Multilevel societies: different tasks at different social levels

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Keywords: Multilevel sociality, partner choice, animal societies, social complexity, task performance, cooperative relationships

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Summary

Multilevel vertebrate societies, characterised by nested social units, allow individuals to perform a wide range of tasks in cooperation with others beyond their core social unit. In these societies, individuals can selectively interact with specific partners from higher social levels to cooperatively perform distinct tasks. Alternatively, social units of the same level can merge to form higher-level associations, enabling individuals to benefit from large social units without always maintaining a large core social unit. The reasons why multilevel sociality evolves in some systems but not in others are not well understood. We propose that this is partly due to a lack of data, especially regarding the fitness consequences of cooperation at different social levels. First, we argue that in multilevel societies individual fitness benefits should increase when performing tasks in cooperation with associates from higher social levels. Secondly, as more multilevel societies are documented across taxa, we will continue to find similar cooperative tasks performed at different social levels. By providing compelling species examples, from dolphins to fairy-wrens, we underscore that despite the diversity of multilevel social organisation, convergence in task performance across social levels will become clearer with more data. Finally, we highlight the role of multilevel sociality in buffering fluctuating environmental conditions by enabling flexible social associations to emerge according to need.

Main Text

Introduction

Multilevel sociality describes social systems that consist of groups (herein social units) which can merge in a predictable way and form distinct higher social levels, exhibiting thus fission-fusion dynamics along the boundaries of social units as per Grueter et al. [1]. The composition and size of social units in a multilevel social system must remain stable over time within at least two social levels [1–3], although different levels of social organisation may differ in their cohesion and the stability of their membership over time [3]. The formation of distinct social levels may be driven either by active social preferences (e.g., as shaped by age, sex, genetic relatedness, or by associating with individuals with similar phenotypes) or by non-social phenomena [1,3], such as the attraction of multiple social units of the same level to the same food resources and habitat geometry [4,5]. Being composed of nested social units, multilevel societies can offer individuals the benefits of fission-fusion dynamics, such as reduced competition and increased information transmission [6], by allowing some of the social levels to remain stable and cohesive when interacting at higher-levels of social organisation. These benefits mainly derive from having the flexibility to decide with whom to associate in response to changing social and ecological pressures [7,8], whilst still benefiting from strong long-term social bonds within the core social unit and weaker long-term social bonds between individuals that are members of the same higher-level unit.

Classically, the capacity to form multilevel societies was thought to be exclusive to large-brained mammals, as navigating preferential and differential dyadic relationships with conspecifics is cognitively demanding [9], both within and across levels of social organisation. However, recent research on social systems of some birds and fish has provided evidence that smaller-brained species may also form multi-level societies offering potentially valuable insights into the evolution of these societies [1,10–13]. The majority of the studies on multilevel sociality, either on large brained mammals or beyond, have so far focused on describing the social organisation [14] and the delineation of the distinct social levels (see for example [15]), rather than on the tasks that are achieved by individuals participating in them—following Loftus et al. [16], we define tasks as "any behaviour that positively affects the fitness of conspecifics within a social group by providing a good or service to those conspecifics". By looking beyond social organisation, we expand the idea that has already been proposed but not thoroughly explored yet [2,17] that comparing the distinct tasks that individuals perform at different social levels across species can shed light on the evolution of multilevel sociality.

Different tasks at different social levels

In several eusocial insect societies, members of a social unit (e.g. a nest or colony) share a common inclusive fitness interest in their social unit achieving a specific objective (such as successfully rearing a brood cohort). Reaching this objective requires completing a series of interconnected tasks, which often leads to emergence of division of labour between members. Splitting these component tasks between individuals can boost efficiency, by allowing individuals to become specialists – much like workers performing separate tasks on a factory floor. Ant superorganisms, which constitute a group of individual organisms that possess the fundamental characteristics of an organism itself, as per Kennedy et al. [18], offer the prime example: by maximising the colony's reproductive output, workers increase their inclusive fitness. This implies that they maximise the sum of both their own direct fitness, as well as their own indirect fitness, as measured by their individual effect on the fitness of others, weighted by genetic relatedness [18]. The ability to increase inclusive fitness through division of labour has allowed for extreme levels of behavioural and morphological specialisation to evolve (see physical soldier castes in [19]). Even in social units where inclusive fitness benefits are less aligned (such as cooperatively breeding vertebrates), some degree of behavioural specialisation can evolve: individuals can adopt different social roles (e.g. sentinels and babysitters in meerkats) in the course of their lifetime [20–22].

