Fission-Fusion Dynamics

New Research Frameworks

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Renewed interest in fission-fusion dynamics is due to the recognition that such dynamics may create unique challenges for social interaction and distinctive selective pressures acting on underlying communicative and cognitive abilities. New frameworks for integrating current knowledge on fission-fusion dynamics emerge from a fundamental rethinking of the term "fission-fusion" away from its current general use as a label for a particular modal type of social system (i.e., "fission-fusion societies"). Specifically, because the degree of spatial and temporal cohesion of group members varies both within and across taxa, any social system can be described in terms of the extent to which it expresses fission-fusion dynamics. This perspective has implications for socioecology, communication, cognitive demands, and human social evolution.

The term "fission-fusion" was first used by Hans Kummer (1971) to describe the social system of a few taxa of nonhuman primates, such as chimpanzees, geladas, and hamadryas baboons, that change the size of their groups by means of the fission and fusion of subunits (called parties or subgroups) according to both their activity and the availability and distribution of resources.[1] Social systems characterized by such fission-fusion dynamics are considered rare among mammals, but they are typical of some primate (Smuts et al. 1987) and other mammalian species (e.g., some bats [Kerth and König 1999], dolphins [Connor et al. 2000], elephants

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[Moss and Lee n.d.; Wittemyer, Douglas-Hamilton, and Getz 2005], and spotted hyenas [Holekamp et al. 1997]). Among primates most studies on fission-fusion dynamics have focused on chimpanzees (Boesch and Boesch-Achermann 2000; Mitani, Watts, and Muller 2002; Nishida and Hiraiwa-Hasegawa 1987) and spider monkeys (Chapman, Wrangham, and Chapman 1995; Symington 1990). Similar patterns also seem to occur in bonobos (Hohmann and Fruth 2002; Nishida and Hiraiwa-Hasegawa 1987; Stumpf 2007) and some populations of muriquis (Milton 1984). Fission-fusion dynamics are likewise typical of modern humans, including hunter-gatherers (Marlowe 2005), although they are not often explicitly recognized. The following quote captures this apparent anomaly: "Fission-fusion sociality seems so natural and necessary to humans—including anthropologists—that it hardly demands explanation, if it is noticed at all" (Rodseth et al. 1991, 238). The sharing of this flexible social nature with our closest living relatives suggests that fission-fusion dynamics were characteristic of the social system of the last common ancestor of chimpanzees, bonobos, and modern humans.

Given the potential role of fission-fusion dynamics in human social evolution, we organized a symposium at the Twentieth Congress of the International Primatological Society and a postcongress workshop to explore from a broad comparative perspective whether fission-fusion dynamics create unique challenges for social interactions or distinct selective pressures for specific underlying communicative and cognitive abilities. In this section, we emphasize that the variation in fission-fusion dynamics goes beyond the modal types of societies that have traditionally been described as "fission-fusion." We therefore suggest a revision of the way the term "fission-fusion" is used to reflect such variation, and we propose a new framework to stimulate the quantification of the relative degrees of fission-fusion dynamics in different taxa in order to facilitate future comparative research.

Although the distinctions among modal types of "fission-fusion societies" (for a brief review, see CA+ online supplement A) are useful for describing the degree of flexibility in the social system of certain species, many other systems characterized by fission-fusion dynamics do not fit within these modal types. In fact, there is pronounced variation in the degree of fission-fusion dynamics both across and within species (for examples, see CA+ online supplement B), and this poses a difficulty in using the modal terminology. Given this variation, we propose a fundamental rethinking of that terminology. We suggest that the term "fission-fusion" be abandoned as a label for a particular modal type of social system (i.e., "fission-fusion societies") and that the term "fission-fusion dynamics" be used to refer to the *extent of variation in spatial cohesion and individual membership in a group over time.* This will allow any animal society to be characterized by its degree of fission-fusion dynamics, which can vary from highly cohesive with stable group membership to highly fluid with either relatively stable or flexible subgroup membership.

This perspective on the use of the term "fission-fusion" fits well with Kappeler and van Schaik's (2002) definition of social organization, which explicitly incorporates the degree of spatiotemporal cohesion of a social system. In particular, this perspective emphasizes that simple dichotomous distinctions of social organizations as cohesive versus flexible are neither realistic nor accurate (Strier 1989). Moreover, it highlights that flexible spatiotemporal grouping patterns in primates and other vertebrates are more common—and more complex—than generally recognized (Kinzey and Cunningham 1994; Struhsaker and Leland 1979; Sussman and Garber 2007). The critical issue is that spatiotemporal variation in grouping patterns influences the opportunities for group members to interact with one another and, ultimately, the resulting social system.

This modification of the use of the term "fission-fusion" requires the development of new conceptual frameworks for studying the implications of variation in fission-fusion dynamics across groups and species for their socioecological, communicatory, and cognitive aspects. As a start, it is necessary to develop basic heuristics for describing the degree of fission-fusion dynamics seen in a group or species and thus the opportunities that individuals have for close-range social interaction. Any such conceptual framework will, of course, be multidimensional. Here we propose a framework involving three dimensions that together capture potential temporal variation in spatial cohesion and membership in a given environment: (1) the temporal variation in spatial cohesion among group members, (2) the temporal variation in party size, and (3) the temporal variation in party composition (fig. 1; for detail on the three dimensions, see CA+ online supplement C).

The accumulation of data for the dimensions of the proposed framework or other variants will permit the relative placement of species and populations of the same species within a complex multidimensional fission-fusion space (e.g., fig. 1), which is an essential first step toward the systematic investigation of whether social systems characterized by different degrees of fission-fusion dynamics are quantitatively or qualitatively different from one another in terms of socioecological conditions, social interaction, and cognitive abilities. However, because the relative positions of most species and populations within this multidimensional space have yet to be empirically determined, a simplified terminology is used throughout the following sections for ease of notation in comparing social systems characterized by a higher degree of fission-fusion dynamics (hereafter "higher-FF" groups or taxa) and those characterized by relatively higher temporal stability in group cohesion and membership (hereafter "lower-FF" groups or taxa). The terms "higher-FF" and "lower-FF" represent *relative* points within multidimensional fission-fusion space and therefore need to be interpreted in terms of different degrees of fission-fusion dynamics (i.e., higher and lower in at least one of the three dimensions); in other words, they do not reflect an actual dichotomy.

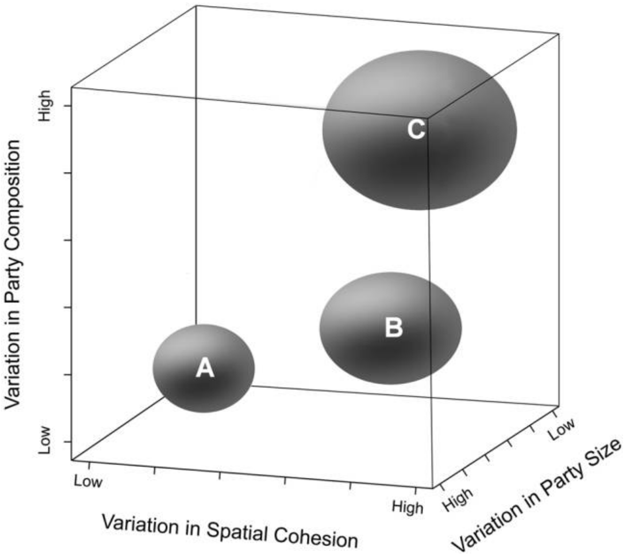

Figure 1. A three-dimensional conceptual framework to represent the degree of fission-fusion dynamics of groups and taxa. The *X*-axis represents the temporal variation in spatial cohesion among group members, the *Y*-axis represents the temporal variation in party size, and the *Z*-axis represents the temporal variation in party composition. Region A illustrates cases that are low in all three dimensions, such as very cohesive groups or constantly dispersed situations (e.g., territorial, solitary species). Region B would include cases that are highly variable in spatial cohesion and party size but not in party composition, such as the multilevel societies of hamadryas baboons, which are based on relatively stable one-male units. Region C represents cases that are high in all three dimensions, such as the highly fluid communities of chimpanzees, spider monkeys, and spotted hyenas, characterized by highly variable party membership. Groups of modern humans, bottlenose dolphins, and elephants would likely be located between regions B and C. Comparative data for each dimension are needed for the accurate relative placement of species and populations.

The three-dimensional framework proposed here is a useful first step, but additional frameworks are needed depending on which aspects of fission-fusion dynamics are being considered. The following sections propose several new frameworks that are relevant to exploring and understanding variation in fission-fusion dynamics in terms of socioecology, communication, and cognitive demands. The concluding section explores the implications of fission-fusion dynamics for human evolution.

The Socioecology of Fission-Fusion Dynamics[2]

Over the past 25 years, studies of primate behavior and ecology have contributed greatly to the development of socioecological theory, whose principal goal is to explain grouping patterns, range use, mating behavior, dispersal tendencies, and inter- and intrasexual social relationships as adaptive responses to features of the ecological and social environment. Primate socioecology historically has taken a reductionist perspective, recognizing a discrete set of modal social systems and seeking to explain, for example, the "nepotistic" female social relationships of many cercopithecines as a consequence of the competitive regime engendered by food resource distribution. The discipline has come a long way using this categorical framework, but the framework plays down the fact that many aspects of social systems (e.g., the spatiotemporal variation in the association patterns of individuals) can vary dramatically both among populations of a given taxon and within the same population over time. Primate socioecology is currently at an important juncture (Janson 2000). If primatologists are to continue to contribute to the development of socioecological theory, it is crucial for us to reevaluate past assumptions about how ecological variables influence social systems and to expand our efforts to understand the first principles that shape movement and grouping patterns. In the past, the study of higher-FF taxa has offered a useful tool for exploring such issues, since their responses to ecological changes take place over very short timescales. Here we return to the example of higher-FF taxa and suggest a new framework that derives more explicit null models of association by using spatially explicit agent-based simulations that begin from assumptions about the state of resources in the environment.

