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## Multilevel Organisation of Animal Sociality

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# 1 **Multilevel organisation of animal sociality**

2

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51

52 **Abstract**

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

63

64 **Keywords:** multilevel society; social complexity; socioecology

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## 74 ***Multilevel sociality in nature***

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

83 MLSs are best known from primates but have recently been reported in a range of animals  
84 [2-7]. Here we synthesise current knowledge on MLSs, critically evaluate their causes and  
85 consequences, and offer prospects for future research. We build from socioecological  
86 principles emphasizing ecological—resource distribution, predation threat—and social—kin  
87 selection, sexual conflict—factors in organising individuals and relationships in space and  
88 time [1]. We focus on Mammalia given the predominance of MLSs in this class. As this very  
89 system also characterises our own species, mapping the causes and consequences of MLSs  
90 provides a valuable reference point for tracing human social evolution.

91

## 92 ***Defining multilevel societies***

93 MLSs are social systems characterised by nested social entities comprising a minimum of  
94 two discernible, consistent levels of social integration between the individual and the  
95 population (Fig. 1). The terms describing these nested social levels are inconsistent across  
96 species, thus, to facilitate comparison, we propose a standardized terminology: *core units*  
97 and *upper levels* for these two mandatory levels, and *intermediate levels* and *apex levels* for  
98 the facultative levels described below (Table 1).

99 In non-human primates, the primary entities of MLSs are usually small *core units* comprising  
100 one reproductive male and multiple females—called one-male units or OMUs [8]. In other  
101 mammals there is greater variability: in African elephants (*Loxodonta africana*) and sperm  
102 whales (*Physeter macrocephalus*), core units comprise closely associated breeding females

103 and their calves, with occasional male visitors [9, 10]. Core units are usually highly cohesive  
104 and stable: individuals show strong fidelity to their units, and socio-positive interactions are  
105 far more frequent within than between units [2, 11]. In terrestrial MLSs, core units are  
106 usually spatially discrete, defined by spatial and social proximity among members [12].  
107 Closely associated core units may form a secondary, less consistent level of organization  
108 with various names [11, 13, 14], herein called an *intermediate level*.

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

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

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

130 Shared space use can set the stage for the emergence of MLSs [3, 23, 24]. However,  
131 **aggregations** of social units without active social preferences—e.g. attracted to the same  
132 localised resource or co-occurring due to constraints of habitat structure—cannot be

133 considered MLSs, nor can social units that occasionally encounter and mingle non-  
134 agonistically [25] be MLSs, because these encounters are infrequent and transient.

135 The term 'multilevel society' is sometimes used interchangeably with '**fission-fusion**,' but  
136 this is a conceptual error. Fission-fusion is not a type of social system, but instead describes  
137 how social units cleave and coalesce over time to form subunits with variable size and  
138 composition [26]. Fission-fusion dynamics unfold over various time scales, from hours to  
139 months, and are generally found in MLSs [10, 12, 17] as well as in uni-level societies [27]. In  
140 non-MLSs, fission-fusion is individualistic and subunits vary widely in composition  
141 (*atomistic*), whereas in MLSs fission-fusion usually happen along the boundaries of the core  
142 units or intermediate levels without compromising the integrity of those units (*molecular*)  
143 [8, 28].

144

#### 145 ***Taxonomic distribution***

146 MLSs are relatively uncommon and patchily distributed on the mammal phylogenetic tree  
147 (Fig. 2). First described for hamadryas baboons in the pioneering study by Hans Kummer in  
148 the 1960s [17], they have subsequently been documented in other primates (papionins,  
149 colobines, humans), cetaceans, elephants, and equids [2, 10, 13, 29-31] (for a full list see Fig.  
150 2). Some taxa show MLSs in only some ecological contexts (e.g. [2, 32]). Bottlenose dolphins  
151 (*Tursiops* sp.), for example, are generally characterized by atomistic fission-fusion dynamics  
152 [33]. Some populations, however, exhibit **multilevel alliances** among males embedded into  
153 an open fission-fusion network, with up to three levels of social integration between the  
154 individual and the population. In Shark Bay, males form stable 2nd-order alliances of 6-14  
155 adult males. Nested within these 2nd-order alliances, two to three males form 1st-order  
156 alliances with varying composition for the purpose of coercing females in reproductive  
157 condition. To this end, Shark Bay dolphins deviate from our MLS definition in that the highly  
158 cohesive and stable units in Shark Bay dolphins occur on a higher level. Second-order  
159 alliance members may cooperate in attacking, or defending against, other 2nd-order  
160 alliances, sometimes even cooperating on a third level [34].

