



# Groups, grouping and networks: dynamic unanswered questions for primatologists

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Defining primate groups has been the focus of considerable effort for at least the last 75 years (Carpenter 1945; Imanishi 1957, 1960; Crook and Gartland 1966): my aim is not to summarise or critique that work, but rather to enthuse those who think that this question has already been answered. I consider, from the perspective of a group member: What does a group mean to the individuals within it? Do individuals have choice in grouping? Why and how has an individual chosen its particular group at any moment in time?

Early observational studies of primates remarked on their “highly social nature” (Kawamura 1958), while the functions of primate grouping [Tinbergen’s (1963) “why” question] have long been explored (Clutton-Brock 1974; Itani 1977; Wrangham 1980; van Schaik 1983; Isbell 1991; Sterck et al. 1997) and are elegantly summarised by Kappeler (2019). More atomistic questions about individual choices or constraints on those choices about being in a group have often focused on two features of groups: fission–fusion dynamics which enable choice of group size (e.g. Aureli et al. 2008; see Fig. 1) and mixed-species groups (e.g. Chapman and Chapman 2000; Stensland et al. 2003; Daoudi-Simison 2020), as distinct from processes such as dominance and leadership operating to structure groups. Group size is considered here to be an outcome variable of individual processes and highly flexible due to local variation in ecology (e.g. Strier et al. 2014).

## Measuring groups, defining grouping

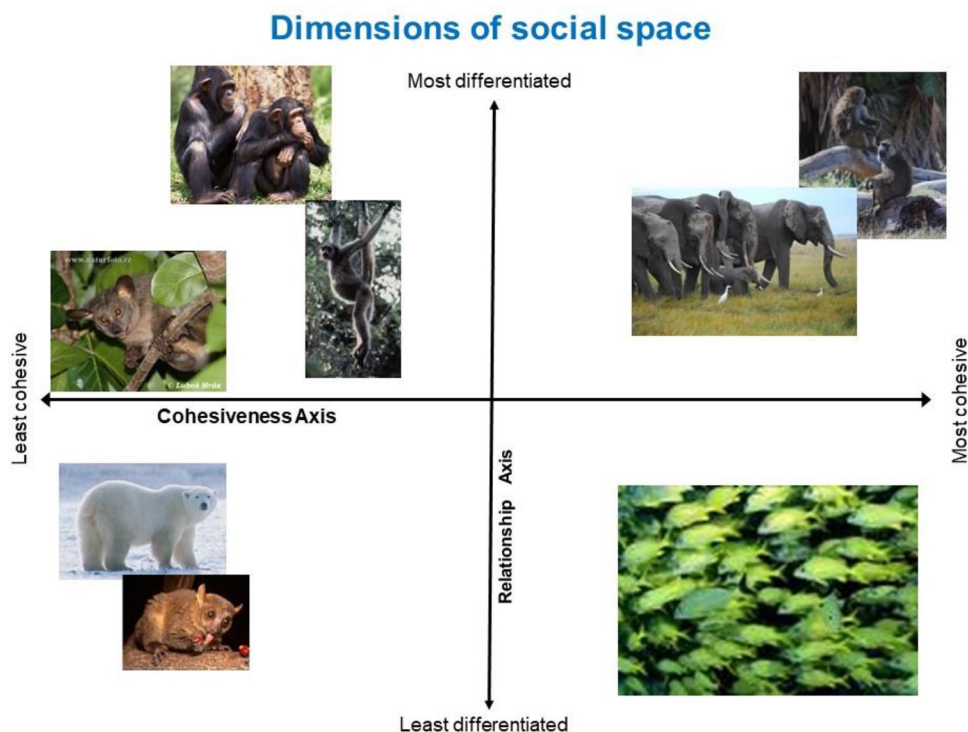
The first, and possibly most challenging, question remains: What is a group? Two or more individuals in association is a typical first approach, but this is tricky when “association” potentially includes individuals who recognise the presence and location of others by scent, sign, vocalisations or knowledge over distance and time [e.g. male orangutans (Mitani et al. 1991); elephants (McComb et al. 2003); sperm whales (Whitehead et al. 2012)]. Another possible criterion is the existence of differentiated roles among individuals, useful for the social insects but perhaps less so for primates (Krause et al. 2009; Pinter-Wollman et al. 2014). Individuals who commonly interact with each other (Di Fiore and Rendall 1994) and share a common home range (Dunbar and Schultz 2021) provide another perspective when identity is known; but what then becomes of the individuals who rarely interact but apparently still live in the same group? Or when individuals of another species (mixed-species groups) join the group? It thus becomes even more difficult, from the observer’s perspective, to categorise or distinguish a group, given the necessity to recognise and differentiate individuals and their interactions.

