A conceptual guide to studying multilevel societies

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Abstract

1. Multilevel societies—social systems composed of multiple nested social units—have long intrigued scholars in anthropology, behavioral ecology, and evolutionary biology. Classically described in mammals, new evidence shows that multilevel societies are more widespread across taxa than previously acknowledged, raising both conceptual and methodological challenges for comparative research.
2. We propose a taxonomically-inclusive framework for detecting and studying multilevel societies, expanding on the existing definitions to accommodate diverse life histories, seasonal dynamics, and levels of spatial cohesion. The proposed refined criteria consist of a core social unit, temporal stability in group membership, and consistent inter-unit relationships that together form higher social levels within a larger social entity.
3. We synthesize current evidence for multilevel societies in mammals, birds, fish, and insects and demonstrate underappreciated or newly discovered cases—e.g., polydomous ant colonies and seasonal associations in cooperative birds—that meet the criteria for multilevel societies. We also present diagnostic field signatures that can guide early-stage detection of multilevel sociality in under-studied populations, while emphasizing the importance of maintaining definitional rigor to avoid diluting the concept.
4. We offer detailed guidance for how to measure and validate multilevel societies using social network analysis, spatial data, and stability metrics. We suggest approaches to help navigate challenges in conflating social systems and spatial overlap, and describe experimental, modeling, and comparative procedures for testing hypotheses on the function and evolution of multilevel societies.
5. By sharpening definitions, outlining sound empirical approaches, and broadening the theoretical scope and the conceptual toolkit for identifying for multilevel social systems this synthesis aims to foster more consistent and systematic cross-taxonomic social comparisons. A better understanding of the drivers and variation of multilevel societies will shed light on the evolutionary mechanisms that underlie animal sociality more

broadly, while offering novel avenues for testing general principles of collective behavior, cooperation, and social complexity.

Keywords: Animal social networks, Collective behavior, Group living, Multilevel sociality, Social evolution, Social organization, Social structure, Social systems

Introduction

Multilevel societies (MLSs) are societies composed of nested social units (Kummer, 1968; Grueter et al., 2020). Multilevel sociality is thought to be a key feature of human social systems that has contributed to the global expansion of our species, such as by enabling cumulative cultural evolution (Migliano et al., 2020). MLSs stand out because social processes and decisions are made at the level of stable social units, rather than at the individual level as in 'other types' of societies. Such dynamics are also found in a range of non-human animals.

MLSs have been described since at least the 1960's in hamadryas baboons (*Papio hamadryas*) where one-male-units (OMUs) join in predictable ways to form clans, and these clans can, in turn, form bands (Kummer 1968). Similar social patterns were later found in other primate taxa (Kawai et al., 1983; Kirkpatrick & Grueter 2010; Patzelt et al., 2011) and in other large mammal species, such as African elephants (Wittemyer et al., 2005), ungulates (Rubenstein & Hack 2004; Maeda et al., 2021), and cetaceans (Tavares et al., 2017; Whitehead et al., 2012). More recently, birds have been shown to form MLSs (Papageorgiou et al., 2019; Camerlenghi et al., 2022) and some ant (Robinson 2014) and fish species (Jungwirth & Taborsky 2015; Josi et al., 2021) have been reported to form multilevel social systems. Although the concept and definition of mammalian MLSs were well covered in a recent review (Grueter et al., 2020), the application of the MLS terminology to a wider set of taxa (Camerlenghi et al., 2022; Jungwirth & Taborsky 2015; Camerlenghi & Papageorgiou 2025; Rodrigues et al., 2022; Robinson et al., 2024) has raised novel questions and also introduced potential confusion over what constitutes an MLS and how to define and study MLS (Papageorgiou & Farine 2020; Grueter et al., 2021).

One reason for broadening the theoretical scope of MLS is that taxonomic groups vary substantially regarding the temporal and spatial scale, seasonal dynamics, and life history characteristics. These can offer opportunities to better understand different aspects of the evolution and functional importance of MLSs. However, we also require strong theoretical foundations because this variation can also impact how and when a multilevel social system is expressed. The logistical challenges inherent in studying each social system—and the methods developed to overcome these—also vary considerably. Thus, data from different social systems are produced with different assumptions and definitions. While such issues are common when addressing questions in ecology and evolution that span taxa, they are particularly challenging to overcome when studying MLSs because of the large numbers of individuals that are typically involved, making individual marking and recognition difficult (Zhang et al., 2024). Thus, to understand the evolution and consequences of multilevel societies, we urgently need a framework that allows taxonomic breadth without sacrificing conceptual coherence.

Here, we address this gap by providing a guide on how to study multilevel societies across taxa. Firstly, we propose expanding the classical definition of MLSs to better encompass non-mammalian taxa while delineating the criteria that distinguish multilevel societies from other types of social systems[1]. Secondly, we review the literature where MLSs have been discovered, outline the signatures of potentially undescribed MLSs, and discuss how to quantify and define the stable social units and nested social levels that underlie an MLS. Third, we offer guidance on common mistakes that can be made when describing societies with nested social structures. Fourth, we call for more studies that explicitly test hypotheses, including those on the function and evolution of

[1] Kappeler (2009) distinguishes social systems according to social organisation (the size and composition of a social unit) and social structure (content, quality, and patterning of social relationships emerging from repeated interactions between pairs of individuals belonging to the same social unit). As multilevel societies encompass parts of both of these elements of social systems (e.g. group composition and relationships among groups), we use the broader label of social systems but acknowledge that past and future work may refer to each element more specifically where necessary.

MLS. We conclude by outlining areas where conceptual and methodological development is critical to develop a robust framework for studying multilevel animal societies.

What are multilevel societies?

According to Grueter et al., (2020), MLSs are social systems composed of at least two distinguishable and consistent levels of social integration between the individual and the population. These two required levels must be nested, and include the core units—the lower-level social unit, such as the OMU in hamadryas and the unit in Guinea baboons (*Papio papio*) or the breeding group in superb fairy-wrens (*Malurus cyaneus*)—and the upper level—such as the bands in hamadryas and gangs in Guinea baboons or the communities in fairy-wrens. Additional, but not mandatory, social levels may be referred to as intermediate and apex levels. Following this definition, at each level of social integration, social units can predictably merge to form higher-level social units and split back into their original units. Still, the composition and size of the unit must remain stable over time—despite natural demographic changes due to mortality or eventual dispersal—for at least the core social unit and the upper level (Grueter et al., 2020).

