Social Components of Fitness in Primate Groups

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fitness (i.e., at the end of its lifetime) than pursuing more individualistic strategies.

What Microneurobiology Has to Tell Us

There has, of course, been growing interest in recent years in some of the neurobiological correlates of social bonding. Particular interest has focused the role of oxytocin (and its male equivalent, vasopressin) in pairbonded species (*40*), but other neuropeptides have also been identified as playing an important role in social bonding [e.g., endorphins (*41*)]. In addition, a parallel interest has been developing in the role of several specific neuronal assemblages, including mirror neurons (*42*) and so-called spindle cells in the anterior cingulate cortex (*43*), as well as in specific genes such as GLUD2 [a retrogene, derived from glutamate dehydrogenase, which is responsible for clearing the by-products of neuron activity (*44*)] and the abnormal spindle-like microcephaly-associated (ASPM) gene and microcephalin, which are implicated in brain growth (*45*).

Each of these has been seen by their respective protagonists as the holy grail for understanding both social cognition generally, and, in particular, for explaining the differences between humans, apes, and monkeys (*43*, *46*). There is no question that these are individually important and novel discoveries, and they undoubtedly all play a role in the nature of sociality. However, there is a great deal more to how and why humans are different from other apes, or why apes are different from monkeys. We will need better studies of cognition and behavior to answer these questions. More important, perhaps, is one key point: Species differences in a handful of very small neuronal components do not explain the apparent need for massive species differences in total brain size. Most of these studies fall into the same trap as the developmental explanations for brain size did in the 1980s: They mistake mechanistic constraints for evolutionary function. It is unclear why this point continues to be ignored, but we will still have a lot of explaining to do about volumetric differences in brains.

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REVIEW

Social Components of Fitness in Primate Groups

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There is much interest in the evolutionary forces that favored the evolution of large brains in the primate order. The social brain hypothesis posits that selection has favored larger brains and more complex cognitive capacities as a means to cope with the challenges of social life. The hypothesis is supported by evidence that shows that group size is linked to various measures of brain size. But it has not been clear how cognitive complexity confers fitness advantages on individuals. Research in the field and laboratory shows that sophisticated social cognition underlies social behavior in primate groups. Moreover, a growing body of evidence suggests that the quality of social relationships has measurable fitness consequences for individuals.

Life in primate groups rivals the best television soap opera—the weak are often exploited by the powerful; strong alliances and lasting bonds are formed; dynasties are established, but are occasionally toppled; and not all of your favorite characters survive the season. Ecological constraints generate the dramatic tension, and natural selection crafts the plot. The complicated storylines reflect the fact that primates have evolved large brains, sophisticated social cognition, and complex social relationships (Fig. 1). There has been considerable discussion of the selective pressures that favor the evolution of large brains in social species (*1*–*4*), but it has has not been clear how large brains, social cognition, and social relationships are translated into fitness advantages for individuals. New evidence indicates that the competitive success and reproductive performance of individuals in primate groups is affected by the nature and quality of the relationships that they form. These data enable us to tie together what we have learned from comparative analyses of brain morphology, experimental studies of social cognition, and naturalistic observations of the structure of social relationships in primate groups.

What the Social Brain Knows

The capacity to develop complex social relationships may be an important benefit derived from having a "social brain." According to the social

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intelligence hypothesis, the challenges of living in social groups have favored the expansion and reorganization of the primate brain (*1*, *2*). The hypothesis is supported by comparative analyses that show that various measures of brain size are positively related to the size of social groups in primates and other taxa. But if it were only the size of social groups that mattered, wildebeest would be wizards. Instead, small-brained wildebeest graze the plains in largely anonymous unstructured herds. The primate's social brain is specially designed to enable individuals to manage social relationships. Thus, brain size is also connected to what goes on within social groups and is correlated with the size of grooming networks that primates form and the frequency of coalitions, social play, tactical deception, innovation, and social learning (*2*).

Primates are endowed with cognitive abilities that are especially well suited to tracking social information. For example, primates are able to recognize individuals; identify kin; compute the value of resources and services; keep track of past interactions with group members; make transitive inferences; discriminate between cooperators and defectors; and assess the qualities of prospective rivals, mates, and allies (*3*–*5*).