161 MLSs have been proposed for other mammal species, but some were based on vague  
162 definitions. For example, reticulated giraffe (*Giraffa camelopardalis*) are found in social

163 cliques embedded in larger subcommunities and communities and show partner  
164 preferences; however, the composition of core units (cliques) is highly variable [3].  
165 Observations of members of different social units of western gorillas (*Gorilla gorilla gorilla*)  
166 interacting non-aggressively and co-visiting forest clearings have been used as evidence for  
167 MLSs [7, 35], but whether associations are durable across contexts remains poorly known.

168

### 169 ***Social dynamics within multilevel societies***

170 The proximate mechanisms underlying MLSs can vary widely. Geladas and hamadryas  
171 baboons, for example, differ considerably in their micro-level **social structure**. In geladas,  
172 core units are shaped by kin bonds among closely related females [36] whereas in  
173 hamadryas baboons the pair bonds between a leader male and his females underpins core  
174 unit stability, with male-male bonds linking the higher social levels [17, 37]. Females are  
175 philopatric in geladas, whereas males are philopatric in hamadryas [11, 36, 38]. Guinea  
176 baboon MLSs are similar to those of hamadryas and geladas, but differ from hamadryas in  
177 the greater social freedom of females, and from geladas in the presence of male-male bonds  
178 across units [39].

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

184

### 185 ***Evolution, maintenance and adaptive functionality***

186

187 The evolutionary pathways leading to the emergence of MLS across mammalian taxa are  
188 variable. In hamadryas baboons, for example, phylogenetic reconstructions suggest that  
189 ancestral multimale-multifemale groups fractionated into OMUs with stable breeding  
190 bonds. Increased group sizes due to localised resources or greater predator pressure in  
191 open habitats may have elevated feeding competition, aggression, and harassment by  
192 unfamiliar individuals. To mitigate these costs, individuals would have formed subgroups,

193 with females tightening their relationships with a single male capable of protecting them [8,  
194 42]. In colobine monkeys, by contrast, MLSs likely evolved via a merger of ancestrally  
195 autonomous OMUs [8], with persistent threat from potentially infanticidal bachelor males  
196 as a formative factor. Through communal defence or the safety-in-numbers effect, leader  
197 males could have collectively reduced bachelor threat, thereby prolonging their tenure and  
198 attenuating the risk of infanticide [23].

199 MLS maintenance requires a unifying social network spanning the boundaries of social units,  
200 and kinship has likely played a major role in shaping such networks. In hamadryas baboons,  
201 these links are provided by male-male social and kin relationships, evident at the clan level  
202 [14, 16, 38]. Similarly, strongly-bonded Guinea baboon males are more likely to be related,  
203 although kinship is not a prerequisite (Table 1) [43]. Another unifying force may be  
204 limitations on female dispersal to within the confines of the highest social levels, which may  
205 increase relatedness among females and strengthen tolerance among core units. This may  
206 explain occasional affiliative exchanges between females across units, as among snub-nosed  
207 monkeys [18] and hamadryas baboons [19]. Multi-year field studies suggest that kin  
208 selection among females can be an organising principle of MLSs. Female kinship predicts  
209 associations between gelada core units [36], and hamadryas females within core units are  
210 more closely related than expected despite being coercively transferred by males [44].  
211 Similarly, aggregation of plains zebra family groups to reduce sexual harassment is driven by  
212 females, not males, and female half-siblings usually reside together [45]. Relatedness also  
213 predicts association between core units of African elephants [46], though it may be less  
214 instrumental in shaping social bonds within higher levels. In sperm whales, kinship  
215 influences social organisation within nearly-matrilineal social units, but associations  
216 between units are not strictly kin-based [47]. Future research on how kinship links core units  
217 in MLSs will elucidate both the maintenance and the evolutionary origins of these systems,  
218 with implications for the evolution of our own [42, 48].