Expanding existing definitions of multilevel societies

With growing interest in studying MLSs across a broader range of taxa (e.g., Camerlenghi & Papageorgiou 2025; Robinson et al., 2024), we propose a revision of the definition of MLS to accommodate species with different life history characteristics. First, the core social unit does not necessarily have to be the lowest-level social unit. For example, in vulturine guineafowl (*Acryllium vulturinum)*, the core social unit (social group), comprising up to 60 individuals, is the most stable unit in terms of composition over time (Papageorgiou et al., 2019). However, these social groups function as an intermediate level of social organization because they can split into subgroups during

breeding seasons, each consisting of distinct cooperative breeding subunits (Papageorgiou and Farine 2020; Nyaguthii et al., 2025). This split is driven by the need for females to nest, incubate their eggs, and then raise their precocial young.

Second, we propose that while core units must maintain compositional stability, they do not need to be spatially cohesive at all times—though many often are, particularly in primates. For instance, in hunter-gatherer societies, individuals from the same family unit may be spatially dispersed during the day but regroup in a shared space at night (Kelly 2013). A similar pattern is observed in male Indo-Pacific bottlenose dolphins (*Tursiops truncatus)* in Shark Bay, where the second-order alliance that functions as the core unit is stable in membership despite individuals regularly splitting from and merging with their second-order allies (Connor & Krützen 2015). However, these alliances still operate as a unit when confronting rival males (King et al., 2021; Connor et al., 2022), meaning that they serve a distinct function. The lowest-level social unit is the first-order alliance, which consists of two or three males from the same second-order alliance, and cooperatively herds females in events termed consortships. Such consortships can last from a few days to several weeks, and individuals can form new consorting pairs or trios even within the same breeding season.

Third, we propose being more stringent about the temporal stability of core social units, suggesting that these should remain largely stable—despite occasional membership changes—for a substantial portion of individuals' lives. For example, second-order alliances in Shark Bay dolphins persist for decades, representing a substantial portion of their ~35-year lifespan (Connor & Krützen 2015). In hamadryas baboons, the median tenure of OMU leader males is six years (Pines et al., 2015), and in golden snub-nosed monkeys (*Rhinopithecus roxellana*), leader tenure averages around three years, with some lasting up to ten (Fang et al., 2019). Breeding subgroups in vulturine guineafowl reform into the same social groups after the breeding season, with males remaining in the same group for life (Papageorgiou et al., 2019; Nyaguthii et al., 2025). Thus, the identity of these groups is robust to temporary splits, such as when key life history stages (e.g.

nesting in birds) prevent spatial aggregation, and individuals can be assigned to one social unit for a meaningful period (i.e., longer than temporary or seasonal changes in ecological conditions).

A (refined) definition of multilevel societies

We propose that to define a society as multilevel, it must satisfy the following five criteria:

1. have a core social unit, i.e. a group of individuals that maintains its composition over a substantial portion of the individuals' lives;
2. individuals (except floaters, dispersers, or unattached individuals[2]) must be clearly assignable to a core social unit;
3. inter-unit spatial cohesion and interactions must be consistent and give rise to one or more distinct levels;
4. core social units should, in combination, form a higher-level social unit; and
5. Key social processes, such as dominance hierarchies and group decisions, should generally operate at the level of core units or at higher levels, such that outcomes are determined collectively by the unit rather than by individuals acting alone.

Our major extension is to better capture the distinct processes and consequences of MLSs (notably through point 5). As a rule-of-thumb, for a society to be considered an MLS, many key decisions that affect individual fitness—such as who to merge with to form an aggregated unit—should generally be expressed collectively by core unit members rather than individually by its members. For example, dominance hierarchies, collective movements, and decisions to fission from or fuse with others are expressed by the core social unit in vulturine guineafowl (Farine 2025) and killer whales (Brent et al., 2015). Similarly, in humans, decisions to share food within a community are made by family units (Kaplan et al., 2005), and nests of ants which have maintained long-term

[2] Not all individuals of a given species necessarily have to be in a social unit to satisfy the requirements of a multilevel society. For example, in a number of species males are solitary during some parts of their lives.

stable food-sharing interactions with neighboring nests may collectively cease these interactions when the resource environment changes (Burns et al., 2020, 2021). We note that collective decisions can take various forms along a spectrum from unshared decisions (e.g. where all individuals in the social unit follow a despot) (Huchard et al., 2008) through to shared decision-making (where all individuals can contribute to the decision) (Papageorgiou et al., 2024), but these are collective decisions because the outcome is shared by all individuals. Individual contributions to decisions by social units can vary over time, but the shared outcome arises because individuals do not leave the social unit if or when their preferences misalign with those of the group (Farine et al., 2025). A consequence of living in a social unit is therefore that core social unit outcomes disproportionally determine each individual's fitness, as outcomes are more consistent among individuals within the same social unit versus those between social units. This feature distinguishes MLSs from other forms of nested or multi-tiered societies, which might show similar structural properties in the aggregate but where processes such as group movement decisions, and their consequences, are more directly reducible to each individual's actions.

A taxonomic survey of multi-level societies beyond primates

Despite a growing interest in MLSs over the past decade, these societies appear patchily distributed across the mammalian phylogenetic tree (Grueter et al., 2020). This pattern—originating in anthropology and primatology and later extending to other taxa—may reflect the high status of primate research in animal behaviour, which likely led researchers working on other species to adopt the same terminology to draw meaningful parallels. It may also stem from a longstanding bias that complex social systems evolve only in large-brained, large-bodied animals (Papageorgiou et al., 2019). Alternatively, the patchy distribution of MLSs across mammals may reflect a real biological pattern that warrants further investigation.