The modeling approach that we advocate will accomplish several goals. First, it will allow us to assess the validity of currently recognized modal types of primate social systems, particularly the so-called fission-fusion societies of chimpanzees and spider monkeys. Second, it will let us explore, *in silico*, new metrics for describing patterns of sociospatial association that might then be applied across taxa and be used for quantifying the fission-fusion space discussed above; using these metrics, we can begin to evaluate the importance of observed deviations from expected null models. Finally, through this approach we expect to be able to explore whether apparently similar social systems might arise for very different reasons and by different evolutionary routes (Lee 1994).

Are Higher-FF Taxa "Special"?

Because higher-FF taxa are relatively uncommon among primates and other mammals, researchers tend to imagine that the socioecological pressures they face may be somehow different in form or degree from those faced by lower-FF taxa. Some higher-FF groups (e.g., those falling into region C of fig. 1) have historically been incorporated into the general socioecological model as follows. First, the flexible association patterns of these higher-FF groups are commonly interpreted as a solution by large-bodied primates—who face a relatively low risk of predation—for coping more efficiently with patchily distributed and temporally varying food sources (Dunbar

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[2] Anthony Di Fiore, Colin A. Chapman, S. Peter Henzi, Phyllis Lee, Julia Lehmann, and Gabriel Ramos-Fernandez have principal responsibility for this section.

1988; Klein and Klein 1977; Milton 1984; Strier 1992; Symington 1988; van Schaik 1989; Wrangham 1977, 1980). Under these circumstances, females are suggested to spread out from one another when resources are scarce to reduce feeding competition and possibly to aggregate and forage together when resources are plentiful. More recently, fission-fusion dynamics in these taxa have been viewed as affording flexible responses for optimal solutions to the usually contrasting pressures of avoiding predators and minimizing feeding competition when there is temporal or spatial fluctuation in predation pressure and food availability (Boesch and Boesch-Achermann 2000). For some higher-FF taxa (e.g., chimpanzees, spider monkeys), males are or are presumed to be philopatric and cooperate with male relatives to defend access to the ranges of several females against males from neighboring groups (Ghiglieri 1984; Strier 1994; Wrangham 1979), which in turn is thought to force the dispersal of maturing females (Pusey 1979; Pusey and Packer 1987). Additional social and demographic factors (e.g., overall community size, presence of cycling females) have been shown to affect fission-fusion dynamics and party size (Lehmann and Boesch 2004). For other higher-FF taxa (e.g., geladas and some baboons, which live in multilevel societies; region B of fig. 1) the risk posed by nocturnal predators is seen as the selective pressure favoring the aggregation of large numbers of animals at communal sleeping sites, while competition drives fissioning of these large groups into smaller, cohesive foraging parties during the day (Dunbar 1988; Kummer 1968) and the risk of infanticide prompts the consistent association of particular males with particular females (Henzi and Barrett 2003).

There are a number of problems inherent in the notion that higher-FF groups face "special" ecological pressures. First, past socioecological models of higher-FF groups in primates offer only post hoc and incomplete explanations for observed patterns of association and kinds of social relationships. For example, the existence of a positive relationship between habitat-wide fruit availability and foraging party size in both spider monkeys and chimpanzees is taken as evidence that resource distribution constrains grouping patterns, and yet resource patch density and distribution explain less than half the variance in party size in these taxa (Chapman, Wrangham, and Chapman 1995). In addition, long-term primate studies are increasingly revealing that considerable flexibility in grouping patterns and within-group social relationships may exist both between populations and within the same population of higher-FF taxa over time (Strier 2003; supplement B). Thus, models of the way ecological conditions shape even such basic aspects of social systems as group or party size are less than straightforward.

Moreover, as primatologists pay more attention to work on nonprimate taxa, we are coming to appreciate that a wide variety of other vertebrates are also characterized by fission-fusion dynamics (see supplement B). The extent to which socioecological models developed from primate studies can be applied across taxa is unknown, but it is very unlikely that any one set of ecological conditions determines superficially similar fission-fusion dynamics in these disparate taxa. Having identified a number of limitations to current socioecological models (see CA+ online supplement D), we outline a research framework that may help us to address these limitations.

A Way Forward? Deriving an Inclusive Spatial Null Model

Our proposition is to develop a new set of null models of association and sociality that begin from first principles to explore links between ecological, social, and demographic variables, on the one hand, and sociospatial relationships, on the other. Given that there is a great complexity in the environments in which grouping takes place, producing null expectations of grouping patterns should take as a starting point a spatially explicit description of the environment inhabited by a species. Spatial analysis is a mature field that offers many tools useful to socioecologists for describing how resources (e.g., food, watering holes, sleeping sites) or predation risk vary in space and time (Dale et al. 2002; Fortin, Dale, and van Hoef 2002). From this description of the environmental complexity faced by animals, null models can be produced that predict what grouping patterns may arise simply as a consequence of the environment. One possible null model might be summarized as follows:

> Within a primate social group, patterns of association across time are a consequence solely of individual decisions that maximize access to resources (i.e., they are not influenced by social factors, such as individuals' relative dominance rank or their relatedness to other group members). The temporal variation in spatial cohesion and membership characteristic of higher-FF groups emerges in response to a specific subset of all possible patterns of resource dispersion.

Subsequently, deviation from what is predicted from these first principles can be analyzed to understand the factors that, in addition to environmental variation, influence grouping patterns and social relationships. Some of these deviations will not lead too far (e.g., sleeping sites may physically constrain spatial dispersion), while others may be fascinating (e.g., quantitative descriptions of how alternative social strategies, such as infanticide avoidance, might influence grouping).

One way to develop null models of movement and grouping patterns against which empirical data can be compared is through the use of spatially explicit agent-based simulations. Throughout the history of primate socioecological research, these kinds of models have been used by various researchers (Boyer et al. 2004, 2006; Ramos-Fernandez, Boyer, and Gómez 2006; Rodman and Di Fiore 1993; te Boekhorst and Hogeweg 1994; reviewed by Dunbar 2002), but they have yet to gain widespread acceptance (Bryson, Ando, and Lehmann 2007). We stress that these are null models that need to be used as *tools* to begin to understand the behavior of real animals rather than as actual descriptions of an animal's behavior (Peck 2004).

The central elements of a spatially explicit agent-based simulation model include a habitat in which various kinds of resources (e.g., depleting food patches, sleeping sites) and agents (e.g., individual model animals, predators) occupy particular locations (fig. 2). The construction of such a model will begin by explicitly designating the distribution of food resources because food necessarily drives travel patterns—even if every other factor were missing from the environment, animals would still need to move to feed. On the basis of the spatially explicit descriptions of environmental variation, a set of model parameters or dimensions that capture this variation is developed. Multiple agents within the simulation are then given simple foraging rules (e.g., "move to the next available patch" or "move to the largest patch within a certain distance"), and the emergent spatial structuring of those individuals (association patterns) is assessed after the model is run for a number of steps. The model is then iterated many times, and the resulting grouping patterns of the agents are recorded for different values of the environmental parameters, generating a surface that reflects what association patterns are predicted to be associated with what combinations of environmental variables. Observed field data can then be examined for concordance with this model surface. If we start with realistic values for meaningful environmental parameters and notice that the particular grouping patterns arise only in certain environments, we obtain testable predictions about the effect of the environment on grouping, and this provides a means of understanding deviations from a purely ecological explanation. For examples of the use of spatially explicit agent-based simulations see CA+ online supplement E.

As with traditional socioecological models, accurate empirical measures of environmental variables of interest (e.g.,

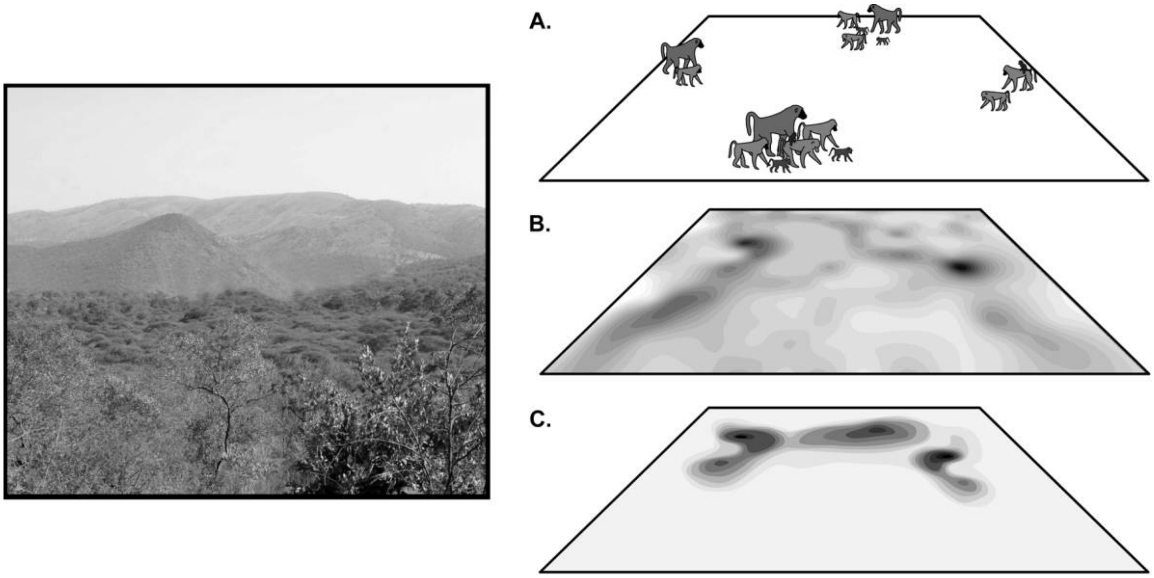

Figure 2. Hypothetical components of a spatially explicit agent-based simulation model. On the left is a photograph of the landscape being simulated. The top layer on the right side of the figure (*A*) shows "baboon" agents distributed across the landscape at one point in time and varying degrees of spatial association (e.g., four "parties" containing two to six independently moving animals). The bottom two layers on the right represent the spatial distribution of two key resources presumed to be important to baboons at that same point in time, where *B* represents the gradient of food resource availability across the landscape, with the degree of shading proportional to average energy return rate (e.g., calories per unit time) that "baboons" could receive by foraging at that location and *C* represents the locations of possible sleeping sites (e.g., cliffs) where predation risk is lower (i.e., the degree of shading is inversely proportional to the degree of predation risk experienced at that site). In running a simple simulation, individual "baboons" are given a foraging rule that moves them across the landscape (e.g., "move to an adjacent location where the return rate is higher"). At each step, the positions of all "baboons" and the details of each resource layer are updated, and various measures of association (e.g., average interindividual distance, average party size, etc.) can be calculated.