In contrast, individuals' interests in vertebrate multilevel societies are often in conflict. For example, a helper-at-the-nest foraging to provision its siblings (usually the lowest social level beyond the pair in avian multilevel societies) may be hostile or indifferent to the success of other nests as these often contain unrelated broods. Therefore, the success of a nest may not offer any, or only limited, opportunities to increase the inclusive fitness of individuals from neighbouring nests. When labour is divided it usually occurs within the lowest-level social unit of a multilevel society, in which there are often shared inclusive fitness benefits by completing tasks in cooperation (e.g., brood care for shared offspring or for offspring highly related to the helpers). However, despite a lack of indirect fitness benefits between individuals from different social units, situations may regularly occur when there is a synergistic increase in direct fitness benefits from cooperating on specific tasks across levels of social organisation. Multilevel sociality offers flexibility: it provides a wide and heterogeneous pool of potential partners, on different social levels, for completing specific tasks, such as obtaining information about resources or collectively defending against predation and intruders. When an individual's interests align with those of others from this pool of potential partners, cooperative social units can form to achieve a specific objective. Cooperation between individuals from different groups (see Figure 1A and bonobos [23]) or between entirely different groups (see Figure 1B and dolphins [24–26]) without immediate payoff (i.e mutualism) may thus be widespread in multilevel societies (see current debate on [23] and corresponding e-Letter by Connor et al. 2024).

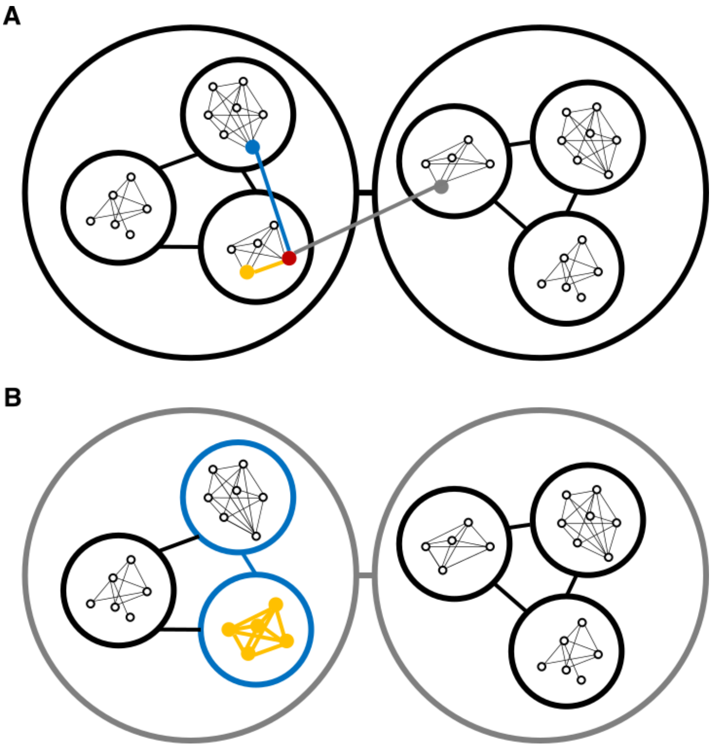

Figure 1. Individuals from multilevel societies perform different tasks when associating with individuals from different social levels. Here we present one multilevel society that exhibits three levels of social associations: individuals (small white nodes with black outline) associate preferentially with others from their own core social unit. Then, core social units (intermediate sized nodes) associate preferentially with each other and form higher level units (large nodes, termed as communities here), which also have contacts with other neighbouring communities. In panel (A) a focal individual (red) performs "Task A– yellow" only when associating with individuals from its own core social unit, "Task B– blue" when associating with individuals from its own community and "Task C– grey" when associating with individuals from neighbouring communities. In panel (B) we depict a slightly different scenario where all individuals from one core social unit or community merge together with another unit of the same social level and collectively perform tasks A, B or C.