The recent alignment of birds with the MLS literature occurred following the description of MLSs in vulturine guineafowl (Papageorgiou et al., 2019) and superb fairy-wren (Camerlenghi et al., 2022). While the description of bird MLSs occurred considerably after the identification of MLS in mammals, it is essential to note that very similar definitions with different terminology were used to describe bird social systems for almost as long as MLSs have been described. For example, buff-rumped thornbills (*Acanthiza reguloides*) were previously described as having societies structured as breeding groups nested within clans (Bell & Ford 1986). Unlike in mammals, it is likely that MLSs are widespread in birds, particularly among cooperatively breeding species (Camerlenghi et al., 2022). One reason why birds have largely been overlooked is likely due to the focus of much of ornithological work being on birds' breeding season, with studies of social behavior outside the breeding season remaining limited (Camerlenghi et al., 2024; Farine 2025; Ramellini et al., 2025). Yet, it is during the non-breeding season—when territoriality is often relaxed—that higher-level social units are most likely to form.

Among social insects, stable patterns of tolerance and cooperation between individuals of spatially distinct nests have likewise a long history of study, particularly in wood ants (Kneitz 1964; Chauvin 1965; Cherix 1980; Rosengren 1985). However, this phenomenon is not usually framed using the MLS terminology (but see Lengronne et al., 2021; Rodrigues et al., 2023). It is instead referred to using a variety of terms, such as *polydomy*. Polydomy describes the non-aggressive, mutual exchange of workers across nests (Debout et al., 2007; Robinson 2014) and is seen in many ant, and some bee, wasp, and termite species (Debout et al., 2007; Lengronne et al., 2021; Brand & Chapuisat 2016). In polydomous species such as wood ants, intergroup cooperation can include exchanging workers and transferring brood and food along inter-nest trails that can persist over several years (Ellis & Robinson 2015; Burns et al., 2020; Piross et al., 2025). These characteristics are consistent with the definition of an MLS in that each nest is distinct, nests of ants make collective decisions, multiple nests combine to form complex social networks, individuals can be

assigned to one nest (or colony), and both interactions and multi-nest colonies are stable over long periods (Burns et al., 2020; Burns et al., 2021; Piross et al., 2025).

While MLSs will undoubtedly continue to be discovered across different taxonomic groups, there may also be undiscovered cases within well-studied species, for example in new populations or at different times of the year. Marine mammal examples include Indo-Pacific bottlenose dolphins that typically form unstable groups in which individuals often leave and join (Wiszniewski et al., 2009) but can, in some populations form multilevel male alliances with up to three levels of social integration embedded within a broader fission-fusion network (Connor et al., 2022). Similarly, both killer whales (*Orcinus orca*) and female sperm whales (*Physeter macrocephalus*) show population-specific expressions of social systems shaped by the local ecological and environmental conditions. Killer whale ecotypes differ markedly in their social systems from highly stable, kin-based multilevel societies in resident populations to looser, more fluid associations in offshore and Antarctic populations (e.g., de Bruyn et al., 2013; Tavares et al., 2017; Jordaan et al., 2023). In sperm whales, female social units are typically stable and matrilineal, but the extent and structure of higher-level associations vary between ocean basins—likely influenced by differences in habitat use, prey and risk distribution (Whitehead et al., 2012). One example of how easily MLSs can be to overlook is the most studied bird species in the Southern Hemisphere, Superb fairy-wrens. Cooperatively breeding groups are strictly territorial during the breeding period, but breeding groups aggregate with other breeding groups during the non-breeding season (Camerlenghi et al., 2024). Thus, capturing the diversity of MLSs may require a wide(r) search; replicating the search across populations experiencing environmental and seasonal gradients will answer whether variation in social systems is the rule or the exception.

Key factors that shape multilevel societies across taxonomic groups

Given the taxonomic diversity of species that form multilevel societies, the selective pressures that favour or are linked to their emergence may often be taxon-specific. However, there may be some commonalities that will provide a rich substrate for future studies.

Several factors likely shape the emergence of MLSs, and life history is particularly influential., Species with an accelerated life history trajectory may lack the longevity necessary to build stable intergroup relationships, and with few opportunities to establish long-lasting relationships, short-lived animals are better off investing more in behaviors that contribute towards survival., In contrast, long-lived species with more protracted life history stages are more likely to accrue the benefits associated with living in an MLS.

Resource heterogeneity across space and time and the need for reciprocal resource access can also facilitate intergroup tolerance, thus favoring the emergence of higher-level social units (Ellis et al., 2014; Grueter, 2022; Pisor & Surbeck, 2019). In other words, spatial asynchrony in resource availability can promote inter-community alliances. For example, for human communities in southwestern Africa, water availability can vary asynchronously over distances of just tens of kilometers, making social relationships between members of different communities crucial for accessing water during local droughts (Cashdan et al., 1983). In addition, resource heterogeneity across time can drive resources to be scarce or unpredictably distributed, with the costs and benefits of forming higher-level social units changing across seasons. This is the case, for example, of some bird species, which lay eggs and defend territories from neighboring groups during times of resource abundance, but relax territoriality to form cooperative higher-level social units during the harsher time of the year (Camerlenghi et al., 2024). Relaxed or absent territoriality appears to be a general requirement for MLS formation. Strict year-round territoriality at the pair or group level likely constrains the development of higher-level social units (Tobias et al., 2016), whereas the need to re-form territories each breeding period may be a driver of MLSs (Ramellini et al., 2025).

One of the benefits of association between groups is joining forces to defend resources against other conspecifics. In many cases, higher-level social units arise when males from different

groups unite to defend females against bachelor groups. For example, collective defense against competitors (e.g., bachelor males in snub-nosed monkeys) is thought to drive the formation of higher-level social units in some primates (Grueter & van Schaik 2010; Xiang et al., 2014; Qi et al., 2017) but also in plains zebras (Rubenstein & Hack 2004) and in bottlenose dolphins (Connor et al., 2022). This defense may also extend to defending future breeding space or resources—for when conditions become suitable—in other taxa, such as birds

Predator pressure could also represent a direct driver of MLS formation. While group living can help reduce per capita predation risk, being part of a higher social level could further reduce mortality, as suggested for pelagic matrilineal cetaceans (Whitehead et al., 2012). This can occur if individual investment in antipredator behaviors increases with familiarity between core social units (Camerlenghi et al., 2023) and because some beneficial group functions scale with social unit size (Hooper et al., 2015; Cantor et al., 2021).

