units [40], whereas, in snub-nosed monkeys, proximity to breeding units reduces social cohesion among bachelor males [41], both reflections of male competition.

Evolution, Maintenance, and Adaptive Functionality

The evolutionary pathways leading to the emergence of MLS across mammalian taxa are variable. For example, in hamadryas baboons, phylogenetic reconstructions suggest that ancestral multimale–multifemale groups fractionated into OMUs with stable breeding bonds. Increased group sizes due to localised resources or greater predator pressure in open habitats may have elevated feeding competition, aggression, and harassment by unfamiliar individuals. To mitigate these costs, individuals would have formed subgroups, with females tightening their relationships with a single male capable of protecting them [8,42]. By contrast, in colobine monkeys, MLSs likely evolved via a merger of ancestrally autonomous OMUs [8], with persistent threat from potentially infanticidal bachelor males as a formative factor. Through communal defence or the safety-in-numbers effect, leader males could have collectively reduced bachelor threat, thereby prolonging their tenure and attenuating the risk of infanticide [23].

MLS maintenance requires a unifying social network spanning the boundaries of social units, and kinship has likely had a major role in shaping such networks. In hamadryas baboons, these links are provided by male–male social and kin relationships, evident at the clan level [14,16,38]. Similarly, strongly bonded Guinea baboon males are more likely to be related, although kinship is not a prerequisite (Table 1) [43]. Another unifying force may be limitations on female dispersal to within

Box 1. How to Identify Levels in Animal Societies

Detecting social levels requires combining qualitative and quantitative methods with high-quality empirical data from long-term studies. Researchers often apply clustering methods to direct observations of social data: interaction rates [14] or frequency of associations of individuals in proximity [10,13,72] or temporally clumped [12,81]. Popular methods include, but are not limited to, network modularity, data cloud geometry, and knot analysis.

Modularity measures how well a network of individuals connected by social relationships is structured into densely connected subgroups, with values ~ 0.3 – 0.5 representing feasible subdivisions [82,83]. The Louvain method creates hierarchical subgrouping of individuals iteratively (Figure 1A), maximising the density of connections within versus between groups at each hierarchical level [5,84]. Data cloud geometry identifies subgroupings at multiple scales with random walks through a network [3]. Hierarchical cluster analysis can be combined with knot analysis displaying the cumulative bifurcations, where significant changes in the rate of bifurcation ('knots') suggest distinct levels [10,32] (Figure 1B). At the population level, these methods can reveal separate social groups [80]; to delineate stable core units, they should be applied at the most inclusive social level.

Identifying stable substructuring from preferential associations does not necessarily make a society multilevel. This is contra permissive definitions that 'any society in which an individual differentially associates with more than one set of companions is in essence a multilevel society' [85]. We highlight the need for stringent delineations of social levels, in which within-unit social connectivity is significantly higher than between units.

It is also necessary to demonstrate that social levels are not artefacts. First, one can use resampling techniques or null models to show how the level delineation differs from random [83]. Subsequently, their biological meaningfulness must be backed up by empirical observations and correspond to groupings derived from naturalistic observations. 'Ground-truthing' is critical, but one should not over-rely on subjective visual impressions, because social units distinguished by observers may not be salient to the animals [76].