Proximity, plus directionality of movement captured within diameters of distance, allows for mathematically determined criteria for inclusion in groups when identity, history, kinship or relationships are unknown (Viscido and Shrestha 2015). The temporal dynamics of proximity are thus one critical focus of our understanding of grouping. How close, for how long, and does this matter to each individual in proximity? To answer such questions, researchers have applied social network analysis (see Kasper and Voelkl 2009; Krause et al. 2009; Kurvers et al. 2014; Pinter-Wollman et al. 2014; Sueur and Pele 2016, among others). Social network analysis is especially useful for assessing within-group sociality (Wey et al. 2008), as a tool for comparative

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**Fig. 1** Dimensions of fission–fusion and grouping (modified from Aureli et al. 2008) [muriqui (photo by K. B. Strier); elephant, baboon (photos by PCL); other images (stock photos)]



analysis (Kasper and Vokel 2009), and for defining complexity (Puga-Gonzalez et al. 2019) in the study of animal societies where the units of interest (individuals, colonies) can be defined a priori (e.g. Finn et al. 2019). It can also be a useful tool for determining whether two or more species are merely overlapping in time and space (Fig. 2a), behaving as a clearly distinctive, integrated and interacting, mixed-species group (Fig. 2b), or undergoing permanent separations or fissions.

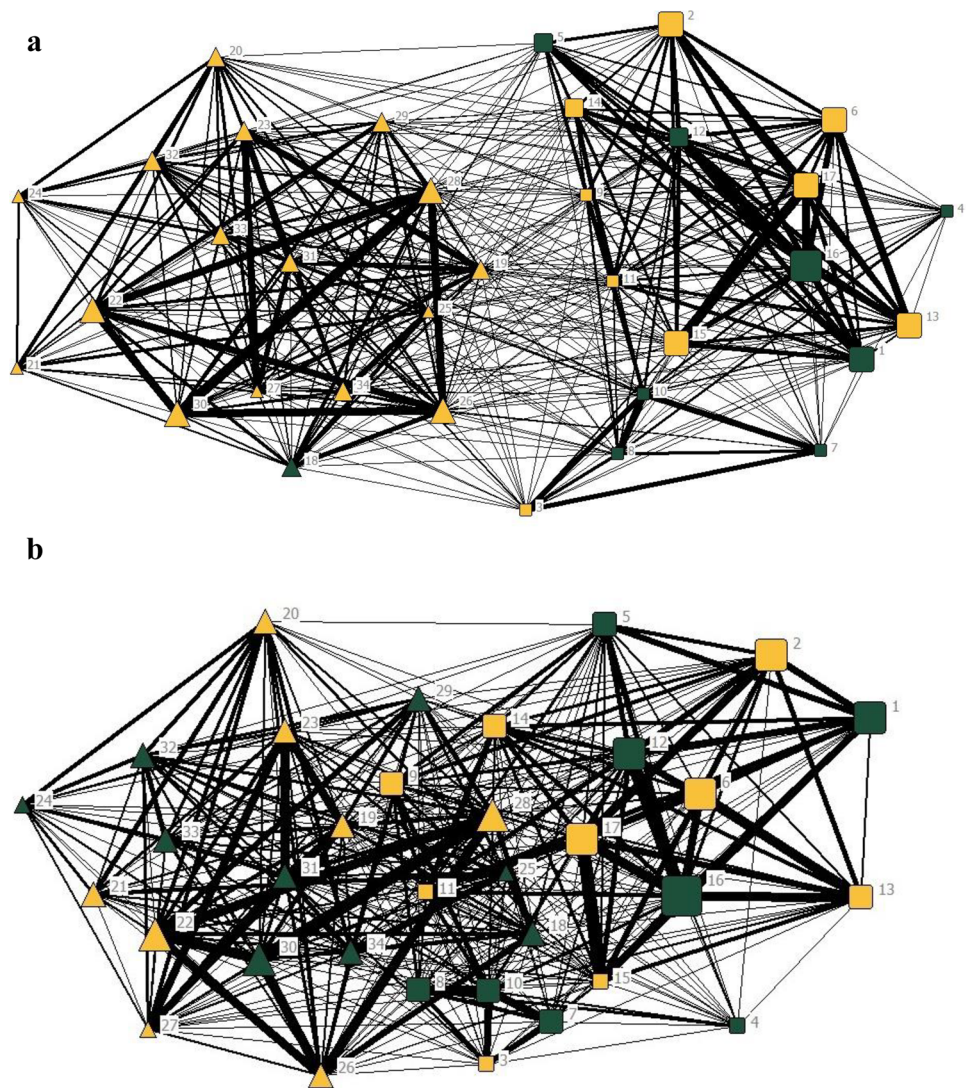
As noted above, an additional question relates to whether individual recognition is required to understand groups, networks and social dynamics in primates and other species. If we require knowledge about relationships [individually discriminated and structured interactions that are repeated over time (e.g. Hinde 1976)], then identity is necessary. When metrics such as size, age or sex represent mechanisms for discriminating associations, then patterns can be revealed even in the absence of knowledge of individuals (Lusseau and Neumann 2004; Coles et al. 2012). While group membership may be determined from simple metrics, membership solely defined as “within some distance” provides little perspective on costs or benefits accruing to individuals in relation to the functions of the grouping pattern (see below). Insights into grouping require teasing out these individually based trade-offs.