In multilevel societies of vertebrates, individuals can perform a wide range of tasks in their daily routines but the tasks they perform may differ according to whom they interact with and which level of social organisation they share with their co-operators (see examples in Table 1). Different social levels may function as entities that collectively specialise on distinct tasks. Thus, individuals in multilevel societies may not need to specialise in completing tasks that can otherwise be taken care of collectively by one of the levels of social organisation. Preferences for cooperatively completing tasks at a social level may therefore allow individuals to gain fitness benefits which would otherwise be inaccessible. The potential benefits stemming from different levels of social organisation specialising in distinct tasks suggest two predictions:

Table 1. Examples from vertebrates that form multilevel societies and engage in tasks with individuals in different social units. Social units are termed as is in the original studies.

		Definition of social units and tasks performed within...			
Species	**Number of social levels**	**...social level 1:**	**...social level 2:**	**...social level 3:**	**... social level 4:**
Hunter-gatherer societies [17,27] (*Homo sapiens*)	3 or 4	Household: male-female complementarity and sex division of labour.	Cluster: social units formed by extended family. Assistance from kin and intergenerational division of labour.	Camp: cooperation with both related and unrelated individuals. Selection of foraging partners.	Between-camp visits. Information sharing and cultural innovations.
Hamadryas baboons [28,29] (*Papio hamadryas*)	4	OMU: one male unit which hosts multiple females. Breeding unit.	Clan: two-three OMUs led by kin males, observable during resource scarcity. Foraging as OMUs or Clans.	Band: multiple clans together, like troops in olive baboons. Communal sleeping, movement coordination, some affiliative interactions.	Troop: two bands sharing sleeping sites. Predator detection and defence, but no other group tasks.
Geladas [30] (*Theropithecus gelada*)	4	OMU: one male unit which hosts multiple females and potentially also a few follower males. Breeding unit. AMG: all-young-male units are an alternative first-level structure.	Team: aggregation of two or more first-level units that associate with each other at least 90% of the time. Tasks not specified.	Band: collection of first-level units that spend between 50% and 90% of their time together. Communal sleeping and foraging, not more specific tasks. Like band in Hamadryas baboons.	Community: the set of units with overlapping home ranges that are found together <50% of the time. Tasks not specified.
Guinea baboons [31–33] (*Papio papio*)	3	Reproductive unit: one male, one to several females, young, and many secondary males.	Party: three to five reproductive units. Foraging, socialising, collective movement.	Gang: several parties together. Predator detection and defence in communal sleeping sites.	
Snub-nosed monkeys [34,35] (*Rhinopithecus roxellana*)	3	OMU: one male unit which hosts multiple females. Breeding unit.	Band: social units formed by different OMUs. Males within bands likely defend females from bachelor males.	Troop: several bands together. Females disperse between troops to breed.	

African elephants [36,37] *(Loxodonta africana)*	up to 6	Breeding females with calves are listed as the first level. We kept the paper’s definition for the first level here, but we would not characterise mothers with calves as a distinct social level.	Family: small size compared to third and fourth levels. Not affected by seasonality. Raising offspring and coordinating movement.	Bond/kinship social units: affected by seasonality. Predator defence, territoriality, knowledge sharing and rearing of young.	Clans: broader compared to third but functional differences have not been identified.
Indo-Pacific bottlenose dolphins of Shark Bay [24–26] (*Tursiops aduncus*)	3	First order alliance: Duos or trios of males consorting females in a cooperative manner.	Second order alliance: Pool for forming first order alliances. Socializing and supporting second order allies to defend females. Stable membership.	Third order alliance: Individuals from two or more second order alliances come together and fight against intruders from neighbouring third order alliances.	
Pacific Sperm whales [38,39] (*Physeter macrocephalus*)	3 to multiple	Permanent social units: contain around 11 females and immatures from unrelated matrilines. Caring for offspring.	Temporary intermediate social units of multiple first-level units of the same cultural clan: defence from killer whales.	Clans: can contain up to 20.000 individuals. They have culturally determined vocalizations and distinct movement patterns.	There is a big difference in size from the second- to the third-level units and the literature suggests that intermediate levels might be missing.
Superb fairy-wren [10,11,40] (*Malurus cyaneus*)	3	Cooperatively breeding unit: individuals that assist a breeding pair to raise a brood of young.	Supergroup: two neighbouring breeding units that merge stably. Tasks not specified.	Community: emerge from repeated interactions between three to four breeding units and supergroups. Likely cooperative defence against predators, and communal male defence against competitors.	
Bell Miner [41,42] (*Manorina melanophrys)*	3	Cooperatively breeding unit: individuals that assist a breeding pair to raise a brood of young.	Coterie or Clan: occupying a discrete area within the colony. May contain one or more breeding pairs and nonbreeders. Members associate preferentially with each other, and helpers may assist more than a single pair within a coterie.	Colony: a geographically discrete aggregation of between 20 and 200 individuals that together inhabit and communally defend an area against avian intruders and predators.	