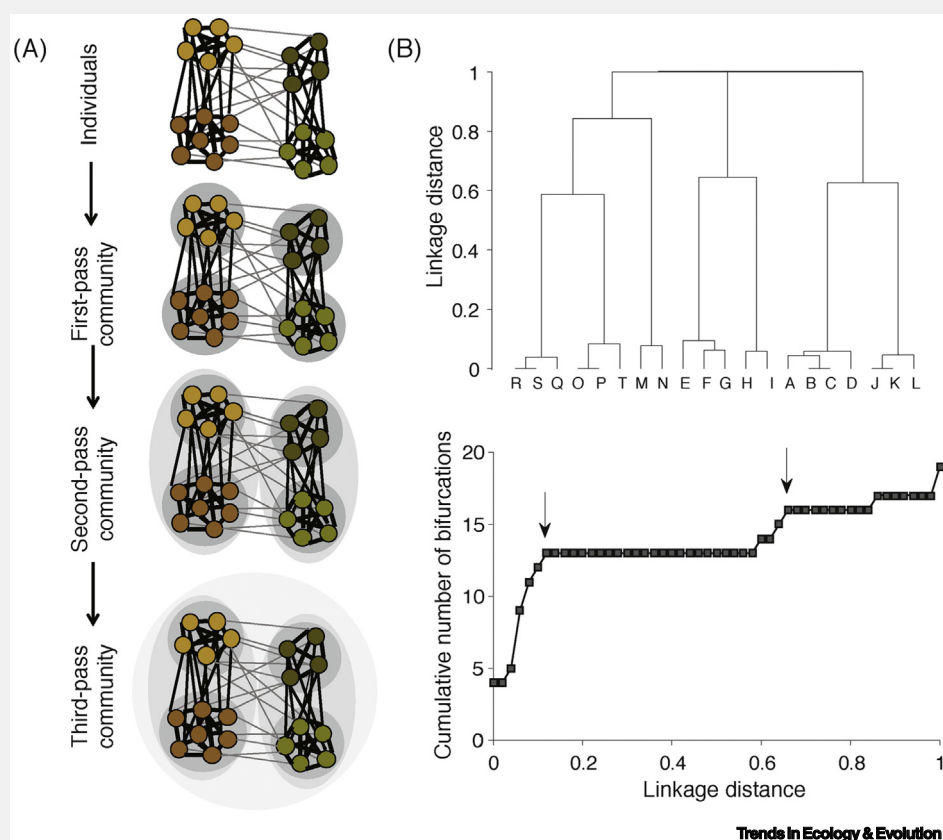


Figure 1. Delineating Social Levels. (A) Louvain method. Individuals strongly connected among themselves comprise 'first-pass communities' (core units); some are strongly connected to one another and detected as 'second-pass communities', until the apex community. (B) Hierarchical clustering and knot analysis. Dendrogram in which linkage (here, 1-association index) is depicted by a knot diagram showing the cumulative number of bifurcations (arrows).