219 In contrast to uni-level societies with one single optimal grouping size, in MLSs different  
220 functions can be optimised at different levels. Given that additional levels of sociality above  
221 the core unit can afford adaptive possibilities that core structures in isolation cannot,  
222 members of MLSs are well equipped to balance the costs and benefits of group-living [49].  
223 Hamadryas baboons illustrate how each social level makes possible different types of



224 collective interests shared among individuals: the core unit offers access to reproductive  
225 partners, the clan is a substrate for the maintenance of male-male relationships, the band  
226 serves an anti-predator and resource-defence function, and the troop optimises predator  
227 protection at sleeping sites while providing opportunities for gene flow via female takeovers  
228 [14, 17]. Reduction of predation through dilution or communal defence is likely a key driver  
229 of higher levels in many MLSs ([2, 50]; but see [23]). In zebras and some snub-nosed  
230 monkeys, males in OMUs that are part of a band, compared to those not in a band, are  
231 better able to prevent intrusions of coordinated bachelor males vying for reproductive  
232 opportunities [20, 29]. In African elephants, the highest ‘level’ may be an epiphenomenon  
233 or a by-product of individual predispositions to socially interact [10]; in contrast, for marine  
234 mammals—whose social lives depend on acoustic communication—the highest social level  
235 can provide the coarse-grained information needed to distinguish between familiar and  
236 unfamiliar conspecifics (Box 2). While atomistic fission-fusion dynamics provide an  
237 alternative means of flexibly responding to socioecological pressures [26], MLSs allow  
238 maintenance of core units, providing a greater consistency in social relationships and  
239 cleavage points.

240

#### 241 ***Consequences of living in multilevel societies***

242 MLSs bring new challenges and opportunities and may have follow-on effects in a variety of  
243 domains including male-male competition, intersexual conflict, and cognitive abilities. First,  
244 while male-male tolerance appears in many—but not all—MLSs, this does not preclude  
245 male-male competition. Mating competition in MLSs occurs in a context of close proximity  
246 among reproductive units and between reproductive units and bachelor males within the  
247 larger society. This crowded, competitive environment can also be fertile ground for the  
248 evolution of signals of male quality and physical prowess. For example, Asian colobine  
249 species with MLSs exhibit greater sexual dimorphism in body mass (a key indicator of male-  
250 male competition) than those without MLSs [51]. A comparative analysis among primates,  
251 controlled for phylogeny and group size, revealed that sexually dimorphic ornaments are  
252 also most pronounced in MLSs compared to other societies [52]. Such ostentatious traits  
253 include the mantles of hamadryas and Guinea baboons, red chest patches of geladas,  
254 extended noses of proboscis monkeys, and red lips of black-and-white snub-nosed monkeys

255 (Fig. 2f). These traits likely allow males to quickly, reliably and remotely assess the fighting  
256 ability of competitors, while females can gauge the quality of potential mates. Such  
257 ornaments are adaptive when individuals are confronted with a high density of competitors  
258 and surrounded by unfamiliar conspecifics [52, 53].

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

270 The cognitive consequences of MLSs have received attention in few taxa despite the  
271 possibility of considerable cognitive capital in these systems due to the presumed necessity  
272 of managing relationships across a complex social landscape (*sensu* [57]). It remains  
273 premature, however, to view MLS as more cognitively taxing than other social systems,  
274 particularly compared to uni-level societies with atomistic fission-fusion [26]. In taxa in  
275 which higher levels have a clear social function and require cultivation via affiliative means  
276 (e.g. multi-level alliance networks of bottlenose dolphins), selection for social intelligence is  
277 expected [58]. On the other hand, the concentration of social interactions within small core  
278 units rather than the wider social sphere may have reduced selection for across-the-board  
279 social cognition and correspondingly reduced the cognitive load of individuals [59-61].  
280 Evidence of this derives from the presence of MLSs in vulturine guineafowls (*Acryllium*  
281 *vulturinum*), a relatively small-brained bird [62]. The omnipresence of morphological  
282 indicators of individual viability in primate MLSs [52], as noted above, as well as behavioural  
283 indicators of social levels in cetacean MLSs [63], further suggest a limited need for  
284 cognitively-demanding abilities. Using group-level relationships to manage interactions (e.g.  
285 treating all members of the same level as mutually substitutable to some extent) and relying

286 on shared markers to identify social units may release the cognitive challenges of managing  
287 tens or hundreds of individual relationships.

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

305

### 306 ***Concluding remarks and Future perspectives***

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

311 First, the partitioning of the physical landscape among higher levels of MLSs remains poorly  
312 understood. In particular, whether and how members of different social levels coordinate  
313 their movements, how dispersal opportunities emerge, and how shared spatial preferences  
314 (e.g. for sleeping sites) differ from social preferences in producing higher social levels  
315 warrant further study. Technologies to collect high-resolution movement, inter-individual

316 proximity, and social association data [62, 72, 73] can help detect interactions among social  
317 units and tease apart the relative effects of the physical and social environments [74].  
318 Additionally, developing empirically grounded and spatially-explicit agent-based models can  
319 shed light on the interplay between collective decision-making, movement and social  
320 interactions that may underlie the upper and apex social levels.

