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Variation in the Degree of Fission-Fusion Dynamics

Nocturnal prosimians, such as some bushbabies, lorises, and mouse lemurs, display a certain degree of fission-fusion dynamics because they live in loose social networks where individuals associate in parties at least some of the time (Bearder 1987; Müller and Thalmann 2000; Schülke and Ostner 2005). For example, mouse lemurs (*Microcebus* spp.) show intra- and interspecific variation within a common pattern of dispersed-foraging individuals with overlapping home ranges that sleep in permanent groups. In certain cases males are mainly solitary, whereas in others they associate with females during foraging and/or sleeping. Similarly, all-female groups are typical, but in some cases females do not associate with one another (Schülke and Ostner 2005).

Sleeping together and foraging mainly solitarily are also typical of several bats, but fission-fusion dynamics are more flexible at least in some species. For example, colonies of forest-dwelling big brown bats (*Eptesicus fuscusi*) and Bechstein's bats (*Myotis bechsteinii*) consist of multiple parties roosting on different trees. Although there are preferential associations between individual bats, party compositions change during frequent roost switching (Kerth and König 1999; Willis and Brigham 2004).

Fission-fusion dynamics are manifest in African savannah elephants (*Loxodonta africana*), where individuals within large populations continuously gather together and separate in parties of all sizes. Families are the building blocks of elephants' societies, but females can also be found in parties with nonkin. The nature and composition of the parties in which a female finds herself vary over 24 hours and seasonally (Moss and Lee n.d.). Adult males have social dynamics that are largely independent from those of females. They may be solitary but most often associate with peers or older males in small parties for foraging or with females for mating opportunities (Poole, Lee, and Moss n.d.). A stronger segregation between the sexes is found, for example, in red deer (*Cervus elaphus*) and bighorn sheep (*Ovis canadensis*), probably because of better activity synchronization among same-sex individuals (Conradt 1998; Ruckstuhl 1998).

Sex differences in fission-fusion dynamics have also been reported in chimpanzees, with males more often found in parties and females more often solitary (Goodall 1986; Nishida and Hiraiwa-Hasegawa 1987). There is, however, variation in this pattern across populations, with some West African chimpanzees showing a higher degree of female presence in parties (Lehmann and Boesch 2008; Stumpf 2007; Sugiyama and Koman 1979). Fission-fusion dynamics in bottlenose dolphins (*Tursiops* sp.) are similar to those of chimpanzees in that party size and composition change often (Connor et al. 2000). However, in at least two populations some males form very stable associations of two to three individuals (called alliances) that join and leave parties as a unit. There is also interpopulation variation within this common pattern. Some male alliances are more labile in the Shark Bay population than in the Sarasota Bay population, and "nested" alliances, in which sets of male allies form regular associations with other such alliances, are evident only in the Shark Bay population. In both populations, female-female associations are weaker than male-male alliances but are highly variable (Connor et al. 2000).

In addition to the multilevel societies of some primate species, which are centered on one-male units as stable associations (Grüter and Zinner 2004; Stammbach 1987), there is the case provided by several bird species that show fission-fusion dynamics with breeding pairs as the basic units. For example, spectacled parrotlets (*Forpus conspicillatus*) form flocks of up to 150 individuals at common night roosts and split into several daily parties of up to 25 individuals. These parties consist of several breeding pairs, and their composition seems to be stable over years. This pattern changes during the breeding season, when pairs establish small territories and the degree of social contact with other party members decreases (Wanker 2002). Another variation within the pattern of fission-fusion dynamics with relatively stable associations is the case of ruffed lemurs (*Varecia variegata*), in which a variable number of adult males and females live in dispersed "core groups" that use restricted ranges and basically do not interact with other community members for most of the year. During the warm season,

however, they form temporary parties with variable size and composition, including members of different core groups (Morland 1991; Vasey 1997).

Macaques are usually described as moving in rather cohesive groups. However, large groups of long-tailed and Japanese macaques may form temporary parties that regroup at night or sleep separately but do not show high fluidity in party composition during the same day (Fokuda 1989; van Schaik and van Noordwijk 1988). Similar patterns of fission-fusion dynamics have been described in large groups of baboons and howler monkeys, which are more cohesive when they live in small groups (Aldrich-Blake et al. 1971; Anderson 1981; Chapman 1990; Dias and Rodriguez-Luna 2006). Spotted hyenas (*Crocuta crocuta*) share a number of characteristics with the baboons and macaques, but their grouping patterns are much more fluid. Their parties have flexible composition, and members of the same matriline are not often all together (Holekamp et al. 1997). Their party size varies seasonally with prey abundance, and the largest parties are formed at the largest ungulate carcasses (Smith et al. 2008). There is also variation in party composition, with lower-ranking individuals being more solitary (Smith, Memenis, and Holekamp 2007; Smith et al. 2008).

Variation in party size within the same community is also common in species that live in habitats where there are strong seasonal differences in food availability. An extreme case of this variation has been witnessed in communities of spider monkeys at two different locations in Central America, where during periods of great food shortage the typical pattern of multiple daily changes in party size and composition is replaced by long-lasting small parties (F. Aureli and C. M. Schaffner, unpublished data).