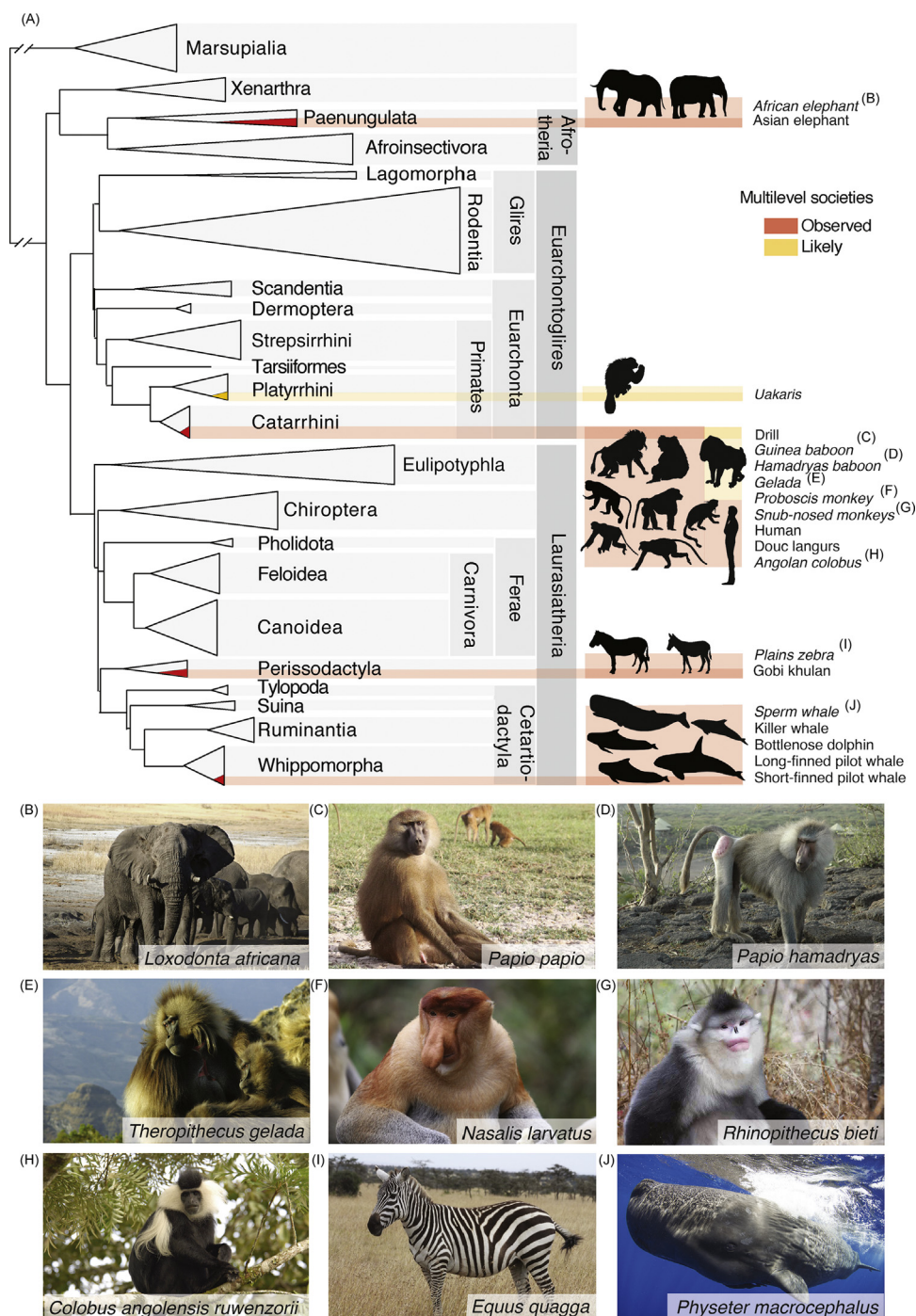


Figure 2. Distribution of Multilevel Societies (MLSs) across the Mammalian Phylogenetic Tree. (A) Phylogram based on [101] shows taxa with strong and likely evidence of MLSs, illustrated by (B) African savanna elephants (*Loxodonta africana* [10]; photo: C. Schradin); (C) Guinea baboons (*Papio papio* [43]; photo: J. Fischer); (D) hamadryas baboons (*Papio hamadryas* [17]; photo: L. Swedell); (E) geladas (*Theropithecus gelada* [13]; photo: T. Bergman); (F) proboscis

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the confines of the highest social levels, which may increase relatedness among females and strengthen tolerance among core units. This may explain occasional affiliative exchanges between females across units, as among snub-nosed monkeys [18] and hamadryas baboons [19]. Multiyear field studies suggest that kin selection among females is an organising principle of MLSs. Female kinship predicts associations between gelada core units [36], and hamadryas females within core units are more closely related than expected despite being coercively transferred by males [44]. Similarly, aggregation of plains zebra family groups to reduce sexual harassment is driven by females, not males, and female half-siblings usually reside together [45]. Relatedness also predicts association between core units of African elephants [46], although it may be less instrumental in shaping social bonds within higher levels. In sperm whales, kinship influences social organisation within nearly matrilineal social units, but associations between units are not strictly kin based [47]. Future research on how kinship links core units in MLSs will elucidate both the maintenance and evolutionary origins of these systems, with implications for the evolution of our own [42,48].

By contrast to unilevel societies with one single optimal grouping size, different functions can be optimised at different levels in MLSs. Given that additional levels of sociality above the core unit can afford adaptive possibilities that core structures in isolation cannot, members of MLSs are well equipped to balance the costs and benefits of group living [49]. Hamadryas baboons illustrate how each social level makes possible different types of collective interest shared among individuals: the core unit offers access to reproductive partners; the clan is a substrate for the maintenance of male–male relationships; the band serves an antipredator and resource-defence function; and the troop optimises predator protection at sleeping sites while providing opportunities for gene flow via female takeovers [14,17]. Reduction of predation through dilution or communal defence is likely a key driver of higher levels in many MLSs ([2,50], but see [23]). In zebras and some snub-nosed monkeys, males in OMUs that are part of a band, compared with those not in a band, are better able to prevent intrusions of coordinated bachelor males vying for reproductive opportunities [20,29]. In African elephants, the highest ‘level’ may be an epiphenomenon or a by-product of individual predispositions to socially interact [10]; by contrast, for marine mammals, the social lives of which depend on acoustic communication, the highest social level can provide the coarse-grained information needed to distinguish between familiar and unfamiliar conspecifics (Box 2). While atomistic fission–fusion dynamics provide an alternative means of flexibly responding to socioecological pressures [26], MLSs allow maintenance of core units, providing a greater consistency in social relationships and cleavage points.