Vulturine guineafowl [15,43–46] (*Acryllium vulturinum*)	3	Cooperatively breeding units and stable clusters of males: breeding pairs can be stable from one breeding season to the next and raise young cooperatively with specific non-parents. Clusters of males (potentially highly related) remain stable across years.	Groups: can contain from 13 to 65 individuals that forage and decide collectively and move as single entities.	Stable between-group associations: driven by social preferences as well as by resource abundance and distribution. They share communal roosts and information. They also form supergroups and travel together to rarely visited areas.	
Cooperatively breeding cichlid fish [47–49] (*Neolamprologus pulcher)*	3	Cooperatively breeding group: individuals assist a breeding pair to raise a brood of young.	Colony: neighbouring breeding groups jointly defend against predators.	Aggregation: feeding assemblies of members from different breeding groups exchanging social information by sporadic interactions.	

First, performing tasks in cooperation with associates from higher levels of social organisation will increase fitness at the level of the individual: by exploiting the multilevel social organisation, an individual can achieve tasks more efficiently than would be possible were the multilevel social organisation to be eliminated. For example, vulturine guineafowl (*Acryllium vulturinum*) groups (i.e., core social units) merge, thus forming a higher level of social organisation, and explore largely unknown and unfamiliar areas [44]. Theory predicts that they have increased collective intelligence while navigating in the novel environment [50], but they should also be increasing their survival probabilities by being better at detecting predators [51]. In principle, this should be tested by comparing survival rates of individuals when navigating novel environments only with associates from their own core social unit, as opposed to with conspecifics from more core social units than just their own. In the cooperatively breeding cichlid fish *Neolamprologus pulcher*, which forms a multilevel society, breeding groups (i.e., the core social unit) exposed to a larger network of conspecifics in their colony (higher-level associations) have a higher reproductive outcome [47] and joint defence of neighbouring breeding groups saves effort of group members, which corresponds to increased efficiency at the colony level [48]. Further, it is worth examining the ability of lower-level social units isolated from the multilevel network to complete tasks typically carried out cooperatively with individuals from other social units. Such examinations could be done with observational studies or (where feasible) in field and lab manipulations (see cichlid fish examples below). Alternatively, comparing different populations of the same species that differ in whether they form multilevel societies could allow us to identify the social and ecological conditions under which multilevel societies evolve.

Second, as multilevel societies become increasingly documented [3,10], we will consistently find that tasks are being completed cooperatively across social units at different social levels. Despite the diversity of organisms that form multilevel societies and their independent evolutionary paths, there seems to be a functional convergence in that lower levels often provide reproductive opportunities and offspring care, sometimes in the context of cooperative breeding, and higher levels facilitate processes such as information transmission, defence against competitors and predator defence [11,47,48,52]. For example, despite their phylogenetic distance, species from different taxa, such as the colonial cichlid fish *Neolamprologus pulcher* [47], sperm whales (*Physeter macrocephalus*) [39], superb fairy-wrens (*Malurus cyaneus*) [11], and bell miners (*Manorina melanophrys*) [42], likely form higher-level social units to defend against predators and intruders. Additionally, in vulturine guineafowl [44] and African elephants (*Loxodonta africana*) [53], higher-level social units converge in providing individuals with the benefits of information transmission about resources, especially during harsh times. These are broad but not universal patterns, and exceptions can be found: for instance, hamadryas baboons (*Papio hamadryas*) [54], and snub-nosed monkeys (e.g., *Rhinopithecus roxellana*) [34,55] use intermediate or higher-level social units as pools for finding mating partners. Nonetheless, based on current knowledge (Table 1), individuals rarely breed or care for broods with other individuals from different lower-level social units with which they form a higher-level unit, but rather join them to exchange information or mob intruders and predators [56]. While evidence on the convergence of benefits provided by different levels of social organisation to individuals in multilevel societies is still scarce, as most multilevel societies have not been studied through the lenses of task performance at different levels, we expect that as more data accumulates, the pattern of the convergence of tasks will be becoming clearer.