Primates also know something about the nature of relationships between other group members (*3*–*5*). The first evidence that primates know something about the relationships of others, which is sometimes called third-party knowledge, came from playback experiments conducted on wild vervet monkeys (*Cercopithecus aethiops*) (*6*). When females heard the screams of their own offspring played from a speaker hidden in the brush, they peered intently into the bushes. Other females sitting nearby did not look for the distressed juvenile, they looked at the mother. Their reactions indicated that they recognized the identity of the caller, and they were able to match the caller to its mother. Similarly, when monkeys are threatened by other group members, they are more likely to redirect aggression toward a relative of a former opponent than toward a random group member (*7*–*10*), and they are more likely to reconcile conflicts with close kin of their former opponents than with individuals who are unrelated to those opponents (*10*, *11*).

Third-party knowledge extends to dominance relationships. For example, male bonnet macaques (*Macaca radiata*) selectively recruit support from males that outrank both themselves and their opponents (*12*), and female monkeys typically support the higher-ranking of two opponents when they intervene in ongoing conflicts (*4*). These recruitment patterns indicate that monkeys know something about the rank relationship between other group members and prefer high-ranking alliance partners over lower-ranking partners. In playback experiments, female baboons (*Papio cynocephalus*) responded more strongly to sequences of calls that simulated rank reversals between females within their groups than to sequences of calls that fit the existing dominance order. Their reactions suggest that the females were aware of the rank relationships between other females and were surprised when interactions confounded their expectations. Similarly, male baboons' reactions to simulated contests between closely ranked and distantly ranked pairs of males suggest that they can assess the rank distance between other males (*13*).

Primates also monitor the quality of relationships between other group members. Hamadryas baboons (*P. hamadryas*), which form one-male groups, do not attempt to take females from rival males when they see that the male and female have formed close bonds (*14*). Playback experiments conducted on chacma baboons indicate that males keep track of the mate-guarding activities of high-ranking males and respond with alacrity when they hear sequences of vocalizations that suggest that consortships have been disrupted and mating opportunities might be available (*15*). When white-faced capuchin monkeys (*Cebus capucinus*) recruit allies, they take into account the quality of relationships between themselves, their opponents, and potential allies (*16*). They selectively solicit support from group members who have stronger relationships with themselves than with their opponents.

The Structure of Social Bonds

Female baboons, macaques, and vervets provide a particularly well-documented example of the complex adaptive design of social relationships. Females in these species remain in their natal groups throughout their lives, whereas males disperse to prevent inbreeding (*17*, *18*). Groups may number 20 to 100 individuals and usually contain multiple matrilines (sets of females related through maternal kinship lines). Females spend a substantial amount of time each day grooming and resting in the company of other group members. Females discriminate among potential partners and show strong biases in favor of close maternal kin (Fig. 2). Recent evidence indicates that nepotistic biases also extend to paternal kin, as females preferentially groom and associate with their paternal half-sisters (*19*–*21*). Paternal kin ties often cut across matrilines.

In the Amboseli Basin of Kenya, some pairs of female baboons, particularly close maternal kin, form close and stable relationships (*22*). Females' preferences for partners are influenced by the quality of their interactions. Females who form enduring social bonds groom more equitably than females who have more ephemeral relationships (Fig. 3), and this pattern holds for both maternal kin and others. We do not know whether females come to groom more equitably as their relationships become stronger or females preferentially maintain close relationships with those who groom them equitably.

Kin biases in behavior are common among animals, but female macaques, baboons, and vervets take nepotism one step further. They form matrilineal dominance hierarchies in which maternal kin occupy adjacent ranks: When they mature, daughters attain ranks just below their mothers, and younger sisters outrank older sisters (*23*). Coalitionary support plays an important role in this process, because immature females are selectively supported by close female relatives when they are involved in conflicts with members of lower-ranking matrilines. Eventually, young females are able to defeat everyone that their mothers can defeat. The importance of maternal support for females is

Fig. 1. Many primates, like these baboons in the Amboseli basin of Kenya, live in large and complex social groups. Baboons have been studied at multiple sites across Africa for decades.

revealed by what happens when mothers are absent. Small juveniles from high-ranking matrilines can defeat larger juveniles from lower-ranking matrilines when their mothers are nearby, but not when their mothers are some distance away (*24–26*). At one site, several female baboons orphaned early in life did not attain the ranks formerly held by their mothers (*27*, *28*).