Consequences of Living in Multilevel Societies

MLSs bring new challenges and opportunities and may have follow-on effects in a variety of domains, including male–male competition, intersexual conflict, and cognitive abilities. First, while male–male tolerance appears in many, but not all, MLSs, this does not preclude male–male competition. Mating competition in MLSs occurs in a context of close proximity among reproductive units and between reproductive units and bachelor males within the larger society. This crowded, competitive environment can also be fertile ground for the evolution of signals of male quality and

monkeys (*Nasalis larvatus* [102]; photo: I. Matsuda); (G) black-and-white snub-nosed monkeys (*Rhinopithecus bieti* [12]; photo: C.C. Grueter); (H) Rwenzori black-and-white colobus (*Colobus angolensis ruwenzorii* [6,103]; photo: C.C. Grueter); (I) plains zebras (*Equus quagga* [29]; photo: D. Rubenstein); and (J) sperm whales (*Physeter macrocephalus* [2]; photo: A. Cotton). Additional taxa with MLSs include long-finned pilot whales (*Globicephala melas*) [104], short-finned pilot whales (*Globicephala macrorhynchus*) [4], orca or killer whales (*Orcinus orca*) ([105], but see [106]), Asian elephants (*Elephas maximus*) [5], Gobi khulans (*Equus hemionus*) [107], all other species of snub-nosed monkeys (*Rhinopithecus* spp.) [30], douc langurs (*Pygathrix* spp.) [108], and humans [31]. MLSs may also occur in uakaris (*Cacajao* spp.) [109] and drills (*Mandrillus leucophaeus*) [110] but our knowledge of the social organisation of these taxa in the wild is limited.

Box 2. Culture as a Driver of Social Levels

Rich social lives, experienced within complex societies, can stimulate learning. Animals deal with risks and resources by fine-tuning behaviour; social animals do so by tracing their physical and social environments. Learning new information from conspecifics, and using it collectively, increases within-group cohesion and coordination. Socially learned behaviours shared within subsets of a population (culture) can in turn modulate social interactions and demarcate social boundaries [77].

How can culture structure well-mixed populations into sympatric yet distinct groups [77]? One route is the feedback between the tendency of similar individuals to associate and the subsequent opportunities to learn from them that promotes within-group behavioural homogeneity. This is leveraged when individuals are conformists or mark their group identity so that social interactions occur preferentially among members. With increased behavioural similarity comes social cohesion; groups become tighter as members reinforce their social connections and shed ties with outsiders. This way, culture can, directly or indirectly, erect social barriers and delineate a distinct level in a society. Sociocultural boundaries are prominent in human societies, but they can also structure non-human societies.

Several animal populations feature sympatric groups with distinct repertoires of socially learned behaviours, especially foraging tactics and communication signals [86]. Communication is critical in social contexts and, thus, influential in demarcating social groups. For social animals, learning communication signals correctly is essential to maintain group cohesion, reinforce bonds, and aid collective decision-making. Distinctive signals can be necessary to distinguish social levels, from addressing affiliates to identifying which groups one belongs to [63]. MLSs of toothed whales illustrate how learning communication signals can generate such culturally driven social levels.

The MLSs of killer and sperm whales contain stable core units and fluid intermediate levels [2] but differ from terrestrial MLS by featuring upper levels (clans) delineated by socially learned acoustic communication signals. The 'pulsed call' dialects of killer whale clans emerge from innovations and learning errors combined with a tendency to diverge from kin [87]. The 'coda' dialects of sperm whale clans emerge from biased learning in which conformists learn the most common signals from similar individuals [88]. In both, boundaries around clans are unlikely products of stochastic processes alone (i.e., genetic or cultural drift), but instead result from social transmission of behaviour [87,88], making culture a key ingredient of their MLSs. Finding analogous cultural processes shaping societies of species in completely different environments can help uncover parallels between human and non-human MLSs [86].

physical prowess. For example, Asian colobine species with MLSs exhibit greater sexual dimorphism in body mass (a key indicator of male–male competition) than those without MLSs [51]. A comparative analysis among primates, controlled for phylogeny and group size, revealed that sexually dimorphic ornaments are also most pronounced in MLSs compared with other societies [52]. Such ostentatious traits include the mantles of hamadryas and Guinea baboons, red chest patches of geladas, extended noses of proboscis monkeys, and red lips of black-and-white snub-nosed monkeys (Figure 2F). These traits likely allow males to quickly, reliably, and remotely assess the fighting ability of competitors, while females can gauge the quality of potential mates. Such ornaments are adaptive when individuals are confronted with a high density of competitors and surrounded by unfamiliar conspecifics [52,53].