Factors such as social viscosity—limited movement or dispersal that keeps individuals near kin or familiar group members—may act as stabilizers of MLS. Such a dynamic is observed in social insects, where the relaxation of group territoriality appears to arise from population viscosity, as seen in paper wasps (Lengronne et al., 2021) and ants (Helanterä 2009). However, while this pattern is evident in many MLS across taxa—from cooperatively breeding birds to geladas and plains zebras—it is not universal., For instance, free-ranging horses and sperm whales may not have kin-based preferences in the formation of higher-level social units (Konrad et al., 2018; Maeda et al., 2025).

Finally, population density likely plays a key role in increasing the frequency of encounters between groups (Beck et al., 2023). In some systems, high density can lead to greater tolerance and the formation of higher-level social units. For example, a large-scale analysis of the effects of population density on contact rates found that contact rates typically flatten out at high densities (Albery et al., 2024). This finding suggests that repeated associations among the same sets of individuals can occur more frequently than expected by chance.

Despite the variety of evolutionary trajectories that can lead to MLSs, not all the key factors associated with them carry the same weight: some act as drivers, others as facilitators, and others as stabilizers (Grueter & Pozzi 2025). Specifically, facilitators reduce the costs of peaceful interactions (e.g., cognitive abilities, demographics, landscape features); drivers provide direct benefits such as shared defense, mating opportunities, dispersal, or resource access; and stabilizers help maintain these benefits over time (e.g., group familiarity, kin-based indirect fitness gains) (Grueter & Pozzi 2025). Other factors, however, may have a confounding effect. For instance, a modular pattern of associations may emerge simply because population density limits movement or promotes intergroup interactions (Decelliers et al., 2021). Similarly, habitat geometry can either facilitate or constrain the formation of higher-level social units by shaping how individuals encounter one another (He et al., 2019). Thus, population density and habitat geometry can produce the appearance of nested societies, even in the absence of explicit social structuring (see *Avoiding potential mistakes and adopting common criteria and definitions*).

Signature features of MLS to look for in the wild

Recognizing an MLS in a study population often involves identifying specific patterns in the animals being studied. Here, we outline four simple, observable signatures that a naïve observer might look for when watching groups of a species in the field—particularly when the social system is unknown and individuals are unmarked or not (yet) individually recognizable. However, it is essential to note that these signatures can only inform whether a MLS may be present, but not quantify it or formally demonstrate its existence.

One signature feature is a stable distribution of social unit size. In MLSs, the size of the single core social unit, and often also the upper level, remains consistent, at least during certain parts of the day or season. For example, among hunter-gatherer societies, the size of the family unit, the fundamental social building block, may fluctuate during the day, but it remains stable when all

individuals return to the unit at night (Kelly 2013). Thus, observing a predictable pattern of group size, even if only at specific times, is an important initial indicator of a multilevel social system. As a general rule of thumb, the membership of individuals in a social unit of a species that forms an MLS should be relatively straightforward to discern.

A second signature is a consistent composition of males and females within the social units being observed. In species that form mixed-sex groups, a stable sex ratio within each unit through time can signal stable membership even before individuals are individually marked or recognized. For instance, in hamadryas and Guinea baboons, as well as golden snub-nosed monkeys, the core social unit is a one-male unit (OMU), typically composed of one male and up to 10 females, which maintains a stable composition of members over time (Kummer 1968; Qi et al., 2009, 2014; Fischer et al., 2017). Importantly, while sex ratios can vary within a species or across social units within a population, they should be relatively consistent when observing the same social unit over time, even though variation between units is expected.

A third signature is a multimodal distribution of social unit sizes being observed over time and/or space. This multimodal distribution captures the fact that core social units (first mode of group size distribution) in a multilevel society can merge to form larger social units (second mode of group size distribution). For example, in golden snub-nosed monkeys, OMUs composed of one male and three to six females are typically fused into bands of 40 to 400 individuals. The group-size distribution shows two distinct peaks corresponding to OMUs and bands. However, while important, a bimodal distribution is not a necessary condition for MLSs. In some species, individuals from different core units selectively interact across units without the units fully merging into larger, cohesive groups (Camerlenghi & Papageorgiou 2025). Despite the lack of a clear bimodal distribution of group size, these societies can still create a pattern of social structure indicative of MLS detectable through observation of the social network (Dyble et al., 2016; Migliano et al., 2017). Likewise, in the case of wood ants, individuals move between nests, but entire nests rarely merge, and the larger network can be identified by the stable interactions between

pairs of nests (Ellis & Robinson 2014). We also add the caveat that multimodality in group size alone does not provide evidence for the existence of a multilevel society, as many factors can drive temporal changes in group size.

Finally, a seasonal or permanent high spatial tolerance can also suggest the presence of an MLS. In social insects, for example, a quick rule of thumb suggests nests are distributed in a non-randomly overdispersed (regular) pattern, which indicates territoriality, or in a non-randomly underdispersed (clustered) pattern, which indicates polydomy. In many songbird species that form MLSs, the collapse of territorial boundaries is associated with enlarged space use, increased tolerance among units, and the formation of higher-level social units (Camerlenghi et al., 2022). A resident seasonal breeder that consistently associates with neighbours could be a key step toward such structured societies (Ramellini et al., 2025). However, the absence of territoriality alone is inconclusive: groups may still avoid one another despite overlapping spatial use (Ogino & Farine 2024), or group membership may become unstable as individuals roam more widely. Nonetheless, when stable group size and composition are coupled with overlapping home ranges between groups, examining between-group interactions more closely becomes particularly important, as multilevel social systems are increasingly likely under these conditions (Grueter et al., 2020).

Refining field observations of group sizes

In populations of mixed-sex primate social groups, especially those suspected of having an OMU-based multilevel social system, one useful criterion for identifying such a system through observational methods (e.g., scan sampling) is the pattern of spatial proximity among individuals. Specifically, adult males in OMUs are expected to maintain close spatial associations with their associated females, resulting in a significantly higher likelihood that an adult male will have a female, rather than another male, as his nearest neighbour (see e.g. Goffe et al., 2016). This spatial pattern reflects the social cohesion of the OMU, where males maintain exclusive or preferential associations with a subset of females (Grueter & van Schaik 2010). However, this criterion does

not apply in the context of bachelor groups, where males often associate loosely with each other without direct access to females. Thus, when consistent patterns of male-female proximity emerge across multiple scans, they can serve as indirect evidence for the presence of OMUs within a larger, multilevel social system (Grueter et al., 2017b). Interestingly, though, not all MLSs with OMUs also exhibit bachelor groups. In Guinea and hamadryas baboons, bachelors are well integrated into the second or third tier of the society, the "clan, party" gang, band and are essential for maintaining cohesion within parties (Swedell & Plummer, 2012; Dal Pesco et al., 2022).