321 Second, in addition to group coordination [75], the long-standing question of whether the  
322 typical structural complexity of MLS necessitates or promotes higher cognitive abilities  
323 deserves further attention. This would also contribute to elucidating the causal links  
324 between cognition, social complexity, and communicative complexity [64]. Just because a  
325 MLS looks complex from the outside does not mean that it is perceived as such from the  
326 inside unless so demonstrated [76]. Comparing the allocation of social attention and  
327 inferential reasoning capacities in closely related species that differ in social organisation  
328 would be particularly revealing. So far most of the species living in MLSs are large-brained  
329 mammals; should MLSs turn out to be more widespread in other groups (e.g. [62]), then this  
330 could be evidence that elaborate encephalisation is not a prerequisite for the evolution of  
331 MLS.

332 Third, we currently lack an understanding of how social transmission differs between MLSs  
333 and uni-level societies. Theoretical and empirical work has shown that the way social  
334 interactions are structured within a single social level can foster or constrain the spread of  
335 socially transmitted information and pathogens [77, 78]. Whether core groups in MLSs act  
336 as transmission bottlenecks has been virtually unexplored, but could be quantified through  
337 experiments whereby problem-solving techniques are seeded in core units and the diffusion  
338 (or lack thereof) across unit boundaries is monitored. Similarly, while MLSs can structure the  
339 gastrointestinal microbiota [79] that play a role in health and immunity, little is known  
340 about how microbiota are transmitted across social levels. Individual microbiome signatures  
341 may be obscured by living in a large MLS (as a result of co-habitation of reproductive units  
342 and synchronised between-unit behaviour); alternatively, MLSs may crystallise distinct  
343 microbiome signatures between units [80]. The dynamics of other physiological states, such  
344 as physiological stress, within MLSs also remains an untapped area of research. While stress  
345 influences individual behaviour and performance, it is unknown whether belonging to a MLS

346 buffers animals from stressors or further exposes them to indirect stressors emanating from  
347 this wider social environment.

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

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

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

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***Box 1: How to identify levels in animal societies***

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Detecting social levels requires combining qualitative and quantitative methods with high-

399

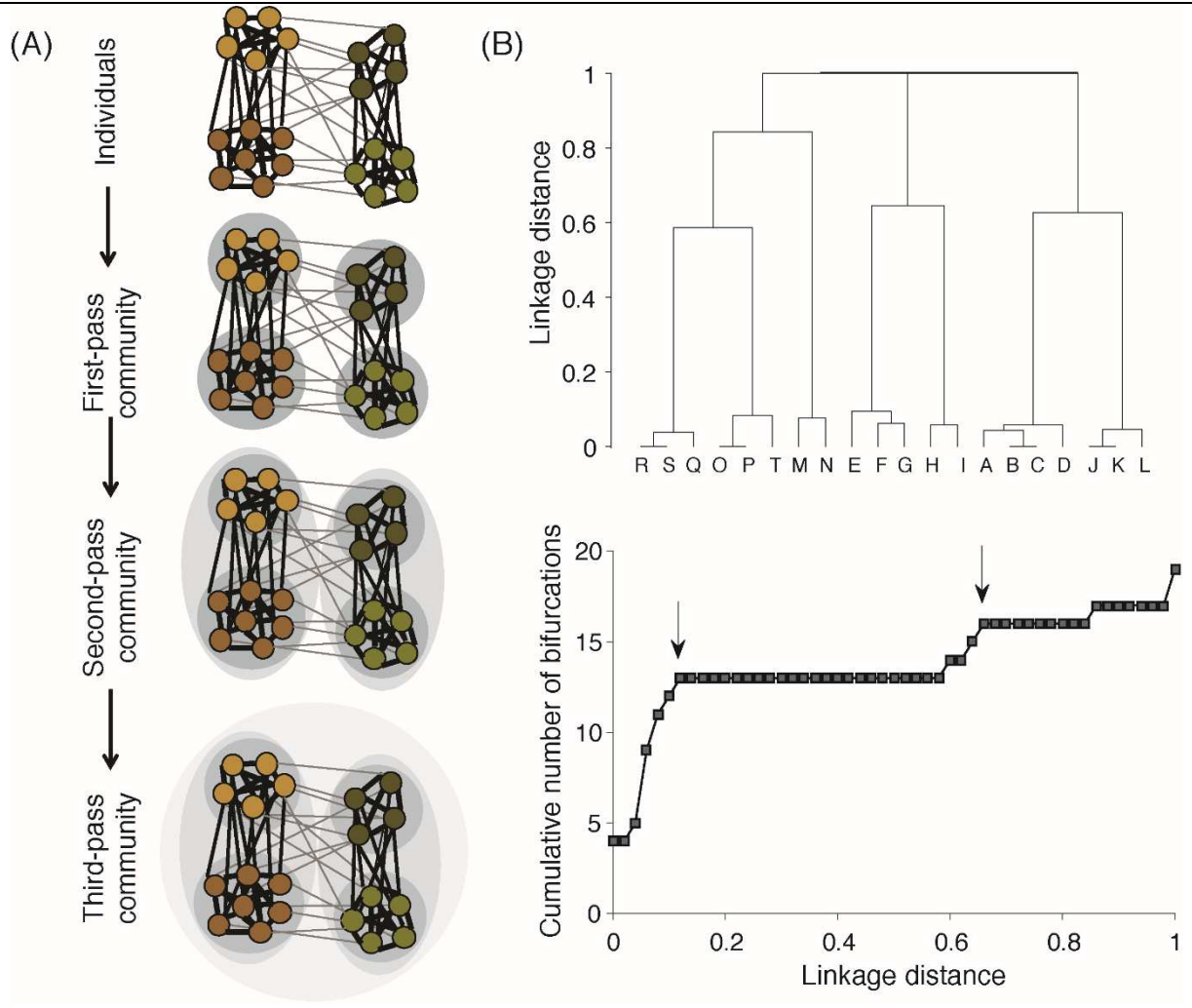
quality empirical data from long-term studies. Researchers often apply clustering methods