One form of sexual conflict generated by asymmetry in reproductive investment is infanticide, common when the highest ranking or sole male in a social unit is replaced, to which females may mount behavioural defences [54]. In MLSs, these counterstrategies include paternity concentration (long-lasting associations with a bodyguard) and paternity confusion (to prevent infanticide from unlikely fathers). Paternity concentration may be used by female hamadryas baboons [55], which may ensure protection against infanticide through (albeit not entirely voluntary) exclusive association with a single protective male. By contrast, MLS-living colobines appear to use paternity confusion: female golden snub-nosed monkeys copulate with males outside their OMU (but within their band), possibly to reduce the risk of infanticide should one of those males subsequently become the leader of their OMU [56].

The cognitive consequences of MLSs have received attention in few taxa despite the possibility of considerable cognitive capital in these systems due to the presumed necessity of managing relationships across a complex social landscape (*sensu* [57]). However, it remains premature to

view MLS as more cognitively taxing than other social systems, particularly compared with unilevel societies with atomistic fission–fusion [26]. In taxa in which higher levels have a clear social function and require cultivation via affiliative means (e.g., multilevel alliance networks of bottlenose dolphins), selection for social intelligence is expected [58]. By contrast, the concentration of social interactions within small core units rather than the wider social sphere may have reduced selection for across-the-board social cognition and correspondingly reduced the cognitive load of individuals [59–61]. Evidence of this derives from the presence of MLSs in vulturine guineafowls (*Acryllium vulturinum*), a relatively small-brained bird [62]. The omnipresence of morphological indicators of individual viability in primate MLSs [52], as noted earlier, as well as behavioural indicators of social levels in cetacean MLSs [63], further suggest a limited need for cognitively demanding abilities. Using group-level relationships to manage interactions (e.g., treating all members of the same level as mutually substitutable to some extent) and relying on shared markers to identify social units may release the cognitive challenges of managing tens or hundreds of individual relationships.

MLSs are structurally complex social systems, but the degree to which their individual members also experience **social complexity** remains another open question. The extent to which individuals face social complexity should have a bearing on individual recognition abilities. One recognition route is through vocal communication; thus, complex societies may foster vocal complexity [64] in terms of acoustic repertoire size, degree of individuality within discrete calls, and use of signals to identify social units. However, the evidence in MLSs is mixed. On the one hand, neither geladas nor Guinea baboons show differentiated responses to vocalisations of individuals outside their core units, suggesting that they are either unmotivated or unable to monitor individuals outside their immediate social sphere [65,66]. Geladas have larger vocal repertoires than baboons [67], but the vocal repertoire of Guinea baboons does not appear more complex than that of non-MLS baboon taxa [68]. On the other hand, African elephants have the neural machinery to vocally distinguish among up to 100 conspecifics [69], and excel at tracking the location of other group members in relation to themselves [70]. Similarly, male bottlenose dolphins in multilevel alliances recognise dozens of individuals from their signature whistles, which are retained for life [71]. However, these abilities may mask complexity in other modalities (e.g., visual).

Concluding Remarks and Future Perspectives

In this review, we have synthesised recent advances in the study of multilevel sociality, proposed a standardised terminology for studies across taxa, and underscored the importance of this topic as a fertile ground for further research (see Outstanding Questions). Here, we highlight three promising avenues for future study.

First, the partitioning of the physical landscape among higher levels of MLSs remains poorly understood. In particular, whether and how members of different social levels coordinate their movements, how dispersal opportunities emerge, and how shared spatial preferences (e.g., for sleeping sites) differ from social preferences in producing higher social levels warrant further study. Technologies to collect high-resolution movement, interindividual proximity, and social association data [62,72,73] can help detect interactions among social units and tease apart the relative effects of the physical and social environments [74]. Additionally, developing empirically grounded and spatially explicit agent-based models can shed light on the interplay between collective decision-making, movement, and social interactions that may underlie the upper and apex social levels.

Second, in addition to group coordination [75], the longstanding question of whether the typical structural complexity of MLS necessitates or promotes higher cognitive abilities deserves further attention. This would also contribute to elucidating the causal links between cognition, social

Outstanding Questions

How can we quantify the relative contributions of social processes and ecological factors in shaping the temporal dynamics of MLS?