An OMU-based multilevel structure can also be inferred from the temporal distribution of individuals in single-file progression sequences, where consistent temporal gaps between successively passing adult males may reflect the boundaries between core units (e.g., Grueter et al., 2017b). Building on this idea, Murphy and Fischer (2025) evaluated the efficacy of using single-file movement data to infer community structure in a group of semi-free-ranging Barbary macaques, applying the Louvain algorithm to estimate modularity and the number of communities. Although the method lacked the resolution to capture fine-scale dyadic relationships, it yielded modularity values and community counts that closely aligned with those obtained through more traditional methods, such as scan sampling and focal observations. These findings suggest that single-file movement data can serve as a practical and low-effort tool for detecting evidence of higher-level community structure in exploratory or pilot studies. In Guinea baboons, for instance, with their clear multi-level structure, single-file movements accurately reflect the association patterns (Montanari et al., 2021). Thus, single-file movement data along with the presence of signature features of multi-level social systems, provides a straightforward, initial quantitative indication of a species' social system—evidence that can help justify more detailed data collection and formal demonstration of its MLS.

How to quantify and demonstrate a species' MLS

Formally describing a multilevel society typically requires long-term, population-scale data on social associations. This is because data generally need to span periods longer than a single field season to obtain evidence for stability in group membership. Space use data can also help to better capture the processes that underpin social dynamics and structure, and the potential interface between these space use and social structure (Webber et al., 2024).

The first step is to identify individual animals, as a prerequisite for measuring their associations is the ability to recognize individuals reliably. How individual recognition is achieved depends on the study species. In birds, individuals are typically marked with color bands (Camerlenghi et al., 2022; Papageorgiou et al., 2019) and may also be fitted with automated tracking solutions, such as RFID tags (Farine & Sheldon 2016) or GPS (Papageorgiou et al., 2019). In ants, researchers use color marking, RFID tags, or, for larger species, small physical tags (Sclocco et al., 2021). In mammals, individual recognition usually relies on natural physical traits and marks, such as scars, differences in facial coloration, fur shading, or body size, but may increasingly rely on individual animal-borne tag data. Deep learning may contribute to solving the identification problem in wild marine (e.g., Patton et al., 2023) and terrestrial mammals (Schofield et al., 2019; Vogg et al., 2025), and birds (Ferreira et al., 2020). Such automated techniques may facilitate expanding beyond studies of single (or small numbers of) groups to allow insights to be gained about patterns of inter-group associations and the stability of these associations at population scales. However, attempts to use camera trap data to recognize individuals and their associations from videos or photos are hampered by the vast amounts of manually labeled data used to train the models. Additionally, in the wild, the presence of unknown individuals in the material may further complicate the classification and recognition of individuals (Ferreira et al., 2020). Self-trained networks may provide a solution to this problem in the future.

The second step is to collect data on the composition of social units. In primates and birds this is typically done through direct observation of individuals identified together (e.g., gambit-of-group approach). In cetaceans this is generally done by capturing temporal sequence of individuals

(photo). As the composition of core social units in MLSs is stable, it should be relatively straightforward to discern. In most studies, individuals will be tied to their group's identity through the group name. In some cases, for example, if an intermediate level is the most stable, social networks may be useful (Ogino et al., 2023). A standard method is the "gambit of the group" approach, where all individuals observed together are assumed to be socially associated during that encounter (Whitehead & Dufault 1999; Farine & Whitehead 2015). It is vital to sample social unit composition regularly and consistently throughout the study to accurately define social units and detect their dynamics over time.

The third step is to collate data on intergroup associations. These can be collected using classical observational methods or, increasingly, are obtained using automated methods. For example, fitting some members of each core group with GPS tags can provide consistent, long-term data on proximity between core groups (Papageorgiou et al., 2019; Loftus et al., 2024; Ohrndorf et al., 2025). One challenge for the study of MLSs is obtaining sufficient data to distinguish between consistent, socially mediated associations and incidental co-occurrence driven purely by shared resource use. Hence, GPS data are instrumental because they collect information about intergroup proximity, social cohesion (e.g., shared movements; Papageorgiou et al., 2024), and spatial overlap of home ranges over long periods.

Social networks are often used to detect and characterize multilevel societies. One approach is to plot a histogram of social association or interaction strengths and assess whether the distribution is multimodal., Multimodality in social bond strength can indicate the presence of distinct social units within the network (Weiss et al., 2019, see also *Signature features of MLS to look for in the wild*). However, this pattern is not definitive, as multimodality can also occur in other forms of multitiered societies (see Fig. 1). Community detection algorithms can then be used to identify the composition of social units across different levels (Grueter et al., 2020). A crucial step is to test the robustness of the composition of these units as a measure of their consistency. A measure for the consistency of membership can be achieved using the method described by Shizuka and Farine (2016), which

involves bootstrapping the association data, constructing a social network for each bootstrapped dataset, applying the same community-detection algorithm, and recording how often each pair of individuals is assigned to the same social unit. By repeating this process on 1,000 bootstrapped networks, it is possible to estimate the stability of the community structure. The *r-com* value describes community stability, a measure of network assortativity that defines how consistent the groupings are across the different bootstrapped networks (Farine 2014). An *r-com* value greater than 0.5 suggests that the population is highly structured into stable social units, indicating consistent individual association preferences (Shizuka & Farine, 2016). However, we expect this value to be substantially higher in an MLS. This procedure can be repeated for each level or by using a community detection algorithm capable of extracting multiple levels (Zhang et al., 2025), such as the Louvain algorithm (Blondel et al., 2008). Finally, it is crucial to test the stability of social unit composition across years, especially when these are only expressed seasonally. One way to achieve this aim is to construct matrices of co-membership (i.e., whether pairs of individuals are assigned to the same social unit) for each year (during the period that co-memberships are expressed), and then utilize matrix correlation tests to evaluate the similarity of social structures across years.