Examples from multilevel societies

Within multilevel societies, units at different social levels have been shown to perform different tasks. Individuals may selectively interact with specific individuals from other social units and engage in diverse tasks with them (Figure 1A), or unite with all members of their own unit, at any social level, and interact collectively with entire other units of the same level to perform various tasks (Figure 1B). These scenarios are not mutually exclusive: it is likely to depend on the type of tasks and the social level involved. We further discuss the multilevel cooperation scenarios described in Figure 1 in the context of observed behaviours in wild populations of animals (such as those listed in Table 1). In doing so, we hope to illustrate the breadth of the taxonomic spectrum of multilevel societies. However, this is not an exhaustive review of all known species that form multilevel societies; instead, we draw on representative examples to demonstrate that units at different social levels perform different tasks in multilevel societies across a range of different taxa.

Indo-Pacific bottlenose dolphins

Male Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) in Shark Bay of Western Australia form three alliance levels [24–26]. The first level consists of pairs or trios of males, who consort oestrus females cooperatively and get mating opportunities with the consorted female. While consorting her, first order allies stay very close to each other for hours to weeks. The intermediate level (second-order alliance) is the core unit of male social organisation, where membership is stable across decades, but spatial cohesion is not always maintained, as second order allies constantly split and merge with each other [26]. Second-order alliances provide a pool of individuals from which males can form first-order alliances (similar as in Figure 1A). Individuals that are second-order allies socialise together and support each other when defending and stealing females from rival alliances. The third-order alliance consists of multiple second-order alliances that preferentially unite to defend females from theft attempts by rival males. Thus, in this system, males consort females together with their first order allies and help their second- and third-order allies steal and defend females from theft by other males, with cooperation occurring both within first and second-order alliances and between third-order allies (more like the synergies in Figure 1B).

Hamadryas baboons

The multilevel society of hamadryas baboons at the Awash National Park, in lowland Ethiopia, has four levels [28,29]. The first, known as One Male Unit (OMU) is the breeding unit and consists of several females and one male. Two to three OMUs led by kin males organise in 'clans' and forage together when resources are scarce. Multiple clans can form a 'band', and members from the same band coordinate movement. Multiple bands merge to form 'troops', the apex social level in the society, often share sleeping sites, and exhibit collective predator detection and defence but no other known social tasks. In each of the four social levels in this hamadryas baboons study system all individuals from two or more society units (e.g. OMUs) merge together, as in Figure 1B.

Humans

In multilevel societies of hunter-gatherers, across several cultures, the three social levels identified may correspond to three kinds of cooperative relationship: (1) male-female sex division of labour within households, (2) assistance from kin within clusters (i.e. extended family), which form the intermediate social unit, often through intergenerational division of labour and (3) selection of foraging partners within a camp, the upper level social unit [17]. Finally, frequent visits between camps allow individuals to share information beyond their specific camp, creating the potential for the emergence of cultural innovations [27,57]. These distinct cooperative relationships (similar to Figure 1A) might represent strategies to cope with three fundamental challenges of foraging groups in most human societies: (a) the differential risks and gains for women and men from engaging in different economic activities; (b) obtaining resources requires a pool of diverse skills, depending on age-related individual experience, within the core social unit, and (c) maximising foraging effectiveness and accessing reproductive opportunities often requires forming large social units [58,59].

Superb fairy-wrens

In superb fairy-wrens, a cooperatively breeding songbird native to South-East Australia, multilevel social organisation provides individuals with access to cooperative relationships that are expressed differentially across social levels [11]. At the lowest organisational level, superb fairy-wrens form breeding units that consist of a breeding pair and some helpers. During the non-breeding season (the harsher time of the year), breeding units can form both supergroups, which involve two breeding units, as well as stable higher level social units, termed as communities [10]. These communities facilitate cooperative relationships among different breeding unit members, when breeding units entirely merge (Figure 1B), including common defence against predators and communal defence against competitors [11]. This likely helps individuals buffer the effects of harsh environmental conditions during winter months, when individual mortality peaks [40,60].