What is the socioecological basis of the emergence and maintenance of vertically tiered stratification in MLS?

How are collective decisions involving multiple associated units made and how is group coordination achieved?

Is the high degree of structural social complexity of MLS, as perceived ‘externally’, by observers also perceived ‘internally’ from the perspective of individual animals living in such societies?

Does the nestedness of social levels reduce or increase the cognitive load that members of MLS experience? Might MLSs impose more limited social complexity compared with large unilevel societies with atomistic fission–fusion dynamics, where frequent changes in association require recognition and monitoring skills?

Does the assorted nature of social connections in MLS shape the diffusion of socially acquired behaviour?

How do MLSs modulate the spread of infectious diseases and individual microbiota? Do cohesive core units in an MLS act as transmission bottlenecks for pathogens and gut symbionts?

What are the physiological consequences of being embedded in an MLS? How does strong substructuring influence stress physiology and social buffering?

If large-scale MLSs require pristine stretches of habitat to compensate for the energetic costs of association, how does habitat loss and degradation, and hunting threaten the social connectivity and persistence of animals living in these social systems?

complexity, and communicative complexity [64]. Just because an MLS looks complex from the outside does not mean that it is perceived as such from the inside, unless so demonstrated [76]. Comparing the allocation of social attention and inferential reasoning capacities in closely related species that differ in social organisation would be particularly revealing. So far, most of the species living in MLSs are large-brained mammals; should MLSs turn out to be more widespread in other groups (e.g., [62]), then this could be evidence that elaborate encephalisation is not a prerequisite for the evolution of MLS.

Third, we currently lack an understanding of how social transmission differs between MLSs and unilevel societies. Theoretical and empirical work has shown that the way in which social interactions are structured within a single social level can foster or constrain the spread of socially transmitted information and pathogens [77,78]. Whether core groups in MLSs act as transmission bottlenecks is almost unexplored, but could be quantified through experiments whereby problem-solving techniques are seeded in core units and the diffusion (or lack thereof) across unit boundaries is monitored. Similarly, while MLSs can structure the gastrointestinal microbiota [79] that have a role in health and immunity, little is known about how microbiota are transmitted across social levels. Individual microbiome signatures may be obscured by living in a large MLS (as a result of cohabitation of reproductive units and synchronised between-unit behaviour); alternatively, MLSs may crystallise distinct microbiome signatures between units [80]. The dynamics of other physiological states, such as physiological stress, within MLSs also remains an untapped area of research. While stress influences individual behaviour and performance, it is unknown whether belonging to an MLS buffers animals from stressors or further exposes them to indirect stressors emanating from this wider social environment.

Current evidence for MLSs in larger-bodied animals varies across species, partially due to the lack of consistency in definitions of social levels, both conceptually and analytically. We suggest limiting the use of this terminology to species with a demonstrably bounded core unit structure and frequent or permanent association among core units into one or more recognisable upper levels. These criteria exclude species in which core units either change in composition or encounter one another only occasionally. To facilitate future cross-species comparisons, we also advocate adherence to the terminology herein proposed for the various levels in an MLS.

While superficially similar across taxa, the underlying social dynamics of MLSs, including the role of kinship, can differ fundamentally, reflecting differing evolutionary origins. Coupling socioecology with phylogenetics using a comparative approach (especially between closely related taxa, e.g., Asian versus African elephants) can help elucidate the ecological correlates of the different routes and the role of phylogenetic inertia in MLS maintenance across lineages. The persistence of MLSs is contingent on their benefits (e.g., protection from predators and conspecifics or optimisation of gene flow) offsetting their ecological costs. By contrast to a one-size-fits-all group, individuals living in MLSs are simultaneously members of multiple levels and, thus, can experience cost–benefit trade-offs of group living at multiple levels. Finally, living in an MLS brings about novel challenges and exigencies that can influence the evolution of precopulatory sexual selection and possibly cognition.

Humans share the same principles of multilevel sociality with other animals (Box 3), thus the study of the evolutionary drivers of MLSs can help elucidate our own evolutionary history. As technology improves the simultaneous tracking and collection of high-definition social and communication data on entire animal groups, it may reveal hitherto hidden social layers in other animal societies. Mapping the taxonomic distribution of multilevel sociality will expand our understanding of its drivers and consequences, providing a valuable reference point for the evolutionary pathways of sociality in our own species.