To conclude, distinguishing between higher-level social units that arise from social attraction among lower-level units and those driven by the shared use of localized resources is essential., One strategy adopted by Loftus et al., (2024) was designed to test whether social tolerance among wild olive baboon groups (*Papio anubis*) was driven by localized resources—sleeping sites. Specifically, they used permutation analyses to test whether the movements of social units were correlated while accounting for attraction to shared resources. For each pair of groups, they randomly shifted the movement data of one group across 1000 permutations, creating 1000 new datasets where the paths and locations were preserved, but the timing was randomized (see Spiegel et al., 2016 and Farine 2017 for more details). These randomized datasets generated a null distribution, representing the distances and space use patterns expected if groups moved independently by chance. They then compared the real movement and space use patterns to this null distribution to assess whether the

groups were more coordinated than expected by chance. A different approach was used by Camerlenghi et al., (2022) to test whether spatial proximity between core social units' breeding territories predicted the strength of social bonds between these units in superb fairy-wrens. During the non-breeding season, Camerlenghi et al., measured the linear distance between the centroids of each territory and tested whether proximity correlated with social bond strength. This analysis helped assess whether closer territories were associated with a higher likelihood of core units joining the same higher-level social groups. Similarly, Papageorgiou et al., (2019) correlated home range overlap values with the strength of between-group associations. Together, these approaches illustrate how spatial analyses can disentangle the roles of resource distribution and social preferences in structuring higher-level social units.

Avoiding potential mistakes and adopting common criteria and definitions

The challenge inherent in detecting multilevel societies also presents numerous pitfalls. Broadly, even if a society has a nested, stable group membership or features regular and consistent patterns of intergroup contacts, it may not necessarily mean that it is a multilevel society. Here, we briefly outline some common ways by which studies with marked individuals can incorrectly conclude that its society displays a multilevel structure.

First and foremost, the ability to assign discrete delineations to define different levels or types of relationships with different functional importance does not satisfy the criteria of a multilevel society. For example, great tits (*Parus major*) can be defined as having three distinct social levels: pair mates, breeding neighbours, and flock mates (Gokcekus et al., 2025). However, while some pairs are maintained across years, and some neighbours prefer helping previous neighbours in mobbing predators (Grabowska-Zhang et al., 2012), these patterns are the exception rather than the rule. If great tits formed a multilevel society, we would expect all pairs and most neighbours to reform year to year. During winter, when birds form flocks, pair mates are statistically more likely to be observed together than expected by chance, and they have repeated associations with specific

other individuals. Still, it is not possible to assign a clear 'group identity' to a set of individuals at any one social level. Thus, while associations with flock mates can play an important role in survival (Firth et al., 2016), none of these levels can predict where a given individual might be at a given point in time (as would be expected if there were clear group identities). These examples highlight that while social networks can be a useful tool for identifying MLSs, relying solely on features of these networks can be misleading.

It is very possible for network structures to emerge visually similar to an MLS without satisfying all, or any, of the criteria discussed earlier. In fact, many social species may exhibit multitiered societies (also called multi-scalar; Madsen & de Silva 2024) with clear levels, without the key features of MLSs such as having a stable core unit. These can be expressed as multimodal distributions of association strengths (*sensu* Weiss et al., 2019) or as social networks that are highly modular in structure. For example, a recent study on zebra finches found that individuals had clear levels of social association: strongest associates, strong associates, and preferred associates, without having any distinguishable group identity (i.e. a core social unit) (Zhang et al., 2025). This highlights the importance of integrating network analyses with behavioural and ecological data and observations to avoid misclassifying social systems as multilevel societies.

Various forms of nested social structures—some of which might superficially appear as MLSs—can arise through a range of processes. For example, there is increasing awareness of spatial effects, such as habitat geometry (He et al., 2019), in driving social structure (Webber et al., 2023). A key feature of multilevel societies is that the social system is not exclusively maintained by spatial drivers because decisions by core social units are made as groups and preferences are expressed among core social units. In zebra finches, higher-level community structures (those that might appear to correspond preferred associations among core social units) can arise simply because individual use space unevenly, even if all individuals can equally access all areas (Zhang et al., 2025. Local differences in habitat can also drive differences in population sizes, which can itself generate patterns of consistency in social structure (Beck et al., 2023). Thus, formally describing nested,

multitiered, or multilevel societies (Figure 1) require careful evaluation not only of social structure, but also of the processes that generate it.

Beyond biological drivers, observational methods could also lead to incorrect inferences. For example, while attracting individuals to resources (e.g. to bird feeders to detect PIT tags) can generate meaningful insights into social preferences among individuals, it could also generate higher-level structures that may not necessarily be realistic (Farine & Sheldon 2016). Key, localized resources could stimulate unusually high rates of intergroup contacts (i.e., aggregation around a predictable resource) that could mimic group-to-group preferences (or multitiered community network structure) and be mistaken for an MLS. Such outcomes are not limited to studies actively attracting individuals. For example, it may be easier to observe animals at important (and predictable) resources, such as a waterhole, where contacts can occur among individuals that may otherwise never associate, let alone interact. Finally, the spatial scale of the study can also play an important role. One common approach in inferring group-to-group social structure will be to test whether there are preferences among groups in who they associate with (e.g., Bejder et al., 1998). However, frequent association between certain groups may reflect spatial overlap rather than true social preference, while lack of association could simply result from non-overlapping home ranges. Thus, disentangling spatial constraints from genuine social preferences or avoidance is necessary to interpret patterns of intergroup interaction and assess whether groups form part of the same social unit. Decisions about data collection therefore need to carefully consider how they might impact the broader-level social structure that is being inferred.

These examples highlight some potential pitfalls that can be encountered when studying MLSs. Avoiding them usually requires taking some additional steps, namely asking about whether the drivers that give rise to the observed social patterns are consistent with an MLS. This brings us back to our definition of MLS, and in particular highlights the importance of being explicit about how structure emerges as opposed to defining MLSs based on only aggregate patterns.