food distribution) are desirable to lend "realism" to a simulation, but one important advantage of a simulation-based approach is that it is possible to explore the effect of a range of values for any model parameter, even one that is very difficult to measure because of observational limitations or the time frame needed for accurate measures (e.g., predation pressure or infanticide risk). Moreover, once a simple model has been constructed, additional environmental variables can be added or removed to explore their effect on the emergent spatial structuring. In sophisticated models, the various resources and agents in the simulation might themselves show temporal variation in their size (e.g., growing and shrinking to simulate food patches such as fruiting trees with ripening and then diminishing crops), location (e.g., moving in space according to behavioral rules to simulate mobile prey or predators), or state (e.g., cycling through varying stages of "receptivity" to simulate female reproductive state).

The power of the agent-based modeling approach lies in its versatility and potential for expansion in ways that are informed by observational studies. For example, although initial null models might not explicitly incorporate social factors (e.g., dominance or kinship relationships among different agents) or demographic factors (e.g., group size, population sex ratio, number of simultaneously receptive females) that are known to influence the degree of spatial cohesion among animals (Lehmann and Boesch 2004), the modeling approach is sufficiently versatile to accommodate the inclusion of these kinds of variables. This can be done, for example, by altering the behavioral rules that agents follow when they encounter one another (e.g., "retreat" when the other agent is more dominant, "follow" when the other agent is in estrus) or by making the behavior of agents contingent on accumulated information about the set of agents previously encountered (e.g., "do X" when the sex ratio of encountered agents is male biased and "do Y" when it is female biased). Indeed, research on other mammalian taxa suggests that broadening our perspective from purely resource-based models to more socioreproductively based ones may have considerable application to the study of primate spatial and social associations. For example, it is clear that various social factors are key determinants of grouping patterns in other social mammals; the risk of infanticide influences grouping in lions (Grinnell and McComb 1996; Packer and Pusey 1983), allomaternal care shapes the social associations of elephants (Lee 1987), and reproductive competition over females shapes male alliances among dolphins (Connor et al. 2000). The potential influence of these kinds of variables on primate associations and sociality could be explored by integrating them into agent-based simulations, which in turn could be used to develop new predictions that could then be tested with field data. We believe that this integration of theory, modeling, and observation will be a profitable way to understand the causes and consequences of higher-FF dynamics in primate and nonprimate taxa and to help identify the range of socioecological conditions under which lower-FF groups are likely to arise.

Implications of Fission-Fusion Dynamics for Communication[3]

Within primate groups, social signals may perform functions as simple as coordinating group movement (Boinski 1996) or as intricate as conveying and negotiating relationship qualities and processes such as formal submission and dominance (Flack and de Waal 2004, 2007), reconciliation (Aureli and de Waal 2000), and trust in the context of coalition formation (Smuts and Watanabe 1990). The kinds of signals and the size of signal repertoires selected to fulfill these functions are expected to be affected by fission-fusion dynamics (Kummer 2002; Milton 2000). Members of lower-FF groups must resolve the conflicts generated by relatively high levels of association and avoid social disintegration. Members of higher-FF groups must have ways to reestablish relationships and resolve uncertainties (e.g., concerning alliances, dominance status, and each individual's relationship to third parties), depending on the frequency and patterns of spatial and temporal separations (Barrett, Henzi, and Dunbar 2003). The interacting effects of the spatiotemporal variation in grouping patterns and social dynamics determine whether communication functions to solve primarily the problems posed by relatively high levels of association or those posed by extended or frequent spatial separations, independent of the sensory anatomy and physiology that different modes of communication (e.g., visual, olfactory, auditory) require.

Differences in communication patterns may reflect distinct evolutionary routes that could have led to both higher- and lower-FF groups, and we begin our consideration of communication with a description of two possible routes. We then present a framework for the evolution of social signaling that illustrates the relative importance of signals for maintaining spatial cohesion, separating from other group members, resolving uncertainty due to low spatial cohesion when individuals reunite, and negotiating social interactions depending on the degree of fission-fusion dynamics and the evolutionary route. We finish by showing the utility of the framework for generating testable hypotheses about the way communicatory signals might vary depending on the social complexity and level of cohesion underlying fission-fusion dynamics. Our framework for the evolution of social signaling is heuristic. It is meant to stimulate research that investigates the extent to which variation in fission-fusion dynamics influences communication because few such data exist at present.

The Phylogeny of Fission-Fusion Dynamics

Figure 3 depicts two hypothetical evolutionary routes by which higher-FF groups can arise and yield a variety of social systems (supplement B). On route A, social relationships became increasingly valuable as the fitness gained through long-

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3. Karen B. Strier, Colleen M. Schaffner, Joseph H. Manson, and Simon K. Bearder have principal responsibility for this section.

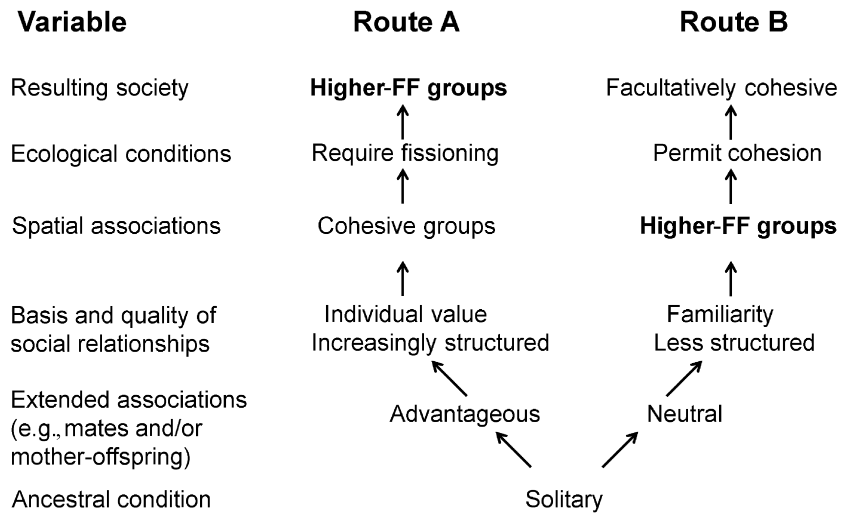

Figure 3. Alternative routes to higher degree of fission-fusion dynamics. The ecological conditions that require fissioning of cohesive groups along route A may also make cohesiveness detrimental for higher-FF groups along route B. In this scenario, extended associations may impose ecological costs that will need to be offset by other advantages, such as increased survival of offspring or reproductive success among mates, to achieve the neutrality required for the social transitions along route B.

term associations—beginning between mates and/or between mothers and their adult offspring—increased. Along route A, then, the driving force behind increasing gregariousness was the increasing value of social relationships for mutual advantages, which over time and with expanding scope could have resulted in lower-FF groups such as those of macaques and capuchin monkeys. The high value of social relationships (Cords 1997; Kummer 1978) selected for increasingly sophisticated relationship negotiation skills, thus permitting group members to remain together unless ecological pressures imposed high levels of resource competition that necessitate fissioning. On route A we can envision two main ways in which higher-FF groups could have evolved: (1) by large groups fissioning into temporary smaller parties such as those observed in the communities of chimpanzees and spider monkeys (Nishida and Hiraiwa-Hasegawa 1987; Symington 1990), or (2) by small groups temporarily fusing into larger bands/clans and then aggregating with other bands/clans to exploit limited safe sleeping locations, with the basic subunits having a relatively fixed composition, as is the case with the multilevel societies of hamadryas baboons (Stammbach 1987). On route A, then, higher-FF groups would have emerged among taxa in which sophisticated relationship negotiation skills formed the background from which the additional skills necessary for resolving relationship uncertainties in the face of periodic separations evolved. This scenario also conforms to the perception of higher-FF taxa evolving along route A having greater social complexity because their communication repertoire requires adeptness at negotiating social relationships while together, signaling departures, and reassessing their relationships following separation (Barrett, Henzi, and Dunbar 2003; Dunbar 2003). The particular signals employed by higher-FF groups need not be more cognitively demanding, but their repertoires may be more extensive than those of lower-FF groups.