400 to direct observations of social data: interaction rates [14] or frequency of associations of  
401 individuals in proximity [10, 13, 72] or temporally clumped [12, 81]. Popular methods  
402 include—but are not limited to—network modularity, data cloud geometry, and knot  
403 analysis.

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

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

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



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427 **Fig. I:** Delineating social levels. A) Louvain method. Individuals strongly connected amongst

428 themselves compose “first-pass communities” (core units); some are strongly connected to

429 one another and detected as “second-pass communities”, until the apex community. B)

430 Hierarchical clustering and knot analysis. Dendrogram in which linkage (here, 1-association

431 index) is depicted by a knot diagram showing the cumulative number of bifurcations

432 (arrows).

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**Box 2: Culture as a driver of social levels**

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

446 How can culture structure well-mixed populations into sympatric yet distinct groups [77]?

447 One route is the feedback between the tendency of similar individuals to associate and the  
448 subsequent opportunities to learn from them that promotes within-group behavioural  
449 homogeneity. This is leveraged when individuals are conformists or mark their group  
450 identity so social interactions occur preferentially among members. With increased  
451 behavioural similarity comes social cohesion—groups become tighter as members reinforce  
452 their social connections and shed ties with outsiders. This way, culture can—directly or  
453 indirectly—erect social barriers and delineate a distinct level in a society. Socio-cultural  
454 boundaries are prominent in human societies, but they can also structure non-human  
455 societies.

456 Several animal populations feature sympatric groups with distinct repertoires of socially-  
457 learned behaviours, especially foraging tactics and communication signals [86].

458 Communication is critical in social contexts, thus influential in demarcating social groups.

459 For social animals, learning communication signals correctly is essential to maintain group  
460 cohesion, reinforce bonds, and aid collective decision-making. Distinctive signals can be  
461 necessary to distinguish social levels, from addressing affiliates to identifying which groups  
462 one belongs to [63]. MLSs of toothed whales illustrate how learning communication signals  
463 can generate such culturally-driven social levels.

464 The MLSs of killer and sperm whales contain stable core units and fluid intermediate levels  
465 [2] but differ from terrestrial MLS by featuring upper levels (clans) delineated by socially-  
466 learned acoustic communication signals. The ‘pulsed call’ dialects of killer whale clans  
467 emerge from innovations and learning errors combined with a tendency to diverge from kin

468 [87]. The ‘coda’ dialects of sperm whale clans emerge from biased learning in which  
469 conformists learn the most common signals from similar individuals [88]. In both,  
470 boundaries around clans are unlikely products of stochastic processes alone—genetic or  
471 cultural drift—but instead result from social transmission of behaviour [87, 88], making  
472 culture a key ingredient of their MLSs. Finding analogous cultural processes shaping  
473 societies of species in completely different environments can help uncover parallels between  
474 human and non-human MLS [86].