Dominance relationships among females remain remarkably stable over long periods, even generations (*18*). There is some dispute about whether coalitionary support plays the same role in maintaining dominance ranks among adult females as it does in establishing rank. Females intervene in conflicts among adult females at very low rates, which might mean that coalitions might play little role in maintaining the stability of dominance hierarchies (*29*). However, the low rate of interventions may underestimate their importance. The presence of potential allies (and knowledge of alliance partnerships) may be enough to deter challenges (*30*). Moreover, females sometimes give vocal threats when they witness agonistic interactions. In the Okavango Delta, vocal responses are considerably more common than active intervention and appear to play a similar role (*31*).

The Function of Social Bonds

Several lines of evidence suggest that affiliative social relationships matter to females. Females preserve time for socializing, even under harsh environmental conditions. In the dry season when food is scarce, female baboons spend more time foraging and moving between feeding sites and less time resting (*32*). However, they do not reduce the amount of time that they spend grooming and interacting peacefully with group members.

Females are strongly affected by the loss of preferred companions. In the Moremi Reserve of the Okavango Delta, where predation rates are high, females who suddenly lost close kin experienced significant increases in glucocorticoid levels (*33*, *34*), indicating increased stress. These females' responses were not simply the result of living through stressful events, because females who were present in the group at the same time, but did not suffer personal losses, were unaffected.

Females make adjustments in their social networks in response to demographic changes within their groups. In the Amboseli basin of Kenya, mothers and daughters form particularly close and enduring social bonds, but relationships among sisters are more variable in strength and stability (*21*, *22*). Pairs of maternal and paternal sisters whose mothers are not present in the group have closer relationships than do sisters whose mothers are present in the group. In Moremi, females also compensate for the loss of favorite partners by adjusting their social networks (*33*). Females who lose close kin devote more time to grooming and expand the number of females that they groom in the weeks after the loss.

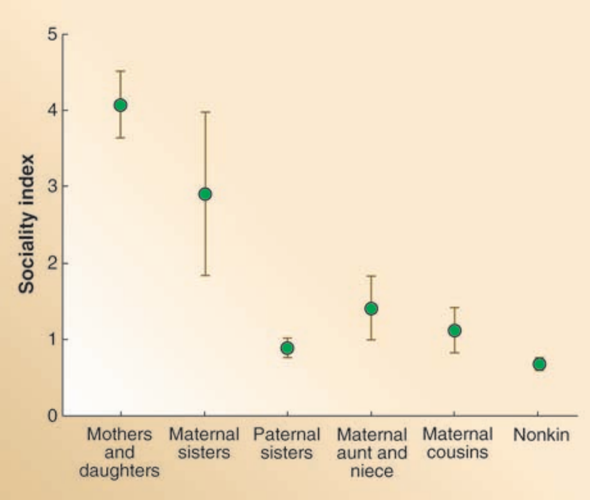

Fig. 2. The relationship between maternal and paternal kinship and the strength of social bonds among female baboons. The category of relatedness is plotted on the *x* axis, and the mean and standard error of values of the sociality index are plotted on the *y* axis. The sociality index is a composite measure of dyadic relationship strength based on the frequency of grooming and proximity. [Redrawn from (*22*)]

Further evidence of the importance of social bonds comes from studies of close associations that mothers of newborn infants form with adult males. Mothers are mainly responsible for maintaining proximity to their male associates, and they groom males much more than they are groomed in return (*35*, *36*). Observational data (*35*) and field playback experiments (*36*) indicate that males preferentially protect their female associates from harassment. The value and scope of such protection may vary across sites (*37*). In southern Africa, where immigrant males often kill unweaned infants and infanticide is a major cause of infant mortality (*38*), new mothers are fearful of immigrant males. Lactating females' glucocorticoid levels rise substantially when new males join the group and acquire high-ranking positions (*39*, *40*). However, mothers who have established friendships with adult males experience smaller increases in glucocorticoid levels than do mothers who have not established such associations. In East Africa, infanticide is much less common, but mothers and their offspring may still gain benefits from their associations with adult males. In Amboseli, adult males preferentially support their own juvenile offspring when they are involved in agonistic disputes (*41*).