By contrast, species on route B in our scenario would move to higher-FF groups from a solitary rather than a group-living condition (Müller and Thalmann 2000; Sterling, Nguyen, and Fashing 2000; fig. 3). Route B does not require that differentiated social relationships become increasingly valuable as gregariousness intensifies, and associations may have been short-lived and random or opportunistic. In some galagos, for example, it may be thermally advantageous or safer with respect to predators to sleep with conspecifics than to sleep alone, but it is the number of conspecifics (as opposed to differences in their individual value as social partners) that leads them to fusion. However, it may also be easier or more efficient to associate with familiar conspecifics than with strangers, and the resulting higher-FF groups may shift into facultatively lower-FF groups if ecological conditions permit (Bearder 1999; fig. 3). Along route B, the transition from solitary to higher-FF groups could have required some enhancement of the minimal social skills (i.e., for distinguishing familiar individuals from strangers) and signals for resolving relationship uncertainties over distance and time, though not to the level attained by lineages traversing route A. Similarly, lower-FF groups that emerge through route B are expected to lack the range of relationship negotiation signals found in both lower-FF and higher-FF groups on route A.

Mapping the Social Landscape

The different evolutionary trajectories by which higher-FF groups could have arisen have implications for the evolution of social signaling. Figure 4 illustrates our framework by depicting a two-dimensional landscape for mapping social systems along two intersecting continua to consider the range and types of signaling mechanisms required to regulate spatial cohesion and social relationships. The *X*-axis in our landscape represents the degree of cohesiveness, operationalized here as the percentage of conspecifics within a given individual's social group that it can communicate with at any given time (which depends on the temporal variation in spatial cohesion, party size, and composition; supplement C). We hypothesize that different kinds of signals are needed, depending on whether they function primarily to resolve relationship uncertainties that arise without constant contact and to convey information about fission events or to maintain coordination within relatively cohesive groups. The *Y*-axis of the landscape represents the complexity and differentiation of dyadic social relationships (sensu Hinde 1979), measurable by criteria such as high between-dyad variation and low within-dyad variation in rates and intensities of friendly and antagonistic behavior. At one extreme of our *Y*-axis dimension, adults will regard adult conspecifics of the same sex, reproductive condition, and possibly degree of relatedness as interchangeable; at the other extreme, each dyadic relationship will be highly distinct along several dimensions (e.g., agonistic asymmetry, tolerance of close proximity, services provided). The *X*-axis demarcates a critical threshold for distinguishing between social environments that either do (upper) or do not (lower) require communication signals for the long-term maintenance of differentiated social relationships. Individuals of species that fall below this threshold may be able to recognize one another and may have signals for mediating their social interactions and coordinating their movements, but it is only among species that fall above this threshold that we expect to find signals that allow for the establishment and maintenance of long-term, differentiated social relationships.

The intersection of the two axes in figure 4 divides the social landscape into four quadrants. Species in quadrant I are low in spatial cohesion and social complexity. Examples include solitary mammals in which adults associate only to mate and to contest access to resources (e.g., shrews [Cantoni 1993], giant mouse lemurs [Schülke and Ostner 2005]). Courtship and assessment signals are used in these contexts, but they communicate only about the current interaction. Among species in quadrant II, signals serve to coordinate activities and maintain cohesive spatial associations, but social interactions are not based on differentiated social relationships. Examples include schooling fish that execute sophisticated antipredator maneuvers (Pitcher and Wyche 1983).

In the upper half of figure 4 we find animals that live in complex societies, defined by de Waal and Tyack (2003*b*) as societies that are individualized, longitudinally stable, and probably characterized by strong learning effects on social behavior and survival strategies. It is only in these societies that we expect to find signals by which individuals can convey the relationship qualities and processes described at the beginning of this section. We expect the evolution of communicative abilities to differ among taxa that fall in quadrants III and IV mainly because of differences in the degree to which individuals need to negotiate conflicts of interest immediately when extended separation is not a common option (quadrant III) or the degree to which they need to resolve uncertainties about relationships in the face of frequent separations (quadrant IV). We suggest that when fissioning is a viable ecological option, conflicts can be avoided instead of deliberately resolved. Prolonged, elaborate displays may be warranted during reunions when fissioning is rare (quadrant III), whereas simple greeting interactions of shorter duration may suffice when fission-fusion dynamics are common (quadrant IV) (Aureli and Schaffner 2007). Finally, different degrees of social complexity and sophistication in signaling should occur depending on whether species arrived in quadrant IV via route A or route B. Individuals from route B (e.g., lesser galagos) will have a more limited range of signals than individuals from route A (e.g., chimpanzees).

Additional Factors

Local ecological conditions can result in interspecific variation that affects the relative placement of taxa within quadrants III or IV. We identify two parallel gradients in our qualitative assessment of primates (dotted lines in fig. 4), each of which reflects the range spanned by taxa with evolutionarily distinct life histories. The upper gradient represents taxa with comparatively slow life histories, such as the atelins, apes, capuchin monkeys, and several Old World monkeys, while the lower gradient represents taxa with comparatively fast life histories, such as galagos and callitrichids. Taxa with slower life histories tend to have more complex and differentiated social relationships, based on their slower rates of development and longer life spans (Charnov 1991), than those with faster life histories when their degree of cohesiveness is similar.

Our landscape accounts for the differences in the employment of signals by populations of the same or closely related species whose cohesion and quality of social relationships affect their respective positions in any of the quadrants. For example, the specialized reconciliation gestures observed in some captive chimpanzees (de Waal and Roosmalen 1979) are apparently absent in wild populations (Arnold and Whiten 2001), possibly because the increased spatial cohesion imposed by captivity necessitates more explicit, unambiguous

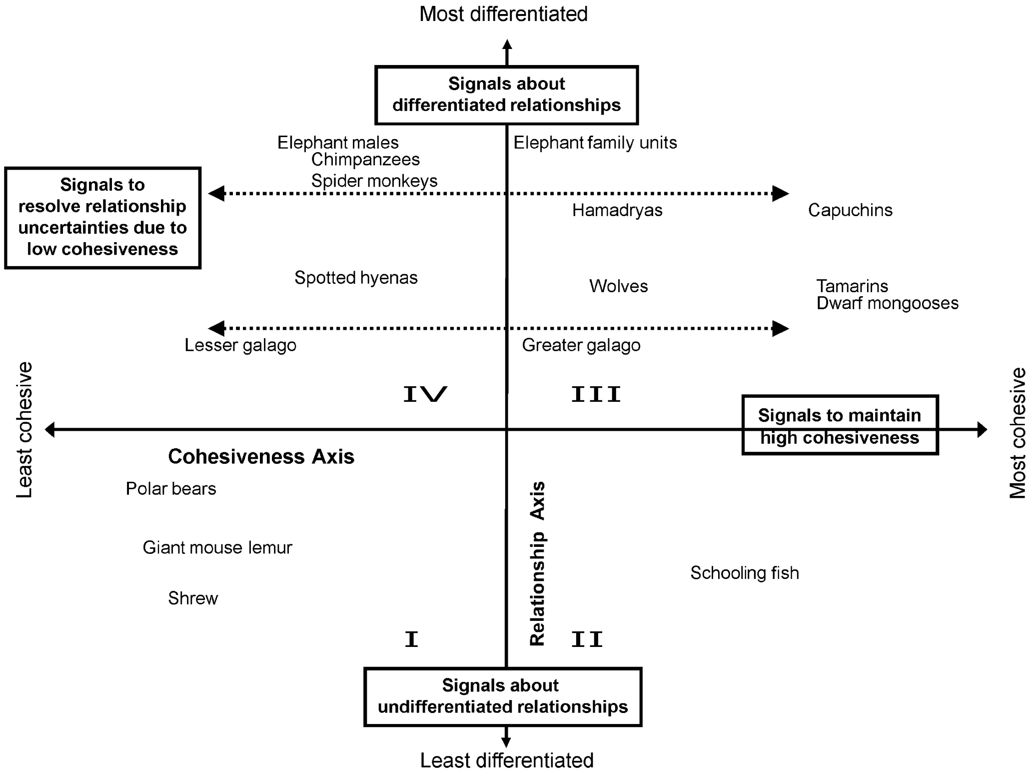

Figure 4. Social landscape and its implications for social signals. The *X*-axis represents the degree of cohesiveness, while the *Y*-axis represents the degree of differentiation of social relationships. The type and frequency of signals required to maintain the corresponding range of social associations emerges as an interaction of the two axes within the social landscape space. The position of species on the landscape is meant to be relative and not absolute. To illustrate the variation that is captured by our framework, several primate species have been placed within the landscape. The utility of the landscape is further demonstrated by the placement of several carnivore species. Polar bears are largely solitary and fall within quadrant I. Dwarf mongooses, wolves, and spotted hyenas fall above the *X*-axis because they are group-living species with highly individualized relationships but differ in the extent of cohesiveness (Holekamp, Boydston, and Smale 2000). Intraspecific variation may also be illustrated within the landscape. For example, female and male African elephants are positioned along the *X*-axis to reflect the sex difference in cohesiveness (see CA+ online supplement B).

reconciliation signals than in the wild, where spatial separation through fission is an option. The gradients, which express the interacting effects of ecology and phylogeny, provide an additional basis for predictions about the way intraspecific variation in signals might vary with a taxon's life-history pattern. An additional factor affecting signaling is an individual's range of social opportunities (see CA+ online supplement F).

This framework for the evolution of social signaling generates a suite of testable hypotheses about the minimum requirements that different kinds of social patterns impose on communication. We have focused on the functions rather than the forms of social signals. However, consideration of the ways in which different modes of communication permit individuals to keep track of one another without maintaining spatial cohesion is a critical next step (Kummer 2002; see CA+ online supplement G for examples). The parallel gradients that distinguish species according to their life-history patterns, the impact of variation in social opportunities (supplement F), the evolutionary route followed to reach their position in the multidimensional fission-fusion space, and the different abilities to coordinate their activities over space and time provide additional variables around which future comparative studies on the role of communication in regulating social relationships can be designed.