Beyond mammal and avian societies

Although inter-group cooperation can have evolved across a range of social species, not many societies beyond mammals and birds have been discussed under the framework of multilevel sociality developed by Grueter et al. [1]. However, species such as the cooperatively breeding cichlid fish (*Neolamprologus pulcher*), fall well within this framework. In *Neolamprologus pulcher*, reproduction occurs at the lowest organisational level (the breeding unit), and predator defence involves synergies between multiple of these different breeding units. When such breeding units act together, as illustrated in Figure 1B, they are termed as colonies [47]. Similarly, in the congeneric *Neolamprologus savoryi*, where groups (the higher social units) are socially and genetically structured into subgroups, members of different subgroups collaborate to defend a larger territory [61,62]. In the Australian ant *Iridomyrmex purpureus*, individuals from the same colony are spread across several separate nests, which remain socially connected [63]. Despite typically showing fidelity to a single nest within the colony, in the face of predation risk individuals across different nests within the colony cooperate to collectively defend their colony [64]. In Neotropical paper wasps (*Polistes canadensis*), workers regularly move from their home colony to neighbouring colonies, which has invited comparisons with vertebrate multilevel societies. Here, the tasks are essentially the same regardless of partners: workers perform standard worker tasks at neighbouring colonies (potentially motivated by indirect fitness benefits of helping neighbouring kin) [65]. In all the above examples, except that of Neotropical paper wasps, individuals adopt different tasks when associating with partners from different social levels. Multilevel sociality, as well as the convergence of tasks at different levels of social organisation, can have evolved in different taxonomic groups that show inter-group cooperation [66], which may include fish, eusocial insects, and social shrimps. However, many animal societies still remain understudied, and often terminologies used to define social organisation are taxon-specific [67], making it challenging to discover multilevel societies beyond the well-studied large-brained mammals, and develop a multilevel sociality synthesis that captures the diversity of social animals.

Emergent properties in multilevel societies

In all the above cases, synergies between individuals across different social levels in the network may facilitate the completion of qualitatively different social tasks at distinct social levels. These synergies arise from interactions among lower social units or individuals [68] and often result in collective behaviours entirely absent at the individual level. Therefore, they could be considered a form of emergent property of social aggregations. However, this doesn't imply that synergies and their emergent properties resulting in qualitatively different tasks in a multilevel society are inevitable features of multilevel social organisation and should become part of its definition, as there could still be systems wherein these phenomena aren't expressed. Nonetheless, the concept of emergent properties might be an important tool for describing and exploring collective behaviour in multilevel societies, across a broad range of taxa.

Enlarging social unit size by avoiding associated costs when environmental conditions require it

Maintaining a large social unit size incurs costs and benefits that are traded off against each other, setting boundaries to social unit size [69–72]. Larger social units face decreased predation risk—see, for example, dilution effects [73] and the many-eyes hypothesis [51]—, higher collective intelligence allowing them to solve problems [50,74,75], and are less likely to go extinct as per classic group augmentation ideas [76]. At the same time, though, large social unit size is also accompanied by larger coordination challenges [71] and intragroup competition [77]. Additionally, large social unit size poses a greater risk of infectious disease [78], and is linked to higher inequality of division of labour among members of the same social unit [79]. Despite these costs, some animal societies invest resources to accommodate excess social unit members, potentially necessary under certain circumstances, as discussed in [80,81] following the concept of redundancy.

In contrast, multilevel societies, characterised by preferential fission-fusion dynamics among social units, facilitate flexible adjustments in social unit size in response to changing environmental conditions, social competition, and resource availability. For instance, in hamadryas baboons [28] and African elephants [37], intermediate social units may fragment into smaller units, mitigating competition during periods of resource scarcity. Conversely, in some species, core social units may coalesce during times of scarcity. This collective behaviour, observed in species such as vulturine guineafowl [44] and killer whales (*Orcinus orca*) [82], facilitates the performance of specific tasks as the need arises, offering, for example, safety against predators and enhancing information transmission regarding the location of vital resources. Territorial species that form multilevel societies, on the other hand, may exhibit increased intergroup tolerance during harsh conditions with limited resources, enabling individuals to exploit larger areas when resources within their territory are scarce [10]. In summary, within the context of multilevel societies, individuals within a social unit can derive benefits like those of large social unit size by forming preferential associations with specific individuals from other social units of the same or higher levels (Figure 1A), or by merging or cooperating with entire other social units when necessary to perform distinct tasks (Figure 1B).