### **Leadership and collective actions: understanding of individual movements in the context of groups**

If we use, as many primatologists will, observed social exchanges to define social structures and the networks that arise from these, then we are dealing with attraction (which maintains proximity), the direct exchange of information (vocal, olfactory, visual) and finally, coordination—the ways and acts of being together. Exploring ways of being together raises interesting questions of dynamic organisation and movement. Much modelling has gone into explaining how individuals in groups move in relation to each other, and whether these movements represent simple rules to coordinate and/or synchronise movements [murmuration, flocks, shoals (Couzin and Krause 2003; Sumpter 2006)], decisions made by individuals (King and Cowlshaw 2009; Pillot and Deneubourg 2010), or leader–follower social dynamics (Rands et al. 2003; Couzin et al. 2005).

Individuals within groups often base their movement decisions on locally acquired cues, such as the position, or motion/change in motion of other group members (Couzin and Krause 2003). Each individual will need to be

**Fig. 2** Illustration of a hypothetical social network of a captive mixed-species exhibit of *Sapajus apella* ( $n = 17$ ) and *Saimiri sciureus* ( $n = 17$ ) if forming **a** associations (some overlap) but not a clear mixed-species group, **b** an integrated clear mixed-species group. *Node size* represents eigenvector centrality, *node colour* represents sex [female (yellow), male (green)], and *node symbol* represents species [*Sapajus apella* (square), *Saimiri sciureus* (triangle)] (from Daoudi-Simison 2020)



close enough to others for information to transfer or diffuse within groups (Claidiere et al. 2013; Firth 2020; Wild et al. 2020) or for the perception of vocal cues, opportunities which may be constrained in larger and more dispersed groupings (i.e. fission–fusion groups). Individuals will have different informational status, and some will not be aware of the informational state of others [i.e. if others are knowledgeable about a resource or a threat (Couzin and Krause 2003; Sumpter 2006)]. For example, predator avoidance, operating both within a group (Cowlshaw 1997) and between species (Heymann 1990; Hardie and Buchanan-Smith 1997; Chapman and Chapman 2000), will depend on shared vigilance or at least some members of the group being vigilant. This enables others to take advantage of those who are more vigilant or are more knowledgeable about threats.