Cognitive Demands of Fission-Fusion Dynamics[4]

Chimpanzees, elephants, and dolphins—all taxa characterized by a high degree of fission-fusion dynamics—are renowned for having relatively large brains and advanced cognitive abilities. One might argue that possessing these characteristics and living in higher-FF groups fit together in a causal manner, but this is not necessarily true. Here we explore this issue and propose a framework for identifying some of the cognitive abilities we expect to find enhanced among animals living in higher-FF groups.

The Role of Evolutionary History

Chimpanzees, elephants, and dolphins are special in that they display an array of cognitive abilities that are not found in many other animals, one of which is the apparently sophisticated manner in which they manage their social relationships over both space and time (de Waal and Tyack 2003*a*). They each have particular evolutionary histories and share a number of characteristics (e.g., slow life histories and long developmental periods), any and all of which may have influenced their cognitive abilities. Living in higher-FF groups, therefore, may be not a causal factor but simply a correlate of enhanced brain power.

Even if living in higher-FF groups has evolutionarily consequences, its effects may well be contingent on what evolution was given to work with in the first place. When considering the whole array of species living in higher-FF groups, as in the case of communication discussed above, we need to recognize the variation in cognitive abilities among these species, which is strongly dependent on the phylogenetic route by which a social organization with a higher degree of fission-fusion dynamics was achieved. For example, the ancestors of modern chimpanzees were likely group-living primates with the cognitive abilities to weigh the costs and benefits of interacting with multiple group members in ways dependent on current circumstances (route A in fig. 3). This capacity could then be used in the fission-fusion context characterized by broader temporal and spatial scales. In this respect, chimpanzees stand in contrast to some other primates, like galagos, which have moved during their evolutionary histories from a solitary state toward a more social state in higher-FF groups (route B in fig. 3; Bearder 1999). In these cases, it is a matter not of employing an already existing set of social skills in a new context but of developing them de novo. We should not assume, therefore, that a higher degree of fission-fusion dynamics automatically endows all species with the same cognitive abilities. Rather, given that a high degree of fission-fusion dynamics evolved multiple times in a wide range of taxa (from fish to birds to mammals), we should expect that cognitive adaptations to such dynamics are both variable and strongly influenced by the species' evolutionary history, in addition to the nature of fission-fusion dynamics (supplement B) and the degree of differentiation of social relationships (from simple aggregations to complex societies; fig. 4). Comparative studies of cognitive adaptations to different degrees of fission-fusion dynamics should therefore use appropriate phylogenetic methods (e.g., Pagel and Harvey 1991; Nunn and Barton 2001).

The Demands of Sociospatial Flexibility

Another important issue is whether species living in higher-FF groups have greater cognitive abilities than species that share an evolutionary history but live in lower-FF groups. We focus here on taxa that derive from group-living ancestors (route A in fig. 3). When comparing species living in higher- and lower-FF groups, we must recognize that each kind of group offers opportunities for new skills to develop but also for certain selection pressures to be relaxed. We should therefore not assume that one kind of group necessarily produces greater cognitive abilities or "social intelligence" than another. With this in mind, we can formulate a framework regarding the cognitive demands that the sociospatial flexibility of different fission-fusion dynamics may impose and use this to develop testable hypotheses.

The degree of fission-fusion dynamics experienced may make different demands on the various cognitive processes involved in the acquisition, storage, processing, and use of social information. At present, it is not clear whether any cognitive abilities are unique to higher-FF taxa, although various suggestions have been made (Barrett, Henzi, and Dunbar 2003; Boesch and Boesch-Achermann 2000; Dunbar 2003; Milton 2000; Skoyles and Sagan 2002), and it seems most parsimonious to assume that we are dealing with relative enhancement of certain cognitive abilities rather than a suite of new skills.

Living in lower-FF groups may impose greater demands on information acquisition than living in higher-FF groups because normally there are more group members present (and for longer periods) in the former than in the latter. Thus, members of lower-FF groups are constantly bombarded with social information that often involves multiple partners engaged in fast-paced interactions. It is even possible that members of lower-FF groups cope with such massive amounts of social information by paying selective attention to certain stimuli and filtering out redundant or unnecessary information. By contrast, individuals living in higher-FF groups may display an enhanced ability to pick up subtle social cues and to use behaviors designed to probe others and extract relevant information from them (e.g., behaviors designed to

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[4] Filippo Aureli, Josep Call, Richard Connor, and Kay Holekamp (in alphabetical order) have principal responsibility for this section.

test bonds; Zahavi 1977). These enhanced information acquisition skills may allow individuals to detect altered relationships among individuals who have temporarily been in a different party (Connor 2007). Among higher-FF taxa, these abilities are likely more important where party composition is highly variable (e.g., chimpanzees) than where the majority of social interactions take place within parties with mostly fixed composition, although such parties fission and fuse with others to form multilevel societies (e.g., hamadryas baboons).

The storage and processing of information appear more demanding in higher-FF than in lower-FF groups. This is a direct consequence of the patchier information gathered by individuals in the former. At the most basic level, these individuals must remember the members of their own group for longer periods because they are not exposed to them continuously. Moreover, because of changing party composition, these individuals have to keep track not only of who was involved in a particular interaction but also of who else was present (or absent) at the event. There is some evidence suggesting that chimpanzees can encode who witnessed an event, such as a particular food-baiting episode (Hare, Call, and Tomasello 2001), but comparative systematic data are needed for appropriate testing of this hypothesis (and the other hypotheses below).

The dispersed nature of higher-FF groups in space and time may have favored an ability to encode information concerning *who* was involved in *what* interaction and to remember such knowledge over longer periods than would be needed in lower-FF groups. Renegotiating important long-standing relationships (sensu Kummer 1978) because individuals have forgotten where they stand with respect to each other is wasteful of both time and energy. Selection should therefore favor individuals living in higher-FF groups who are able to retain knowledge about partners (and their relationships with others, i.e., third-party relationships) over a long period, even in the absence of those partners, so that they can "pick up where they left off" when they meet again.

The patchy nature of information gathered by members of higher-FF groups may also promote enhancement of various information-processing skills. Inferential skills may enable animals to extract information about relationships among others from cues based on limited dyadic and triadic observations, which may be particularly important when not all interactions can be witnessed. For example, spotted hyenas use transitive inference very effectively in social situations (Engh et al. 2005). Thus, although transitive inference is not exclusive to higher-FF taxa (e.g., pinyon jays; Paz-y-Miño et al. 2004), we predict its enhancement in higher-FF taxa.

It is also possible that, for some higher-FF taxa, the ability to understand relations between relations (analogical reasoning) will be enhanced. This can act as a way of reducing cognitive demands while enhancing cognitive capacity (e.g., by storing information on particular kinds of relationships rather than retaining knowledge of many specific individual interactions; Call 2001). In lower-FF taxa, the need to store such information "off-line" may be reduced by the increased likelihood of witnessing interactions between dyads. Furthermore, in taxa in which fission-fusion dynamics involve parties of mostly fixed composition (e.g., the joining and splitting of stable one-male units of hamadryas baboons), cognitive demands can be reduced by forming equivalence classes (cf. Schusterman, Reichmuth Kastak, and Kastak 2003). For example, it would be easier to remember that "party X" was present during an interaction than to remember the presence of individuals A, B, C, D, and E.

Cognitive demands can also be reduced if assessment and updating of social relationships with various partners are achieved via emotional mediation, which is based on the emotion experienced when partners interact and the role of partner-dependent emotional experience in guiding future interactions (Aureli and Schaffner 2002). Under this scenario, individuals' behavior toward other animals may reflect an emotional response akin to Damasio's (2004) "somatic markers," which guide current action by producing a positive or negative "gut feeling" about another individual based on both experienced and observed interactions involving that individual. This emotional response reflects the nature of past interactions but does not require any active recollection of them or indeed any conscious cognitive response at all, merely a linking of a particular individual and situation with a particular emotional experience. Compared with lower-FF taxa, emotional mediation in higher-FF taxa should be based on a lower sample size of direct observations (because they do not witness all interactions of others) and on more indirect evidence (e.g., detectable changes in the behavior of others toward a particular individual after fusion).

Finally, information should be put to good use, and we can also hypothesize possible differences in this regard between higher-FF and lower-FF taxa. Owing to the changing opportunities of social partners in higher-FF taxa, individuals may possess an enhanced capacity to inhibit and control their responses. For example, given that the appropriate response to a situation may vary depending on party composition, the capacity to inhibit responses under less favorable conditions should prove selectively advantageous. Thus, inhibiting prepotent responses, assessing a situation before acting, and possibly concealing changed relationships at reunions would all be expected to be enhanced in taxa experiencing a higher degree of fission-fusion dynamics. Japanese macaques provide an illustrative example of how members of lower-FF groups may react to sudden changes in group composition without showing appropriate behavioral inhibition. High-ranking juvenile macaques whose relatives have been removed from the group invariably continued to challenge subordinate animals with intact matrilines (Chapais 1992). This led to the high-ranking juveniles losing their dominance rank as a result of the lack of support from their absent relatives. Chimpanzees, in contrast, seem to be able to inhibit aggressive behavior under challenging conditions (Aureli and de Waal 1997). As mentioned above, comparative systematic data are needed for appropriate testing of this and other hypotheses.