Outstanding Questions

Much remains unclear about why and how multilevel societies have evolved, under what conditions there is convergence of tasks at different levels of social organisation across species and to what extent cooperating with individuals from different levels of social organisation increases individual fitness. Recent studies have shown that there is scope for detailed observation of multilevel interactions across a wider taxonomic breadth, extending beyond mammals [10,15,48]. Additionally, field or lab manipulations could quantify the decision-making and fitness consequences of social connections at different levels, but to achieve this, studies on multilevel sociality should move beyond characterising multilevel social organisation and rather explore the tasks performed at different levels. Finally, evolutionary modelling could shed light on the transition to a multilevel social organisation [66].

Questions regarding different tasks at different levels

- How common are multilevel societies, and are they all characterised by different tasks at different levels? In which cases is there no differentiation between levels on the tasks they perform?
- Are there fitness consequences of losing access to different levels of a multilevel society across species that form multilevel societies (see [25])?
- Is the early evolution of multilevel sociality driven by individuals choosing different partners for different tasks? Or do individuals tactically choose their partners only once they find themselves in a multilevel society that has largely arisen for other (passive) reasons? If the former, which tasks and which partnerships were decisive?
- Has division of labour evolved among different units of the same organisational level, where, for example, one first-level social unit specialises in one task and another first-level unit in another task, in any multilevel societies beyond humans?
- Does coordinated collective action among members of separate social units in a multilevel society qualify as genuine polyadic cooperation or do individuals simply show independent yet simultaneous defensive action in response to intruders or threats (see [48])?

Broader open questions on multilevel sociality

- Are the evolutionary trajectories to multilevel societies similar across taxa or idiosyncratic to each case?
- To what extent is life in an incipient multilevel society an adaptive choice or a burden for different individuals?
- How do power asymmetries shape multilevel societies? Does multilevel sociality increase scope for achieving private aims only for those with the social power to make or break social connections across levels?
- Are multilevel societies more resilient to environmental shocks compared to unilevel societies?
- Why is there interspecific variation in whether harsh environmental conditions drive social units to split or grow?
- Do individuals in structurally complex multi-level societies have knowledge of the social structure they are embedded within and is such knowledge useful across taxa that form multilevel societies?

Conclusions

Multiple of the presented examples and case studies support the idea that multilevel societies, through cooperative relationships across diverse social levels, enable individuals to accomplish distinct social tasks [1]. By providing individuals within a social unit access to a familiar social pool of potential partners beyond their core social unit, these societies efficiently address challenges related to group living, such as safety against predators, competitors, and information sharing, without incurring the cost of maintaining a large, potentially sub-optimal and stable social unit size. As a promising avenue for further exploration (see Outstanding Questions), we encourage the empirical investigation of two broad hypotheses: 1) task performance in cooperation with associates from higher levels of social organisation increases individual fitness and 2) as additional multilevel societies are documented across taxa, we expect to identify similar cooperative tasks being performed at each of the distinct social levels. By systematically mapping the individual benefits associated with different cooperative relationships across social levels in various taxa, we can gain crucial insights into the social complexity of multilevel societies and into what drives their emergence across the animal kingdom.

Acknowledgments

We are grateful to Patrick Kennedy for inspiring and critical discussions and further contributions while framing the first versions of this manuscript, as well as to Harry Suter, Stephanie L. King and Cyril C. Grueter for their insightful feedback. We also thank two reviewers, one anonymous and Arne Jungwirth and the editor, Michael Taborsky, for their valuable critiques while reviewing our manuscript. D.P. was awarded a Marie Skłodowska-Curie European Postdoctoral Fellowship, funded by UK Research and Innovation (UKRI) under the UK government's Horizon Europe funding guarantee [grant number EP/X021394/1]. E.C was awarded a career bridge doctorate-postdoc, funded by Bielefeld Young Researchers Fund (BYRF), from Bielefeld University.

Ethics

Not applicable as this is an opinion piece that doesn't involve new empirical studies.

Data Accessibility

Not applicable as this opinion piece doesn't include new data.

Authors' Contributions

D.P. conceived the initial ideas of the study. Both authors worked on developing these ideas and contributed equally to writing and revising the manuscript.

Competing Interests

We have no competing interests.

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