Complex patterns of coordination and shared knowledge within groups can occur even when individuals have

different needs. Almost all higher primate species live in groups and therefore reap the multiple benefits of sociality, such as reduced risk of predation and multiple foraging advantages. As such, group members need to synchronise their activities and coordinate their movements despite individual differences in physiological and/or morphological traits, reproductive state, or motivation (Conradt and Roper 2007; King and Cowlshaw 2009; Petit and Bon 2010). Individuals that have the highest nutrient requirements will tend to initiate either more collective movements or be located at the front of movement progression compared to conspecifics [e.g. chimpanzees (Hockings et al. 2006)]. Those with more to lose (e.g. those carrying infants) may mitigate risk via internal position choice as well as through variable group/subgroup composition.

The greater the differences between individuals in traits and states, the more complex the decision-making process will be. In the context of collective actions/movements, we

can study the distribution of leadership, the order of individuals, or other types of organisation such as the existence of subgroups. A leader is “an individual eliciting follower behaviour/exerting social influence on others, by its rank in the progression, its behaviour or its social status” (Pyritz et al. 2011, p. 1270). In primates, the distribution of leadership and the organisation of individuals may be random or homogeneous [no leader and no specific order (Koda et al. 2020)], or heterogeneous, with one or more leaders and a specific/stable order (Hockings et al. 2006; Sueur et al. 2009; Jacobs et al. 2011). This raises interesting questions about whether different rules underlie variance in influence; for example, differentiating those engaging in risk-taking in forward progressions as a function of their hunger in contrast to contexts where foraging movements are problem-solving via socially acquired knowledge about the best food locations. Which rules operate, interact, or covary will influence the resulting visible social networks.

### Constraints on grouping: individual choices vs tyranny of the group

As an individual meerkat, wolf or lion, if you are no longer in a group your chances of survival are greatly reduced (Clutton-Brock 2016). The same phenomenon is largely true for primates [e.g. the risks of mortality when transferring or as a lone male/female are high (Alberts and Altmann 1995)], suggesting that grouping for many individuals is simply making the best of a bad job. The reproductive advantages and disadvantages of grouping are clearly shown in the common inverse U-shaped relationship between group size and average reproductive rates (Dunbar 1988), but even this relationship obscures individual patterns of disadvantage. Individuals who are at “the top” of the hierarchy or are more connected within a group do better, i.e. they have more infants which survive better (Silk 2007), irrespective of group size.

Absolute group size among primates both enables and constrains variance in aggregation tendencies and therefore network stability. Optimum group sizes for energy intake to sustain reproduction, for finding mates, for enhancing infant care, for minimising predation risks, and for effective other-group exclusion from resources can vary as a function of the cost–benefit ratios to individuals for each of these grouping functions (e.g. Sakura 1995; Lehman et al. 2014; Kappeler 2019), leading to fission–fusion and multi-level structures for different activities and contexts. Examples of trade-offs between grouping types are found in species with habitual temporal variation in their group structures: lion or hyena foraging parties, mother–infant pods of dolphins, mating aggregations of elephants, chimpanzee boundary patrols, and multi-species associations of colobus with guenons, or

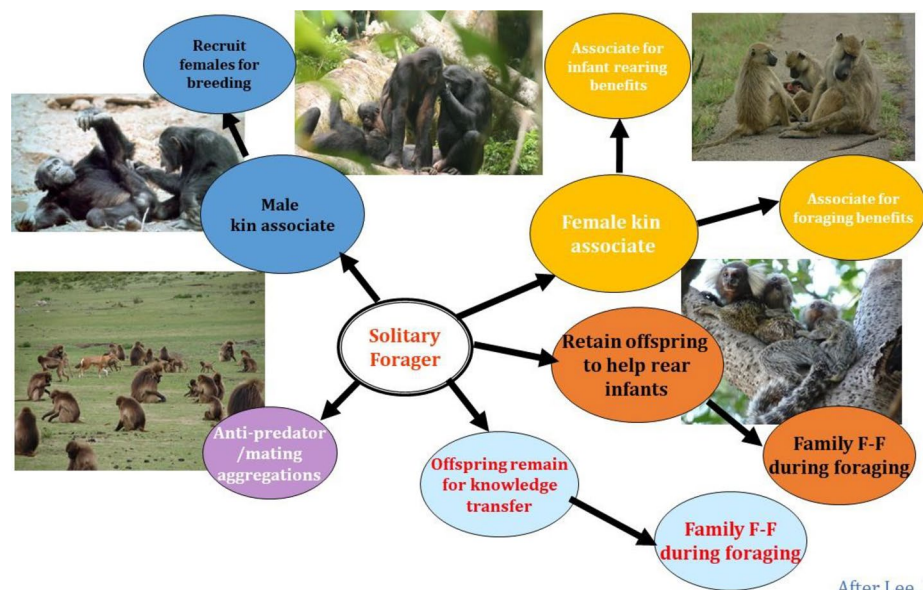
capuchins living with squirrel monkeys (Daoudi-Simison 2020).