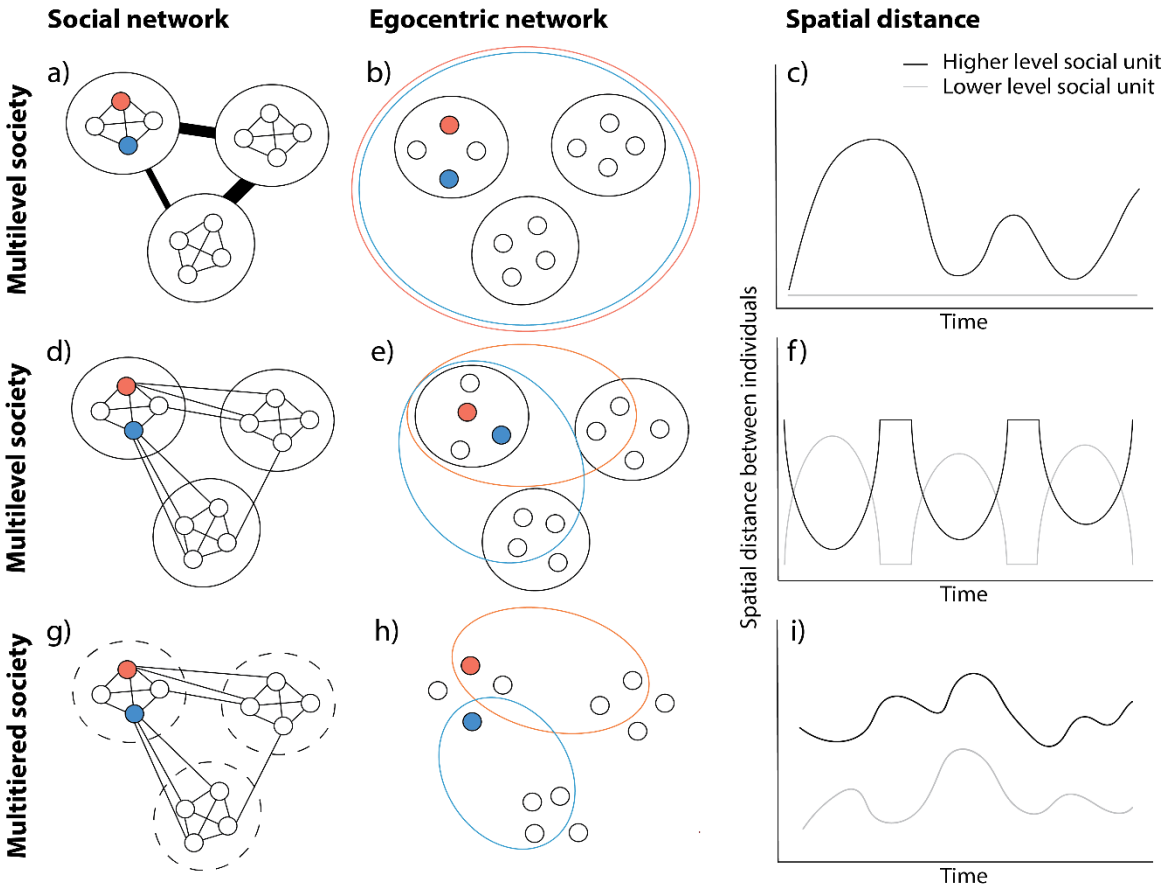

Figure 1. Multilevel and multitiered societies. The first column shows a toy social network; the second column shows egocentric networks, that is, centered on individuals (here, red and blue), highlighting their social ties with the rest of the population; the third column shows a toy graph of spatial distance between individuals over time. In the third column, the black line represents spatial distance between individuals within the same lower-level social unit, while the gray line represents distance between individuals within the same higher-level social unit. Panels **a–c** describe a multilevel society in which stable core social units merge to form higher level social units, as observed in hamadryas and Guinea baboons, superb fairy-wrens, and snub-nosed monkeys. In panel **c**, spatial distance over time between individuals within the same core unit remains nearly constant, whereas distance between individuals from different core units within the same higher-level unit fluctuates. Panels **d–f** show a different kind of multilevel society, where higher-level social structure emerges only when analyzing patterns of association between individuals in different core units. This pattern is typical of human hunter-gatherers, where individuals from different households (core units) associate during the day. However, the core unit remains spatially and socially stable at night, as reflected in panel **f**, when all household members return to sleep in the same location. Finally, panels **g–i** illustrate a multitiered society, which may superficially resemble multilevel social systems like that in panels **d–f**, but lack any consistent temporal or spatial stability at the level of the core unit. The apparent core unit is not a cohesive social entity. In panel **h**, for example, individuals such as red and blue appear to be part of the same core unit, but their strongest social ties do not overlap, indicating that the core unit is only apparent, not real.,

How to test hypotheses about function, costs, and/or benefits

Much remains unclear about the evolution of multilevel societies, the benefits they provide, and the functions of the higher social units. Research on MLSs has primarily focused on characterizing the multilevel sociality of different species, but fewer studies have investigated the specific functions of the higher social levels (Camerlenghi & Papageorgiou 2025). Gaining a deeper understanding of the function of MLSs will often require experimental approaches. Historically, the literature on MLS has been dominated by studies of large mammalian species (Grueter et al., 2017; Grueter et al., 2020), where manipulative experiments are scarce due to ethical and logistical challenges. Instead, most studies have relied on correlational designs, or comparisons between populations (Grueter et al., 2012). One of the few manipulative studies conducted in this context was by Kummer (1968), who translocated female individuals and entire one-male units (OMUs) across bands in hamadryas baboons to investigate the role of familiarity in troop dynamics. He discovered that social familiarity—particularly between females and their associated males—plays a crucial role in maintaining group cohesion and stability in hamadryas baboon troops. These experiments were crucial for establishing a baseline understanding of the social basis of MLSs (though it is important to note that such manipulations would raise ethical and conservation concerns and would not be permitted in wild vertebrates today).

A recent study in Guinea baboons tested the intuitive notion that an MLS proves advantageous, as it provides greater flexibility in responding to variation in environmental conditions. Specifically, that study tested whether Guinea baboon parties would decrease their spatial distance when predators were detected in the baboons' habitat and increase their spacing when food availability was low. Somewhat surprisingly, neither prediction was met, as parties generally remained in close proximity regardless of predator presence or food availability, despite pronounced variation in these ecological factors throughout the year (Ohrndorf et al., 2025). Similarly, another study found that proximity between sleeping sites of Guinea baboon parties likely was not driven by food availability, predator or parasite avoidance, but rather reflected

opportunistic use of abundantly available sites, with parties sleeping closest to other parties they associate most with during the day, indicating social preference as an important driver (Ohrndorf et al., in press). These patterns may reflect high local resource availability, which reduces competition between parties and associated costs, and allows close association year-round, highlighting how the costs, benefits, and expression of MLSs can vary with ecological context.