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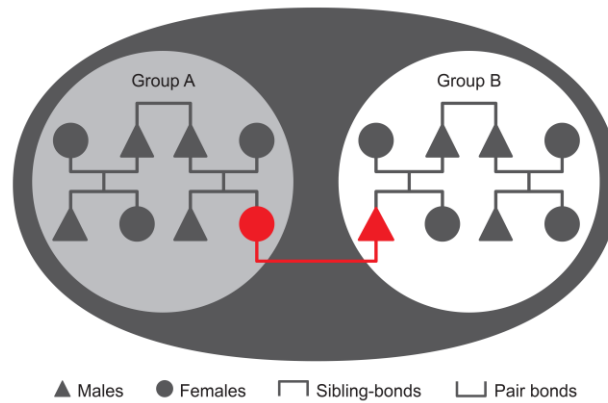
**Box 3: Multilevel societies in humans**

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

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

523 cultural and technological knowledge [99] thus underlie the remarkable success of human  
524 MLSs.

525 A phylogenetic model suggests that human MLSs evolved through a series of transitions  
526 from ancestral multimale-multifemale groups to multi-family groups to strongly bonded  
527 communities [89].



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529 **Fig. II.** Bilocality with exogamy of males and females and the evolution of human MLSs. The  
530 key unit of between-group alliances is a pair bond (red) linking the spouses' kin living in  
531 different groups (A, B) and connecting the two sets of in-laws (modified from [100]).

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544 **Table 1. Names and approximate sizes of the various levels in the MLS of a representative**  
545 **sample of mammals.**

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

546 OMU = one-male unit. Ranges are given where there is dramatic variation in level sizes.

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555 **Fig. 1. Multilevel society as a nested assemblage of at least two discernible social levels**  
556 **between individual and population.** Individuals represented by nodes are connected by  
557 links representing social interactions and/or relationships. The *core units* and *upper level* are  
558 the two mandatory social levels, while (one or more) *intermediate levels* and the *apex level*  
559 are facultative levels. *Core units* are more cohesive than the higher social levels, which vary  
560 in stability and cohesiveness.

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564 **Fig. 2. Distribution of multilevel societies (MLS) across the mammalian phylogenetic tree.**  
565 Phylogram based on [101] shows taxa with strong and likely evidence of MLSs, illustrated by  
566 African savanna elephants (*Loxodonta africana* [10]; photo: C. Schradin); Guinea baboons  
567 (*Papio papio* [43]; photo: J. Fischer); hamadryas baboons (*Papio hamadryas* [17]; photo: L.  
568 Swedell); geladas (*Theropithecus gelada* [13]; photo: T. Bergman); proboscis monkeys  
569 (*Nasalis larvatus* [102]; photo: I. Matsuda); black-and-white snub-nosed monkeys  
570 (*Rhinopithecus bieti* [12]; photo: C. C. Grueter); Rwenzori black-and-white colobus (*Colobus*  
571 *angolensis ruwenzorii* [6, 103]; photo: C. C. Grueter); plains zebras (*Equus quagga* [29];  
572 photo: D. Rubenstein); and sperm whales (*Physeter macrocephalus* [2]; photo: A. Cotton).  
573 **Additional taxa with MLS include long-finned pilot whales (*Globicephala melas*) [104], short-**  
574 **finned pilot whales (*Globicephala macrorhynchus*) [4], orca or killer whales (*Orcinus orca*)**  
575 **([105]; but see [106]), Asian elephants (*Elephas maximus*) [5], Gobi khulans (*Equus***  
576 ***hemionus*) [107], all other species of snub-nosed monkeys (*Rhinopithecus* spp.) [30], douc**  
577 **langurs (*Pygathrix* spp.) [108], and humans [31].** MLSs may also occur in uakaris (*Cacajao*  
578 spp.) [109] and drills (*Mandrillus leucophaeus*) [110] but our knowledge of the social  
579 organisation of these taxa in the wild is limited.

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584 **Glossary**

585 Aggregation: Temporary gathering of individuals and units that is usually the result of some  
586 nonsocial forcing factor, e.g. localised resources.

587 Fission-fusion (dynamics): Spatiotemporal variation in cohesion of group members and  
588 subgroup size and composition.

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

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

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

600 Social organisation: Size and demographic composition of a social group.

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

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

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

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