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News and Views

Importance of Cooperation and Affiliation in the Evolution of Primate Sociality

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ABSTRACT The idea that competition and aggression are central to an understanding of the origins of group-living and sociality among human and nonhuman primates is the dominant theory in primatology today. Using this paradigm, researchers have focused their attention on competitive and aggressive behaviors, and have tended to overlook the importance of cooperative and affiliative behaviors. However, cooperative and affiliative behaviors are considerably more common than agonistic behaviors in all primate species. The current paradigm often fails to explain the context, function, and social tactics underlying affiliative and agonistic behavior. Here, we present data on a basic question of primate sociality: how much time do diurnal, group-living primates spend in social behavior, and how much of this time is affiliative and agonistic? These data are derived from a survey of 81 studies, including 28 genera and 60 species. We find that group-living prosimians, New World monkeys, Old World monkeys, and apes usually devote less than 10% of their activity budget to active social interactions. Further, rates of agonistic behaviors are extremely low, normally less than 1% of the activity budget. If the cost to the actors of affiliative behavior is low even if the rewards are low or extremely variable, we should expect affiliation and cooperation to be frequent. This is especially true under conditions in which individuals benefit from the collective environment of living in stable social groups. Am J Phys Anthropol 127:000–000, 2005. © 2005 Wiley-Liss, Inc.

The idea that competition and aggression, mainly over access to food and sexual partners, are central to an understanding of the origins of group-living and sociality in human and nonhuman primates remains a dominant theory in primatology today. Using this paradigm, competitive and aggressive behaviors are expected to be widespread and relatively common among conspecifics (e.g., Wrangham, 1980; van Schaik and van Hooff, 1983; Janson, 1988; Sterck et al., 1997; Wrangham and Peterson, 1996; Cowlishaw and Dunbar, 2000). As stated by Wrangham and Peterson (1996, p. 130–131), "Territorial fights can be frequent and fierce... The same applies to fights inside groups, where the most frequent aggression is between rival males."

Competition theory is a fundamental tenet of neo-Darwinian theories. Driven by their selfish genes, individuals seek to maximize their genetic contributions to the next generation.[1] In order to accomplish this, they compete with one another, resulting in individual differences in reproductive success. Moreover, because females are required to devote more energy than males to the production and care of offspring, it is argued that they compete principally over resources such as food and water. Males, on the other hand, invest little energy in reproduction directly, and devote more of their efforts to maintaining priority or exclusive access to sexual partners (e.g., Trivers, 1972; Wilson, 1975; Wrangham, 1980, 1999; Cowlishaw and Dunbar, 2000). Overall, within-species competition is assumed to be a primary influence in the evolution of sociality (van Schaik, 1989; van Hooff and van Schaik, 1994; Sterck et al., 1997). As stated by Sterck et al. (1997, p. 291), "Agonistic relationships are an especially important organizing feature in primate groups."

Two types of competition are described: contest and scramble (Nicholson, 1954; Wilson, 1975; Wrangham, 1980; van Schaik, 1989; Isbell, 1991; Cowlishaw and Dunbar, 2000). Contest competition occurs when individuals compete directly over resources, and it is measurable. The result is that subordinate individuals are excluded from exploiting monopolizable resources in the presence of more dominant individuals. Scramble competition,

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[1] Here, it has been said that we have gotten caught up in Dawkin's rhetoric and "who on earth promotes this idea in its strict sense?" In this regard, again, we quote Wrangham and Peterson (1996, p. 22): "A new evolutionary theory emerged, the selfish-gene theory of natural selection... The ultimate explanation of any individual's behavior considers only how the behavior tends to maximize genetic success: to pass that individual's genes into subsequent generations. The new theory ... is now conventional wisdom in biological science because it explains animal behavior so well." We acknowledge that Wrangham and Peterson (1996) wrote a trade book, but worry that the competition paradigm is so prevalent that it is emphasized in popularized accounts of primate behavior and evolution.

on the other hand, is difficult to measure directly. It is based on the assumption that individuals lose access to resources because other group members have already used them. This is more likely to occur at small, ephemeral, or highly dispersed feeding sites at which animals that arrive first, regardless of social status, are able to rapidly deplete the resource. Within-group scramble competition is supposedly an almost unavoidable consequence of group-living (e.g., Janson, 1992, 2000; but see Isbell, 1991). Contest competition is supposed to depend on resource abundance, distribution, and quality (van Schaik, 1989; Sterck et al., 1997; Koenig, 2002; but see Pruetz, 1999).