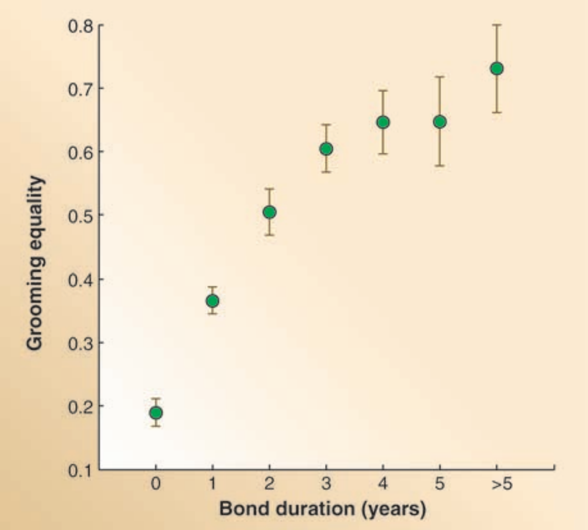

Fig. 3. The relationship between grooming equality and bond stability among baboon females. Bond stability is measured as the number of consecutive years in which the same female was among a given female's top three partners (based on the sociality index measure described in Fig. 2). Grooming equality is a measure of the distribution of grooming within dyads, and varies from 0 when grooming is completely one-sided to 1 when grooming is evenly balanced. The mean and standard error of values for adult females are shown. [Redrawn from (*21*)]

A direct chain of connections links social bonds to fitness outcomes in primate species with matrilineal dominance hierarchies. Social bonds enhance the prospects for obtaining coalitionary support, coalitionary support affects dominance rank, and dominance rank influences reproductive performance. High-ranking females tend to mature at earlier ages, grow faster, produce healthier infants, have shorter interbirth intervals, and have higher lifetime fitness than low-ranking females (*18*, *42–44*). The magnitude of the effects of dominance rank varies over time and across populations. However, any reproductive advantages that high-ranking females accrue will be magnified over time because dominance ranks typically remain stable across generations. High-ranking females will have high-ranking female descendants.

For female baboons in Amboseli, the fitness consequences of sociality extend beyond the relationship between dominance rank and reproductive performance (Fig. 4). Females who were more fully socially integrated into their

Fig. 4. The mother of a young infant (**center**) is groomed by an adult male (**left**) and another adult female. The female in the center wears a radio collar with an antenna, which allows researchers to locate the group on a regular basis.

groups reproduced more successfully than other females (Fig. 5) (*45*). The positive relationship between sociality and reproductive successs might reflect the fact that some females lived in more favorable habitats or during more favorable time periods than others. These females might have been more social and reproduced more successfully than other females. However, the results remain unchanged when the measures of social integration are corrected to account for group membership and changes in environmental conditions over time. The relationship might also arise because high-ranking females have higher reproductive success and belong to larger matrilines than lower-ranking females do. Again, the relationship between social integration and reproductive success remains significant when dominance rank and lineage size are controlled statistically.

There may be similar connections between sociality and fitness outcomes in other primate taxa, although the evidence is less complete. For example, females living in groups of red howler monkeys (*Alouatta seniculus*) with more close kin had higher reproductive success than females living in groups with fewer close kin (*46*). It is not entirely clear why females benefit from living with close kin. Howler monkeys collectively defend their territories and practice extensive allomaternal care, and it is possible that related females cooperate more effectively in intergroup encounters or provide better care for one another's infants.

Male chimpanzees (*Pan troglodytes*) provide an interesting parallel to philopatric female baboons (Fig. 6). Males remain in their natal groups throughout their lives, whereas females usually disperse (*47*). Chimpanzees form fission/fusion communities and frequently break up into smaller parties. Like female baboons, males spend considerable amounts of time grooming one another and spend much of their time in the company of other males. Male chimpanzees also participate in a number of collective activities, including territorial patrols, coalitionary aggression, cooperative hunting, food sharing, and joint mate-guarding. Males that groom one another often also participate in collective activities together, indicating that males form strong and well-differentiated relationships with one another. At Ngogo in Uganda, male chimpanzees preferentially groom, associate, support, share food, and patrol with their maternal brothers but do not show similar preferences for paternal brothers (*48*).