An advantage of the expanded breadth of systems with multilevel societies will be the facilitation of experimental approaches. For example, manipulation of the resource environment on polydomous wood ant (*Formica lugubris*) showed that ant colony networks fragment into smaller components and begin foraging on previously unused food sources (Burns et al., 2021) with a long-term decreased network efficiency (Piross et al., 2025). Playback experiments on the core social units of superb fairy-wrens revealed that higher-level social units promote cooperative behaviour among core social units, as individuals responded to distress calls from other groups by approaching a predator model, thereby potentially improving survival (Camerlenghi et al., 2023, 2024). A recent field experiment with GPS-tagged vulturine guineafowl showed that communal sleeping sites—context in which higher-level social units are expressed—can act as information centers (Papageorgiou et al., 2024). Social units of vulturine guineafowl could learn about the location of novel, experimentally introduced, food sources if they roosted with other units that had already discovered the novel food patch. These recent studies highlight that field experiments should be conducted when possible as they remain one of the most direct and effective ways to understand the adaptive value and the function of higher-level social units within MLSs.

Another useful way to explore the drivers of multilevel sociality is through in silico experiments. For example, agent-based models grounded in empirical data have shown that the higher-level social level in sperm whales—vocal clans, in which social units share acoustic repertoire of communication signals called codas—most likely emerges from biased social learning, as individuals preferentially adopt the codas of their associates (Cantor et al., 2015). Such a simulated experiment then provides support to the hypothesis that socially mediated transmission,

rather than stochastic processes such as genetic or cultural drift, drives the emergence of MLS in a system that is otherwise inaccessible to field experimentation due to the animals' long lifespans, wide-ranging movements, and remote pelagic habitat. Similar computer simulations have lent support to another hypothesis that even simple partner-choice rules, such as continuing to forage with the same partner after a successful attempt, can give rise to one of the building blocks of multilevel structure—stable, long-lasting community structures that persist through demographic changes and become kin-structured over time (Cantor & Farine 2018). A recent modelling study demonstrates that intergroup tolerance and aggregation among mixed-sex social groups can emerge when resource patchiness drives home range expansion and the threat of bachelor males (Grueter in prep). Simulated animal groups expanded their home ranges in response to increasing resource heterogeneity but aggregated when exposed to bachelor males that move independently across the landscape. Intergroup tolerance emerges dynamically through repeated spatial overlap, with encounter histories captured in a familiarity matrix that weights tolerance over time. This new model suggests that resource heterogeneity promotes tolerance by increasing spatial overlap and intergroup familiarity, while bachelor threat drives aggregation; when both pressures are high, groups aggregate frequently and maintain high familiarity-based tolerance (Grueter in prep). Together, these studies show how in silico experiments are a powerful tool to investigate the underlying drivers of higher social units in MLSs.

Finally, comparative and phylogenetically informed analyses—both across populations of the same species and across species—are essential for investigating the evolution of MLSs and their consequences. For example, several species of wood ants show within-species variation, spanning the full range from monodomous to highly polydomous (Ellis & Robinson 2014), offering an opportunity to examine how ecological and social factors drive transitions in social systems. Within primates, a recent phylogenetic study on Asian colobines found that (genomic) adaptations to ancient climatic events, such as the late Miocene cooling and Pleistocene glaciations, likely played a key role in the emergence of MLSs in this group (Qi et al., 2023). However, a challenge for

comparative analyses is that MLSs remain largely under detected outside of mammals, often due to the lack of social network analyses or long-term behavioural data. In birds, for instance, detailed data on social behaviour during the non-breeding season are often lacking (Farine 2025). Nevertheless, valuable anecdotal or descriptive records on non-breeding social structure can often be found in specialist journals or in handbooks. For example, a systematic search on Australian and New Zealand bird species to assess potential evidence for MLSs (Camerlenghi et al., 2022), combining either species common or scientific names with keywords ("social," "winter," "aggregation," or "congregation") revealed that species with cooperative breeding strategies are more likely to exhibit traits consistent with MLSs. Beyond identifying the presence of MLSs, comparative analyses can also shed light on their potential consequences. For example, among 104 primate species, those with greater home range overlap tend to have larger brain sizes (Grueter (2015), suggesting that living in MLSs may select for enhanced cognitive capacities. Additionally, primate species living in MLSs exhibit more pronounced ornamentation dimorphism, indicative of intensified sexual selection (Grueter et al., 2015b). Taken together, field manipulation, in silico experiments, and comparative analyses provide complementary avenues for exploring the adaptive significance, evolutionary origins, and broader consequences of living in multilevel societies.

The way forward

Many open questions remain about multilevel societies. Some are fundamental, such as how widely distributed these societies are across taxa, and whether some taxonomic groups are constrained from expressing such a social system, or whether certain ecological contexts strongly select against it. Many of the questions outlined in Grueter et al., (2020) remain largely unresolved. Expanding the breadth of systems, better understanding the processes underlying their structure, and determining their function will open the door to address a broader range of questions about MLSs. Here we outline some new questions and tractable research directions for studies on MLSs.

- Does the occurrence of MLSs vary across environmental and seasonal gradients? If so, how?
- What is the relationship between MLSs and life-history strategies?
- How does space use — including movement patterns, resource distribution, and spatial fidelity — shape the structure and dynamics of MLSs?
- In what ways do habitat loss and degradation disrupt the social connectivity and long-term stability of MLSs?
- Do MLSs provide distinct costs and/or benefits to individuals in terms of acquiring information about the environment?

The study of multilevel societies has opened an exciting avenue of research, as seen by the recent wealth of studies across a broad range of taxa. Our synthesis brings clarity to the definition of MLSs and therefore promotes a deeper understanding of these social organizations to start making effective comparisons to societies with similar structural properties. Do these have similar drivers, are the mechanisms giving rise to their structure similar, why do some species maintain stable social units, but others do not? These comparisons will be critical for addressing open questions about MLSs and, more broadly, the evolution of animal societies.

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