The particularly fluid nature of higher-FF groups also may allow individuals to model the future and optimize social outcomes in many situations. For these individuals enhanced planning skills could be especially beneficial by enabling them to "engineer" party composition and associate with the most profitable partners. Chimpanzees seem to display such planning skills during boundary patrols, territorial incursions, and cooperative hunting (Boesch and Boesch-Achermann 2000; Wrangham 1999). There is also some indication of planning for future needs from tool use experiments in bonobos and orangutans (Mulcahy and Call 2006) and from the selection of the most helpful partners in a cooperative task in chimpanzees (Melis, Hare, and Tomasello 2006). In addition, further cognitive demands can be encountered when individuals are in parties of varying size and composition because of a biological market of exchanges (Barrett, Henzi, and Dunbar 2003; see CA+ online supplement H).

In conclusion, if different degrees of fission-fusion dynamics make characteristic cognitive demands on animals, then we should expect to see enhanced abilities of the kind described above in higher-FF taxa compared with closely related taxa living in lower-FF groups. Empirical evidence for such a difference in demands and enhanced abilities is clearly needed. Our framework provides guidance on how to gather such evidence and how to carry out "fair" tests to probe these abilities. In other words, species-appropriate tests should be implemented to reflect the potentially different phylogenetic routes to fission-fusion dynamics and their different underlying brain substrates.

Implications of Fission-Fusion Dynamics for the Evolution of Complex Human Societies[5]

Modern humans (and particularly modern foraging peoples; Marlowe 2005) offer what is in many ways an archetypal example of a higher-FF taxon. We therefore build on issues raised in the preceding sections to investigate how human society—characterized by well-structured social relationships but with a low level of spatial cohesiveness during the day—may have evolved. In trying to understand the origins and evolution of human society, we can usefully ask four questions: (1) To what extent does human society differ from that seen in other anthropoid primates (in particular, in chimpanzees)? (2) By what evolutionary route did modern human social systems evolve? (3) What function(s) do higher-FF groups have for hominids? (4) What cognitive demands do higher-FF groups impose on humans? We do not believe that it is possible to provide definitive answers to any of these questions at present; our intention, rather, is to develop a framework that identifies issues that need to be explored in order to provide those answers.

Human and Ape Social Systems Compared

The social systems of great apes and humans share a low level of spatial cohesiveness but strongly developed social relationships (quadrant IV in fig. 4). Orangutans are clearly the least cohesive of the apes, but they are known to aggregate more when ecological conditions are favorable, and there appears to be some form of a community (Delgado and van Schaik 2000). Even the generally cohesive gorilla groups may be part of some form of multilevel society (Bradley et al. 2004). Our closest relatives, chimpanzees and bonobos, whose physiology and food choice are more comparable to those of humans, have a social system with a high degree of fission-fusion dynamics but also a very high level of cooperation and affiliation within communities. Bonobos differ from chimpanzees mainly in having slightly larger party sizes and a generally higher level of spatial cohesion. In addition, while male alliances are important in chimpanzees, female alliances and male-female alliances are more important in bonobos (Hohmann and Fruth 2002; Parish and de Waal 2000). For simplicity, we limit our framework mainly to a comparison between early humans and chimpanzees (including bonobos, unless stated otherwise).

Humans and chimpanzees share a number of features (see also Layton and Barton 2001; Moore 1996; Nishida and Hiraiwa-Hasegawa 1987): an omnivorous diet associated with cooperative hunting, tool use (though cooperative hunting and tool use may not apply to bonobos), large community size, and higher-FF groups within the context of a multimale/multifemale social organization. There are also a number of shared features that are expressed differently in the two taxa: sexual division of labor (only in humans does this entail a form of mutual dependence), hunting (meat sharing occurs in both chimpanzees and humans, but only in humans do we see prey killed elsewhere and brought back to a camp for distribution), and flexible territoriality. To compare chimpanzees and modern humans regarding territorial tendencies, we first need to understand the phylogenetic connection between human and chimpanzee grouping patterns. If the human band (i.e., overnight camp) corresponds to the chimpanzee community, then the territoriality is more relaxed in modern humans than in chimpanzees. In many hunter-gatherer societies, adult humans of both sexes can readily move (temporarily or permanently) between bands (e.g., Lee 1979, 42; Turnbull 1965, 96; Woodburn 1982, 435). However, if the regional hunter-gatherer community (commonly associated with a unique dialect) corresponds to the chimpanzee community, then territoriality of modern hunter-gatherers is more comparable to that of chimpanzees. Relations between regional communities are more constrained (e.g., Andrews 1996), although exchange across community boundaries does

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[5] Amanda H. Korstjens, Robert Layton, Carel P. van Schaik, Christophe Boesch, and Robin I. M. Dunbar have principal responsibility for this section.

occasionally take place (e.g., McBryde 1978). When we assume that chimpanzee communities should be compared to regional communities (and the cognitive evidence suggests that this is the correct equivalence; Dunbar 1993), then human social evolution has moved toward longer-term association in subunits (i.e., subunits have become more stable).

Finally, human societies differ from those of apes in a number of respects: the recurrent assembly of subunits at an overnight base camp, the presence of social and economic pair bonds, significant alloparental inputs in child rearing, exchange of goods as tokens of social relations, and, perhaps rather obviously, the use of language in regulating relationships (see also Dunbar 1993; Marlowe 2005; Rodseth et al. 1991). These differences are numerically and qualitatively sufficiently large that they are unlikely to have arisen at the same time, which raises the second issue of our framework: how were these differences acquired in the hominid lineage?

Phylogeny and Function for Human Higher-FF Groups

At present, we can say little about the sequence of specific events that occurred in the hominid lineage, but it is likely that human higher-FF groups derived from group-living species that depended on cooperation and had various social skills (e.g., conflict resolution [Aureli and de Waal 2000] and alliance formation [Harcourt and de Waal 1992]) useful for maintaining social relationships in spite of low spatial cohesion (route A in fig. 3). The best we can do is to assume that whatever chimpanzee and bonobo societies have in common with those of modern humans resembles those of their common ancestor (Moore 1996) and then ask what changes had to be made and in what sequence in order for the differences to develop. Because these changes are inevitably linked to the *function* of fission and fusion, the third question of our framework is embedded in the discussion below.

Most of the differences we have listed between chimpanzee and human societies are unique features of humans and probably evolved fairly recently in human evolutionary history. The use of sites where the community aggregates at night (i.e., a possible precursor of home bases), however, is common in many primates (although not in chimpanzees or bonobos). The use of a limited number of sleeping sites is driven by predation pressure and the availability of safe refuges that are large enough for the group (Anderson 2000). If the society has a relatively low level of spatial cohesiveness, a lack of safe sleeping sites or extreme predation risk may force the group members to come together at night. Such a situation is especially obvious in hamadryas baboons (Kummer 1995), though similar patterns may be seen in all *Papio* baboons. The fact that baboons live in as large a variety of habitats as our earliest ancestors did (from rain forests to open savannah areas), including more open and drier habitats than those where modern chimpanzees occur, seems relevant, given that *Papio* and our earliest ancestors emerged at about the same time (Jolly 2001; Moore 1996). We envisage an evolutionary path in which a chimpanzee-like hominid ancestor, with a low degree of spatial cohesiveness but highly structured social relationships, started to exploit not just forests but also more open savannah/woodland environments. In such environments, daytime food-searching demands required individuals to forage in small parties, as do contemporary chimpanzees in forested habitats and baboons in dry savanna habitats (Nishida and Hiraiwa-Hasegawa 1987; Stammbach 1987). However, some variable—most likely the rarity of essential resources such as safe refuges at night (with an increased risk of predation in the more open habitat) or waterholes (scarce in savannah habitats but less so in forests)—forced individuals to aggregate once a day in large groups that contained the entire band or community, as happens in hamadryas baboons (Stammbach 1987) but not in contemporary woodland and forest chimpanzees (Nishida and Hiraiwa-Hasegawa 1987).

Coming together at night and at waterholes is not the only difference in fission-fusion dynamics between chimpanzees and baboons: they also differ in the types of parties that are commonly formed. As discussed earlier, in hamadryas baboons large night aggregations split into smaller foraging parties based on one-male units during the course of the day, whereas in chimpanzees community members are very rarely all together and form parties rather independently. This difference can have a major impact on the level of cooperation among community members. A chimpanzee-like system may be more conducive to cooperation (as seen among chimpanzee males during hunting of difficult prey and border patrols) than a hamadryas baboonlike system because all members of a chimpanzee community may regularly interact affiliatively when they meet in different parties. In a baboonlike system individuals always remain in the same party (at the smallest unit level), and there is little affiliative interaction between members of different parties.

We do not know what kind of aggregation or dispersal behavior may have occurred among australopithecines, but most paleoanthropologists agree that australopithecines were highly sexually dimorphic (similar to baboons) and that, therefore, neither a chimpanzee-like social system nor one approximating that of modern hunter-gatherers was found among them. Rather, intermale competition may have been as strong as it is in baboons (Foley and Lee 1989; Plavcan and van Schaik 1997), which tends to reduce levels of cooperation among males. Indeed, what was once thought to be evidence for "home bases" among early Palaeolithic hominids is now discounted because the accumulations of tools and bones are considered to have been caused by transport in streams or flash floods (Binford 1987; Stern 1993). All we can say at this stage is that the typical chimpanzee strategy of building nests wherever individuals happen to find themselves at nightfall would have been constrained by the occurrence of fewer suitable sites in more open savannah/woodland environments. We stress nonetheless that this hypothetical formation of large groups at least once a day at a safe location would, in a society in which cooperation is common, offer a whole new set of opportunities, especially for a large-brained primate like our ancestor. Some of the benefits of aggregating once a day do not require anything as advanced as a home base—only that individuals spend a relatively long period of social time in each other's presence while not engaged in activities such as foraging, hunting, or patrolling their boundaries.

