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A Three-Dimensional Framework

As a first attempt at quantifying the three dimensions of our proposed framework, we offer some suggestions about the parameters to be considered. Here we use the broader term "party" instead of "subgroup" because the former can apply to both well-defined groups/communities and "open" communities, which are characterized by a continuous mosaic of overlapping individual home ranges (e.g., orangutans [van Schaik 1999], dolphins [Connor et al. 2000]).

The first dimension of temporal variation in spatial cohesion will vary from low (region A in fig. 1) in very cohesive groups or constantly dispersed situations (e.g., territorial, solitary species) to high in species where marked fission-fusion dynamics are common. A metric such as the coefficient of variation in interindividual distances across time that incorporates species-specific characteristics, such as body size and sensory capacities (e.g., critical distances are shorter for smaller species than for larger ones or when the main mode of communication is visual rather than auditory), could be used to quantify this dimension, though this may be problematic if all individuals are difficult to locate, as they are in open communities or in dense forests or aquatic environments. This difficulty may not be a critical problem because the temporal variation in spatial cohesion is incorporated into the operational definition of "party" that is fundamental for the other two dimensions (see below). However, whenever possible it is important to quantify the first dimension, because it also identifies groups and taxa that experience high temporal variation in spatial cohesion without fissioning into discrete parties (e.g., some baboon populations, which vary from being rather cohesive to dispersing over large areas; Henzi and Barrett 2003). The identification of such groups and taxa will be critical for determining whether they differ in terms of social interaction patterns or underlying socioecological conditions and communicative and cognitive abilities from groups and taxa that form explicit parties.

With respect to the second and third dimensions, the party will be the same as the entire group if fissions and fusions do not occur. When they do occur, however, various operational definitions of "party" might be used, depending on local factors, among them visibility and dispersion of group members (e.g., Chapman, White, and Wrangham 1993). One possibility is to determine the minimum distance at which two individuals can be considered in different parties by identifying a "break point" in the distribution of the distances between all community members sampled at various intervals. This method would still work if not all the interindividual distances were recorded at each sampling interval, which is always the case in open communities and is likely in well-defined communities in environments where individuals are difficult to locate. Under these circumstances, special effort to sample at least some individuals far apart from each other is needed, and the criterion for identifying the break point needs to be stricter. Computer simulations can be used to inform researchers about the sampling effort in terms of the area that needs to be covered to be able to sample individuals in different parties and thus strengthen the operational definition of "party."

Once the party is operationally defined for a given socioecological condition, we can focus on the temporal variation in party membership. The second dimension of the framework—temporal variation in party size—is related to the rate of fissions and fusions and the relative proportions of group/community members involved in these changes (the latter aspect can only be approximated for open communities). The third dimension—the temporal variation in party composition—takes into account how parties change in terms of the identities of the individuals leaving and joining a party. For example, the multilevel societies of hamadryas baboons would be highly variable in the second dimension, reflecting party-size changes from large night aggregations to small foraging one-male units during the course of the day, but much less variable in the third dimension because the composition of the parties based on the stable one-male units is overall relatively constant (Kummer 1968; Stammbach 1987; region B in fig. 1). By contrast, the communities of spider monkeys and chimpanzees are expected to be highly variable in both dimensions (Nishida and Hiraiwa-Hasegawa 1987; Symington 1990;

region C in fig. 1). These two dimensions also need to take into account that temporal variation in party size and composition may occur during only part of the year, as it does in ruffed lemurs and spectacled parrotlets (see supplement B).

Whereas this three-dimensional framework easily incorporates modal categories such as atomistic and molecular communities, it has the advantage of accommodating the range of variation described above. It also incorporates modern humans; during the day we resemble an atomistic community in which members are very rarely all together and form parties rather independently from one another, but we also have characteristics of a molecular community when we return to the stable family unit at night (Rodseth et al. 1991). In addition, the three-dimensional framework together with the approach outlined in the section on socioecology can also identify levels of fission-fusion dynamics that are inherently unstable and are possibly counterselected by socioecological conditions.