Do subordinate individuals stay because they have few (or no) choices to move—the meerkat dilemma—or do they stay for a future advantage from a potential rise in rank, using a specific primate cognitive capacity for relationship prediction when status transitions are possible (Silk 2007)? This question raises another interesting problem: why is fission–fusion, as a solution to poor choices thrust upon individuals by status differentials or resource competition, so rare in primates? Elsewhere, we have argued that mortality risks of dispersal constrain choices about when to leave and who (of each sex or age) moves (Lee and Strier 2015). Does subgrouping represent similar or different foraging and mortality risks from those of dispersal, especially if during subgrouping you can exploit individuals of other species to manage these risks? Habitual fission–fusion [fluid subgrouping within consistent knowledge-based relationships, as defined by Aureli et al. (2008)] is seen in great apes including gorillas (Forcina et al. 2019), many atelids (Symington 1990; Strier 2009), and some papionines, colobids and macaques (Grueter et al. 2012, 2020). Subgrouping on a temporary basis, with the formation of distinct and separated foraging, sleeping, and socialising units within a habitually associated “group”, is relatively common (Majolo et al. 2008). What may indeed be rare in primates and limited to those with the smallest group size is consistent and sustained “whole group” foraging, socialising and resting (e.g. Zhou et al. 2005; Kamilar and Baden 2014; Strier et al. 2014; see also Fig. 3).

### Conclusions: networks and multi-level sociality

I have tried to demonstrate that from the perspective of an individual, its sociality is effectively the outcome of multiple levels of costs, benefits, choice and tyranny (constraint) (see also Peñaherrera-Aguirre et al. 2020), and simplistic classifications will hide this variation in decisions and contexts. Using multi-level network analysis is particularly helpful for moving from single-state interactions or relationships, and allows us to appreciate primate “groups” in all their dynamic forms. Networks have a deep (evolved) structure as well as a surface structure (linkage, edge, strength). Characteristics of individuals underlie their roles within networks as well as the depth and breadth of their connections. Demographic processes, such as aging, transitions (births, sexual maturation), dispersal and death, create perturbations in networks that can be temporary or persistent (e.g. Periera et al. 2020); networks themselves are as dynamic as the individuals that make them up. As Strier (2009) shows, comparative analysis

**Fig. 3** Social space occupied by primates, from a solitary forager origin [modified for primates after Lee (2009) for other mammals; photos by PCL, H. van Lawick, I. Behncke, M. Ramsay, H. Buchanan-Smith]. Note that several possible branches are unoccupied by primate social space, although these are found in other mammals. *F–F* Fission–fusion



After Lee, 2009

of within-species variation allows us to approach a better understanding of primate sociality from the perspective of the individual. Furthermore, understanding the processes of decision-making within networks contributes to understanding heterogeneity in behavioural strategies (Sueur and Pele 2016; Pasquaretta et al. 2014). This perspective, focusing on the individual, and on variation in network structures and dynamics, enables us to address key questions of conservation and species survival such as cultural variation (Cantor et al. 2015; Brakes et al. 2019).

Networks are powerful descriptive and analytical tools that illuminate the deep evolved structures of grouping as well as surface mechanisms of social maintenance. This is a brief dive into some aspects of grouping and networks; the application of network processes to the evolution of and consequences for primate grouping goes beyond simple socioecological models to enable a deeper understanding of within- and between-group genomics, dispersal decisions and consequences, mate choice, cooperation, personality and culture. Such evolutionary questions are of critical importance to primate persistence in a changing world (Kurvers et al. 2014; Sosa et al. 2021).

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## Declarations

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