As the daily aggregation at a safe limiting resource evolved into a home base in later *Homo* species, fusing at nighttime may have offered the opportunity for sexual division of labor, whereby gatherers and hunters shared their spoils at the end of the day (Key and Aiello 2000). Some degree of resource redistribution would have been allowed by alloparenting (Kennedy 2003), costly signaling by males, and perhaps pair bonding; the latter could have allowed pooling of resources within a domestic unit in a context in which confidence in reciprocity of food transfers was maximized (a feature that may have been reinforced *or* actively selected for by the parental investment demands of increasing brain size; Key and Aiello 2000). Because the weakest individuals no longer had to leave the safety of the home base to forage, the home base would presumably have increased the survival chances of the weakest individuals (e.g., young children, older people, women with newborns, and heavily pregnant women), who could nonetheless have performed essential tasks there such as child care. At this stage, the sharing of spoils means that individuals in the community could distribute themselves optimally over the area to increase efficient use of resources. Eventually, this could have given rise to the multilayered society of modern hunter-gatherers, in which survival risks were further reduced through cooperation between different bands in the form of trading and allowing some trespassing onto each other's territory (Klein 1999; Layton and Barton 2001). Many of these latter changes imply significant demands in terms of social skills and may have selected for the evolution of larger brains (see CA+ online supplement I for archeological evidence).

Cognitive Demands of Human Higher-FF Groups

This leads us to the last of the four questions of our framework, because the scale of human social groups (and, in particular, the size and dispersion of forager *communities*, in combination with a gathering at home bases) must inevitably impose considerable demands on human cognition (Aiello and Dunbar 1993). We would simply stress that a high degree of fission-fusion dynamics may be cognitively taxing and, without the gathering of individuals at night, may undermine high degrees of cooperation for two reasons. First, fission-fusion dynamics do not allow for regular updating of information about social relationships in the community, and this makes it more difficult for individuals to depend on a relationship when individuals are spatially dispersed. Second, regular fission and fusion creates opportunities for free riders (Enquist and Leimar 1993) because it is impossible to monitor each individual's behavior while the group is dispersed. Coming together daily not only allows individuals to reinforce bonds but also provides opportunities to observe the social interactions taking place among other individuals (and thus update reputations) and additionally forces individuals to resolve conflicts in order to reduce tensions in the group instead of simply avoiding one another. In combination with the cognitive abilities of great apes and their tendency toward complex social relationships, this could have been the point of departure for the high level of cooperation and the evolution of complex symbols to indicate intentions that we observe in hominids. Social learning and information exchange at these daily gatherings are likely to have increased the development of a society with highly structured social relationships and elaborate signals. Even though the original need for fusing on a daily basis may have disappeared as hominids came to occupy various environments, the other benefits of doing so may have been the evolutionary adaptation that allowed our ancestors to become a highly adaptable species, capable of spreading across the world.

Conclusions

The five interlinked sections of this article propose several new frameworks within which to pursue research on a range of topics that we believe are particularly relevant to fission-fusion dynamics. In the years since the term "fission-fusion" was first introduced (Kummer 1971), research in this area has been rather patchy and has focused on only a limited number of topics. For example, significant methodological improvement for the recognition of nonrandom association patterns has been made (supplement A), and several socio-ecological factors influencing party size have been identified (e.g., Chapman, Wrangham, and Chapman 1995; Lehmann and Boesch 2004; Mitani, Watts, and Lwanga 2002). Less attention has been paid to other aspects of fission-fusion dynamics, such as the rate of change in party size or the extent to which parties, when they do form, are composed of the same set of individuals.

A possible reason for the lack of more systematic investigation of fission-fusion dynamics is the tendency for researchers to adhere to a dichotomous perspective on flexible versus cohesive organizations and to focus on the so-called fission-fusion societies of chimpanzees and spider monkeys. We believe that much progress can be achieved by acknowledging that this is a false dichotomy and by recognizing that fission-fusion dynamics occur to some extent in most social systems (cf. Kinzey and Cunningham 1994; Strier 1989; Struhsaker and Leland 1979; Sussman and Garber 2007). We reiterate, therefore, that a starting point for a renewed research input is the adoption of a relativistic approach that places species—and even populations of the same species—within a complex, multidimensional fission-fusion space of the sort illustrated in figure 1. Higher- and lower-FF groups refer to relative positions within such a space, and comparisons between taxa and populations need to be interpreted within this framework.

A second critical point we have stressed is the pressing need for primatologists—and other researchers interested in the evolution of flexible patterns of social organization—to develop new null models against which the associations of individuals can be compared. The generalized modeling framework of spatially explicit agent-based simulation is a powerful tool that can be applied to many different taxa. Another critical point emphasized in our frameworks is that the evolutionary route followed to reach a given degree of fission-fusion dynamics has fundamental implications for the types of social and cognitive skills the organism may possess. This means that two species that lie relatively close to one another in the multidimensional fission-fusion space may nonetheless differ in important respects depending on their phylogenetic background. Thus, interspecific comparisons need to take evolutionary history into account (Pagel and Harvey 1991; Nunn and Barton 2001).

The relativistic approach based on the degree of fission-fusion dynamics within such an evolutionary framework provides an effective way to evaluate patterns of communication across taxa. Given similar differentiation of social relationships, we expect that communication in lower-FF groups will be focused on coordinating movement, resolving conflicts, and promoting cooperation, whereas the communication systems of higher-FF groups must accommodate the additional requirements of routinely negotiating separations, reestablishing relationships, and reducing tension at reunions. In addition, while carrying out comparative analyses, we need to be aware that higher-FF groups may have evolved either from rather solitary species with limited social skills or from relatively cohesive groups that already possessed effective means for maintaining differentiated relationships. Furthermore, despite the fact that many animals living in higher-FF groups have large brains and sophisticated cognitive abilities, we suggest that a higher degree of fission-fusion dynamics does not necessarily impose selection pressures that promote the evolution of novel forms of "social intelligence." However, evolutionary enhancement of existing cognitive skills may increase fitness in higher-FF taxa and thus promote cognitive attributes such as long-term memory about who did what to whom and the inferential abilities necessary to put together patchy social information. Finally, the nature of fission-fusion dynamics of early hominids, in particular the suggested combination of both a high degree of interaction among community members due to frequent changes in party composition and a tendency to reunite on a daily basis, may have strongly influenced the evolution of the highly adaptable and cognitively sophisticated species that we are today.

Given these premises, the proposed frameworks we advocate here are expected to stimulate new momentum in the investigation of whether qualitative or quantitative differences in fact exist between species or populations in the underlying socioecological conditions, communication skills, or required cognitive abilities, depending on their degree of fission-fusion dynamics. Because higher-FF groups occur in a wide variety of taxa, a broad comparative perspective, not limited to primates, should help elucidate underlying principles and also highlight fundamental differences due to evolutionary history. This perspective could also be highly beneficial in increasing our understanding of the causes of the variability in human fission-fusion dynamics and the evolution of our complex societies.

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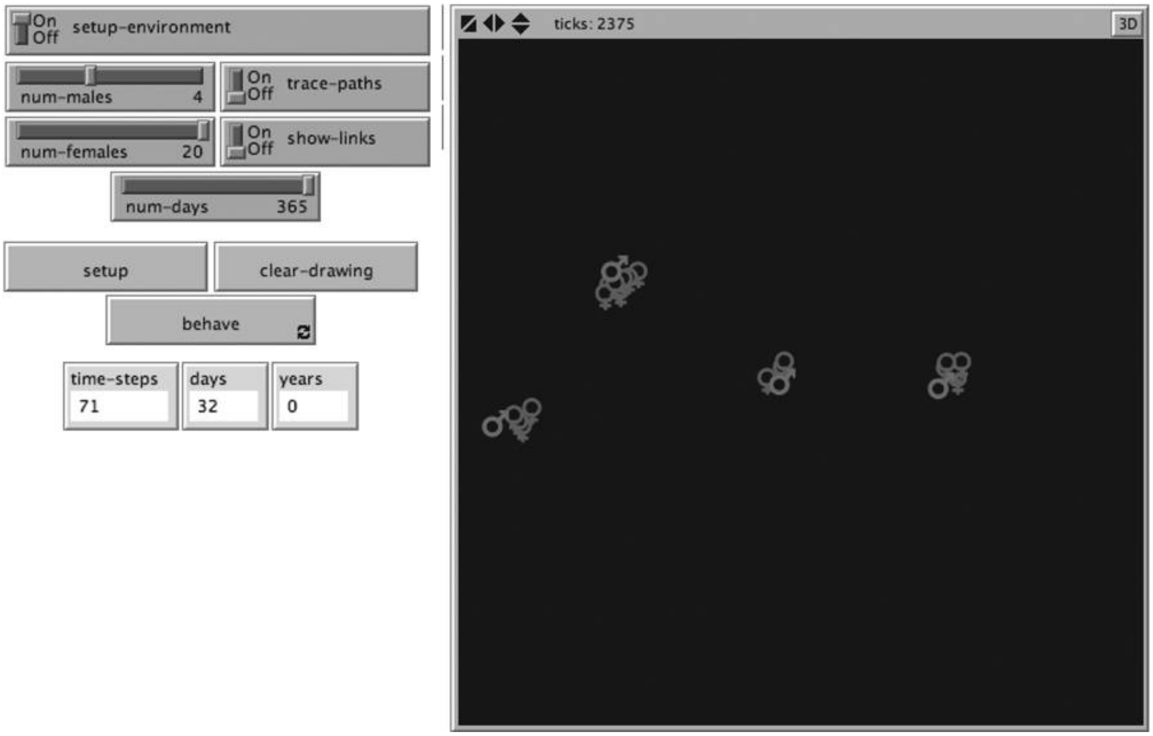
Comments

Reply

Our main aim was to propose new frameworks for the study of fission-fusion dynamics. We are pleased to have Kummer's welcoming words for a comprehensive revival of the topic. We recognized that important starting points for a renewed research impetus are the rejection of the false dichotomy between flexible and cohesive organizations and the adoption of a relativistic approach. Fission-fusion dynamics occur to some extent in most social systems.