Box 3. Multilevel Societies in Humans

Human MLSs differ from those of other animals in that sets of multiple core units bonded through bilateral kin ties form co-operative networks with high levels of between-group coordination [8,24,89]. In hunter-gatherer societies, core family units (mostly monogamous, sometimes polygynous, rarely polygynandrous) are part of relatively fluid local bands of ~50 individuals and of higher-level interconnected multicamps [90]. The high costs of reproduction in humans has promoted cooperation in food procurement, favouring within-unit food sharing and provisioning, thereby constraining polygyny and male dominance. These patterns, reflected in modern hunter-gatherers [89], are associated with a change in residence patterns from sex-biased dispersal to bisexual exogamy: most hunter-gatherer groups are bilocal or multilocal (i.e., both males and females keep close cooperative kin links across camps, helping to offset reproductive costs). Bilateral kin ties bridge between-camp affinities, with nuclear families moving between camps [90,91]. This social configuration promotes within- and between-camp cooperation and large home ranges, while at the same time producing a new social system where neither sex is closely related to their camp of residence [92]. Clustering at the band level of more closely related households facilitates food sharing and cooperative subsistence [93].

Phylogenetic models suggest that modern human societies originated as multimale–multifemale groups and then evolved into MLSs with one-male core units before or during the evolution of pair bonds [48,89]. The evolution of stable pair bonds may have paved the way for bilateral kin and in-law recognition [94]: once pair bonding was established, shared reproductive interests between affinal (in-law) families would extend cooperation beyond kin, promoting affinal kin recognition [95], and strong between-group ties would be cemented via both consanguineal kinship and affinal kinship (Figure 1). This fluid sociality with frequent mobility between unrelated bands would promote cooperation between unrelated families, through resource sharing [91] and reciprocal allomaternal care [96]. Strong bonds between unrelated families [97] in this vastly extended social landscape would lead to a tenfold greater likelihood of encountering role models for social learning compared with chimpanzees [98]. Thus, frequent opportunities for information exchange and accumulation of cultural and technological knowledge [99] underlie the remarkable success of human MLSs.

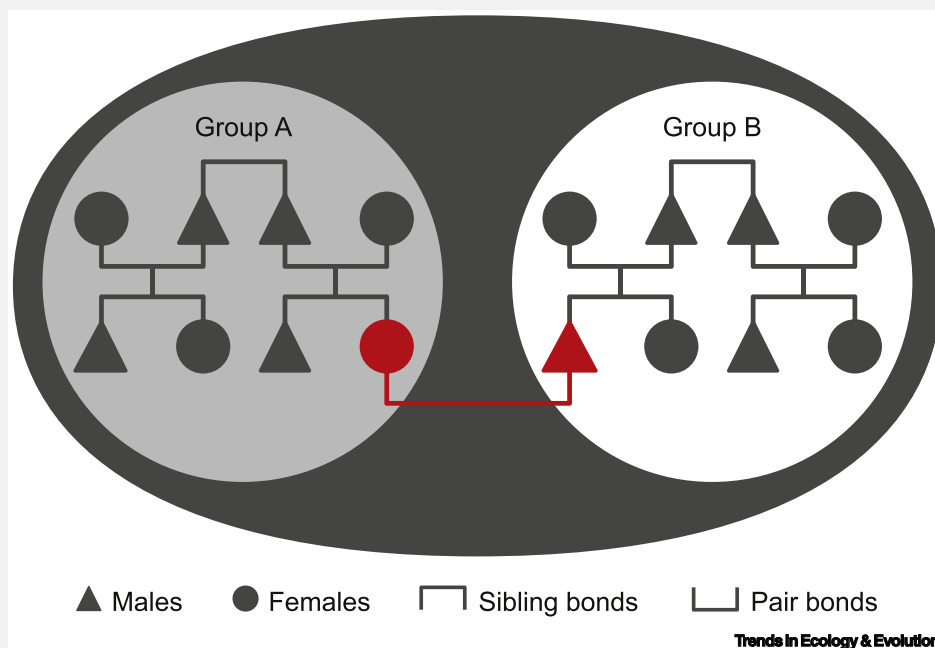


Figure 1. Bilocality with Exogamy of Males and Females and the Evolution of Human Multilevel Societies (MLSs). The key unit of between-group alliances is a pair bond (red) linking the spouses' kin living in different groups (A,B) and connecting the two sets of in-laws. Modified from [100].

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