Given a theoretical perspective of competition, how can we understand the context and prevalence of affiliative behaviors among members of a social group? Over the past two decades, many primatologists have described evidence of affiliation, alliance formation, and cooperation as a reaction or behavioral response designed to counteract high levels of within-group aggression or to secure resources against other group members or other groups. Wrangham (1980) argued that among female-bonded primate species, social groups evolved essentially to allow females (mainly kin) to fend off other groups in competition over resources (see also Wrangham, 1983, 1999; van Schaik, 1983; Dunbar, 1988; Cowlishaw and Dunbar, 2000). Wrangham (1980, p. 291) stated, "Groups have evolved as a result of the benefits of cooperation, between allies competing against others of the same species." Within-group cooperation is seen in much the same way. Wrangham (1980, p. 291) stated that "cooperative behavior arises ultimately because it pays two subordinate animals to form alliances at the expense of a dominant... Ecological pressures favour cooperation, while genetic considerations favour kin as partners." However, as the number of individuals joining such an alliance increases, so does the potential for feeding competition among its members. Thus, the major cost of sociality is increased competition (Gaulin and McBurney, 2001), although the costs of competition or cooperation have rarely been measured.

Using a similar theoretical approach, the new field of research on reconciliation behavior assumes that many friendly or affiliative behaviors are the result of competition and aggression. "The reconciliation hypothesis predicts that individuals try to 'undo' the social damage inflicted by aggression, hence, they will actively seek contact, specifically with former opponents... Reconciliation ensures the continuation of cooperation among parties with partially conflicting interests"(de Waal, 2000, p. 587, 589). Van Schaik and Aureli (2000, p. 314) summed up the relationship between group-living, competition, and cooperation:

> "Theories of social evolution generally start by considering females and add males later... Group living primarily depends on whether females are associating with one another. If predation avoidance favors gregariousness, competition for access to vital resources limits it. Female social relationships in their group depend primarily on the intensity and nature of competition for food, water and shelter."

It is reasoned, therefore, that reconciliatory behaviors evolved to help reestablish social bonds fractured by within-group aggression and competition. In studies of reconciliation, however, it is difficult to differentiate "friendly and affiliative" behaviors from those that are considered "reconciliatory." This has led to problems in identifying and comparing the social function of cooperative behavior within and among primate species (Fuentes et al., 1996, 2002; Fuentes, 2004; Silk, 1997, 2002a; Sanz et al., 2001; Bernstein, 2004).

The framework described above was used to interpret the social systems of many primate species. However, sufficient data required to substantiate the basic assumptions of this model have not been collected, and alternative theories on the causes of aggression and cooperation have not been adequately investigated. For example, considering contest and scramble competition, Chapman and Chapman (2000, p. 28) stated, "The relative frequency of occurrence of these two types of competition has rarely been quantified." Smuts (1987, p. 411) emphasized that "aggression and affiliative behaviors of male and female primates vary depending on the species, the social context, and the individual." Furthermore, she believed that an understanding of this variation "awaits a clearer appreciation and investigation of the complex social environments in which these differences find their varied articulations." Pruetz (1999, p. 201) evaluated the accuracy of models based on scramble and contest competition, and her findings ran counter "to the expectations of theories of feeding competition." Pruetz (1999, p. 249) found that the models were "too broad in the terminology used to describe conditions of food availability predicted to lead to contest competition." Finally, there is evidence that, where resources are distributed heterogeneously in time and space, feeding competition and group-living might be less costly than previously thought (Johnson et al., 2002). Most primates are characterized by tremendous dietary breadth in the type of foods exploited (insects, fruits, flowers, leaves, seeds, gums, corms, nectar, bark, and small vertebrates) and in the number of species consumed (Harding and Teleki, 1981; Sussman, 1987; Garber, 1987). In addition, it is recognized that in many primate species, grouping patterns are flexible and individuals may form subgroups as a facultative response to local ecological and social conditions (Kinzey and Cunningham, 1994; Chapman et al., 1995). Given recent quantitative evidence that resources in tropical forests are found in dispersed, heterogeneous patches (Tuomisto et al., 2003; Wehncke et al., 2003), the existence of food patches of various sizes and quality scattered across the landscape increases the probability that individuals have access to nearby feeding sites and may limit the importance of feeding competition in group-living primates (Johnson et al., 2002).