Males may gain important benefits from the relationships that they form with other males. Males compete intensely for high-ranking positions within their groups, and males' ability to obtain and maintain high rank is influenced by their ability to recruit support from other males (*47*). Although the political maneuverings of chimpanzees may be more complicated than the nepotistic strategies of female baboons, the result is much the same. High-ranking male chimpanzees have priority of access to receptive females and can prevent other males from mating (*47*). Genetic analyses confirm that the top-ranking male sires a disproportionate number of infants (*49*, *50*). Social relationships among male chimpanzees may also enhance the fitness of lower-ranking males. In one community, the alpha male selectively tolerated mating attempts by his allies. As a consequence, the mating success of males was more closely related to how often they supported the alpha male than to their own dominance rank (*51*).

Future Directions

The work summarized here suggests that variation in the quality of social bonds has fitness consequences for individuals in some primate species. For many primate species, our knowledge about the structure and function of social bonds is much less complete. These gaps create difficulties when we try to compare the impact of sociality on fitness in species that live in groups of different size and configurations, or to compare the extent of social complexity across species.

It may be profitable to extend these kinds of analyses to other taxa in which group size is linked to relative brain size, such as cetaceans, carnivores, insectivores, and ungulates (*2*). Moreover, it is important to recognize that primates have not cornered the market on social complexity. For example, spotted hyenas (*Crocuta crocuta*) establish matrilineal dominance hierarchies, form coalitions, reconcile after conflicts, recognize paternal kin, hunt cooperatively, and recognize third-party relationships (*52*); an African elephant (*Loxodonta africanus*) can recognize the vocal-

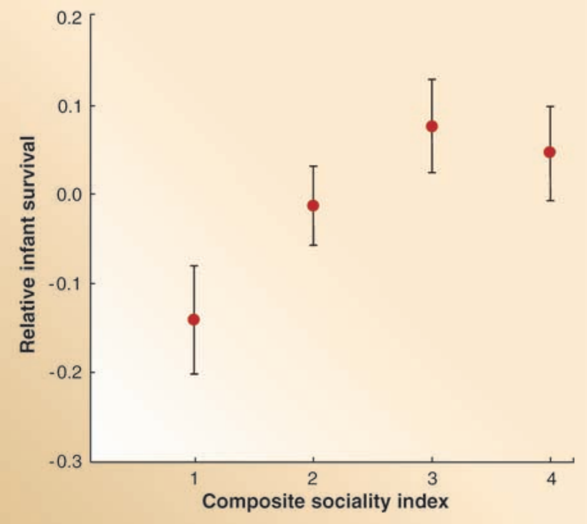

Fig. 5. The relationship between social integration and reproductive success among baboon females. For each female, a composite sociality index was computed. This value represented the frequency of grooming and proximity to all adult partners. Here, composite scores were ranked and divided into quartiles. The mean and standard error of the sociality index for the least social females are on the left, and those for the most social females are on the right. Infant survival is based on the proportion of infants that survived to 1 year of age, a major component of variation in females' lifetime fitness. [From (*45*)]

Fig. 6. Two adult male chimpanzees in Kanawara groom. Male chimpanzees participate in a variety of cooperative activities and form close social bonds. [Photograph taken by Ian Gilby]

izations of at least 100 other individuals (*53*); bottlenosed dolphins (*Tursiops aduncus*) form stable multilevel alliances (*54*); and rooks (*Corvus frugilegus*) console their partners after conflicts with other members of their flocks (*55*). For individuals in these species, there may also be important social components of fitness.

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REVIEW

Prospection: Experiencing the Future

Daniel T. Gilbert[1]* and Timothy D. Wilson[2]

All animals can predict the hedonic consequences of events they've experienced before. But humans can predict the hedonic consequences of events they've never experienced by simulating those events in their minds. Scientists are beginning to understand how the brain simulates future events, how it uses those simulations to predict an event's hedonic consequences, and why these predictions so often go awry.

All animals are on a voyage through time, navigating toward futures that promote their survival and away from futures that threaten it. Pleasure and pain are the stars by which they steer. When animals experience pleasure they hold a steady course, and when they experience pain they tack. With a bit of practice, most animals learn to associate pleasures and pains with their antecedents—the smell of an approaching predator or the call of a beckoning mate—which enables them to steer toward pleasure and away from pain before they actually experience either. When a mouse hides before a cat enters the room it is responding to an event that has not yet happened, and its ability to do so is one of evolution's most remarkable achievements.

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