We are grateful to the commentators for their stimulating comments showing how our proposed frameworks may be expanded in various directions. We find Izar's enthusiasm for applying our conceptual framework of spatiotemporal variation and multidimensional fission-fusion space to the social dynamics of wild populations of tufted capuchin monkeys very encouraging. We hope that others will find our frameworks useful for explaining the grouping patterns of their study species and integrating them with those observed in different populations and different taxa.

We are pleased to receive Izar's and Talebi's comments supporting our proposal of reevaluating the assumptions of traditional socioecological models by using spatially explicit agent-based simulations, and we agree wholeheartedly with Yamagiwa's remark that we need to incorporate multiple factors into null models of association. That is a point we tried to make in our article. In fact, the flexibility of the agent-based approach makes it an especially powerful tool for exploring, in a controlled way, the influence of a range of factors, both individually and simultaneously. Yamagiwa remarks that the same position of different taxa in the three-dimensional fission-fusion space (fig. 1) does not mean that the same exogenous factors are affecting the fission-fusion dynamics of those taxa. We are perfectly comfortable with this position, as different taxa may show the same quantification of fission-fusion dynamics for different reasons. This emphasizes that



num-males 4
num-females 20
num-days 365
time-steps 71
days 32
years 0
ticks: 2375

Figure 5. One frame in the running of a simple agent-based simulation model of association patterns among hamadryas baboons (A. Di Fiore, unpublished data). In this model, 20 females move randomly but also follow a simple flocking algorithm, moving in coordination with other females when they get close to them. When females get close to a male "leader," they preferentially follow the male. The four males in this run of the model also move randomly, but they are intolerant of one another and turn away from one another when they get close. With these two different classes of behavioral rules—one for females and one for males—"harem" subgroups of female agents form around male "leaders." At this point in the run, for example, harem sizes for the four males are nine, four, four, and three females. Harem compositions remain generally stable, but some interactions between males, depending on the spatial details of those interactions, can result in the transfer of particular females between harems.

in addition to being able to describe and compare the actual fission-fusion dynamics across taxa, we need to study why those dynamics take the form that they do. The various sections of our article propose frameworks to address that question.

Kummer's commentary raises a very good point that we did not discuss: the roles that certain key individuals or classes of individuals can play in structuring subgroups (e.g., via mutual attraction of animals to a particular leader). This aspect, however, can easily be incorporated into agent-based models by ascribing characteristics to particular agents. For example, one might add the behavioral rule "agents follow animal A" when they get close to it or set a measure of "intolerance" between animals A and B to be high, such that when they get near each other, they (and their followers) split. The agent-based models can help us explore relevant social interactions or social roles just as easily as we can evaluate the influence of the environment on association patterns—a point we do make explicitly in the article. For example, figure 5 shows the output of a simple simulation model with "male" and "female" agents that follow different behavioral rules. In this model females move randomly but also follow a simple flocking algorithm and coordinate their movement with conspecifics when close to them; when they are close to a male, they preferentially follow the male. Males also move randomly but do not follow a flocking algorithm, and they are intolerant of one another; when males get close to another male, both turn away. With these simple rules, subgroups of female agents form around "leader males."

Kerth and Kummer both correctly point out that observed fission-fusion patterns derive from individual decisions that, in turn, are products of evolved goals and motives that may differ among individuals. Both cite experimental studies that have elucidated the links between ecological variables, individual psychology, and the collective decisions that produce fission and fusion events. We agree that experimental approaches, which we did not discuss in our article, can yield important data with which to address the questions we have raised. For example, Meunier et al. (2006) have shown that captive white-faced capuchins differed in their tendency to follow group members when choosing a travel direction in search of food. Subordinate females were least likely to conform to majority decisions, as would be expected if they had learned to expect exclusion from food while accompanied by dominants. We anticipate and encourage similar research that can be incorporated with our relativistic approach on fission-fusion dynamics.

The social constraints on party size and composition discussed by Kummer are perfectly compatible with the frameworks presented in our article. As we mentioned, agent-based models can include rules instantiating socially differentiated agents. Negotiating travel routes and meeting points, as hamadryas baboons accomplish in the fascinating and intricate ways documented years ago by Kummer and his colleagues, are among the social tasks that drew our attention in "Implications of Fission-Fusion Dynamics for Communication," though space limitations precluded specific discussion of them. Kummer's lead in this area needs to be followed seriously.

Yamagiwa asks us to consider generally the evolutionary origins and functions of primate sociality. Other authors (Dunbar 1988; Isbell 1991; Sterck, Watts, and van Schaik 1997; van Schaik 1989; Wrangham 1980) have tackled these questions, and they remain unsettled. Our point in figure 3 was not to rehash these debates but to draw a distinction between the hypothesized effects on fission-fusion dynamics of two general evolutionary routes to group living that differ in the importance of differentiated social relationships. Yamagiwa also draws attention to sex-differentiated dispersal and its implications for comparative analyses. Clearly, philopatric individuals are more likely than dispersing individuals to be more closely related to—and possibly more familiar with—potential social partners. This variation could influence sex differences in the costs and benefits of gregariousness and therefore could affect fission-fusion dynamics in situations in which party composition is flexible.

We agree with Kerth that more research must be done to test the theoretical prediction that group members should temporarily leave subgroups to avoid group-level decisions that are not in their favor (Conradt and Roper 2005). Fission-fusion dynamics offer opportunities to deal with group-level decisions. For example, and consistent with Kerth, Ebert, and Schmidtke's (2006) findings in bats, the high degree of fission-fusion dynamics permits another nonprimate species, the spotted hyena, to directly benefit the interests of the departing individuals (Smith et al. 2008). Departing from subgroups is typical in the following contexts. First, victims of aggression separate from former opponents to reduce the immediate costs of escalated aggression. Second, mothers reduce infanticide risk by avoiding conspecifics during early lactation. Third, individuals benefit from temporarily departing from group members to hunt alone because lone hunters gain more energy from feeding from ungulate carcasses that they acquire before competitors arrive. Therefore, we suggest that future research must focus on the communication and cognitive demands regarding not only fusion decisions (e.g., Aureli and Schaffner 2007; Smith, Memenis, and Holekamp 2007) but also fission decisions. Both types of decisions should theoretically have large fitness consequences for individuals and, consequently, should strongly affect the way group decisions are made in species from a variety of taxa.

Boehm and Yamagiwa both draw attention to the importance of pair bonding in human social evolution. Boehm is correct to argue that the most basic unit in hunter-gatherer regional networks is the pair-bonded family, which is lacking in great apes. We acknowledge this in our article, and the evolutionary context of pair bonding has been modeled before (e.g., Foley and Lee 1989). We do not dispute the importance of this aspect of human evolution but wish to draw attention to another level of human social organization that we (and Boehm) consider as having received less attention. Social anthropology equated hunter-gatherer society with the band, but early authors (Radcliffe-Brown 1931; Steward 1936) supposed that men remained in the same band all their lives while women transferred from one band to another at marriage. *Pace* Yamagiwa (and in contrast to many previous authors) we do *not* assume such an equivalence; indeed, we suggest rather that it may well be the hunter-gatherer community (or regional grouping) that is the analogue of the chimpanzee community, and that changes what is in need of explanation. As Boehm points out, the band is a much more fluid and permeable grouping than Radcliffe-Brown and Steward appreciated. Despite the advantages of band life, such as developing trust in reciprocal exchange, human adults of both sexes often freely change band membership. Recognizing the evolutionary importance of this aspect, we propose that if the human band is the analogue of the fusion phases in chimpanzee community interaction, then crucial elements in the evolution of human behavior, such as band exogamy and gift exchange, can be explained as responses to the problem of sustaining relationships in a community that is far more dispersed (temporally and spatially) than that of chimpanzees, hence enabling the kind of movement to which Boehm refers. In analyzing these relationships we need to distinguish between function (meat sharing, dispute avoidance) and consequence (gregariousness, long-term kinship relations). The differences in mating strategies between chimpanzees (promiscuity with strong female sexual signals) and humans (small family units with a strong tendency of pair bonding) that Yamagiwa highlights are most likely elements that evolved after humans and chimpanzees diverged from the shared common ancestor. Humans, indeed, are distinguished by their ability to extend pair-bonded-like relationships beyond breeding couples to enduring relationships in wider social networks.

Finally, as pointed out by most commentators and stressed in our article, a broad approach is needed to achieve our main goals. First, we need to populate the multidimensional fission-fusion space with taxa and populations. To do so, we need data from multiple sites for the same species belonging to a large number of primate and nonprimate taxa. With this database comparative analysis of the relation between the extent of fission-fusion dynamics and factors related to socioecology, communication, and cognitive abilities can be carried out taking evolutionary history into account. To understand such dynamics we need long-term field studies, which can be informed by the findings of agent-based simulations and which can, in turn, provide essential data for the implementation of further simulations and generate hypotheses for testing on actual animals. A comparative experimental approach, along with better knowledge of comparative brain structures and functioning, not limited to primates and possibly beyond mammals, complements the endeavor to understand the impact of fission-fusion dynamics on communication and cognitive abilities. We believe that this broad comparative perspective can identify common underlying principles and critical differences as well as improve our position for understanding the nature of human fission-fusion dynamics and their evolution.

—Filippo Aureli, Colin A. Chapman, Anthony Di Fiore, Robin I. M. Dunbar, Amanda H. Korstjens, Robert Layton, Joseph H. Manson, and Colleen M. Schaffner

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