We are concerned that some authors have accepted the competition-aggression/affiliation-reconciliation paradigm as a default explanation without critically evaluating its assumptions or appropriately testing alternative hypotheses. In particular, there can be considerable advantages to both kin and nonkin group members in developing dyadic, polyadic, and group-level affiliative and cooperative behaviors in which partners receive collective benefits (Dugatkin, 1997; Clutton-Brock et al., 2001, 2002; Clutton-Brock, 2002; Korstjens et al., 2002; Bernstein, 2004; Cheverud, 2004; Strier, 2004). Theories on the importance of mutualism and low-cost forms of social cooperation are generally lacking from the discussion of primate sociality. Furthermore, as we discuss later, there are a number of recent studies in which neurological and endocrinological mechanisms seem to have evolved to reinforce and facilitate unselfish cooperative behaviors (i.e., Carter, 1999; Carter and Cushing, 2004; Rilling et al., 2002).

A CALL FOR A NEW APPROACH TO THE STUDY OF PRIMATE SOCIALITY

We believe that there are two major problems with the competition-based model of primate sociality as presently conceived. First, the current paradigm assumes that competition is the main driving force behind both affiliative and agonistic social behavior. For example, as reported in *Anthropology News*, Silk began a symposium on conflict and cooperation at the 2003 Annual Meeting of the American Association of Anthropologists stressing: “The consensus among primatologists is that competition over scarce resources is the key to understanding collective actions, which are a product of cooperation in competitive encounters among groups of individuals bounded by kinship” (Patton and Kohler, 2004, p. 13). Certainly there is no question that affiliative, agonistic, and competitive behaviors are a consequence of social life, and that agonism and competition can have a major effect on the life of individuals. However, there are reasons to believe that competition is not the main driving force of primate sociality and affiliative behavior. We argue that primate sociality, and agonistic, affiliative, and cooperative behaviors, are best understood in terms of the mutual benefits and collective advantages that individuals obtain as members of a functioning social unit. They do not necessarily relate directly to individual fitness or to patterns of natural selection, although the competition paradigm is usually couched in these adaptationist terms (see below).

There is sometimes confusion in the literature over the concept and meaning of natural selection, and this has contributed to confusion in testing evolutionary models of social behavior. The relative importance of competition over food and mates and the ability of group members to form peaceful, affiliative, and cooperative bonds in the evolution of primate sociality is, in the end, a matter of patterns of natural selection. There is, at times, failure to distinguish between variations in individual fitness and the concept of natural selection. When variations in relative fitness of individuals are observed, it is often interpreted as evidence for selection. However, this is not necessarily the case. In evolutionary theory, variation in fitness is referred to as the opportunity for selection (Crow and Kimura, 1970), and not selection itself. This is because selection is the relationship, or covariance, between relative fitness and some phenotype of interest (Falconer and Mackay, 1996), and not just variation in fitness alone. Both selection and random genetic drift occur through differential reproductive success of members of a population. Selection is differential reproductive success causally correlated with a phenotype, through interaction with the environment. The form of this fitness-phenotype relationship determines the kind of selection, with linear relationships defined as directional selection, and quadratic relationships defined as stabilizing selection.

Genetic drift occurs when differential reproductive success is random with respect to the phenotype and its underlying genotypes. The life or death of an individual can even contribute to both selection and genetic drift at the same time, depending on the characters considered. While variant alleles at one locus may be causally correlated with differential reproductive success and thus be under selection, variant alleles at unlinked loci will evolve under genetic drift. In fact, strong selection results in extreme genetic drift at loci not causally correlated to the phenotype. We cannot classify an individual death as a selective death or a random one without reference to a phenotype of interest and without comparison to others in the population with different phenotypes. The relationship between individual interactions and fitness must be understood in terms of specific phenotypes present in a defined population. Behavior and fitness must be correlated at a population level, and not an individual level, because populations, not individuals, evolve. Furthermore, for these interactions to cause evolutionary change, the phenotypes must be heritable, i.e., they must be causally correlated with underlying, variable genetic factors. The results of social interactions normally have not been examined at this level.

Our second problem involves the database presently available to test theories of primate sociality. Data on the contexts, functions, and effectiveness of affiliative and agonistic interactions in wild primates are limited. In this paper, we will focus on the following three questions: How much time do different primate species actually spend in social interaction? How much of this interaction is friendly, and how much is agonistic? How do these numbers vary among populations of the same species and different species? We are not claiming that rates of different types of interactions are directly related to the importance of those interactions in the lives of these animals, but it is useful to know these rates and the context in which they occur. This is simply a first step. Other questions should drive future research on primate sociality. For example, what are the contexts in which friendly and agonistic interactions occur, and are contexts consistent across species? Are there differences in the frequency and quality of social interactions between kin and nonkin? Are primates with closer spatial relationships more or less likely to engage in social interactions than those that maintain greater interindividual distances? When agonism is measured, are distinctions made between mild spats and more violent fights, and what are the patterns of these differences? Can one find consistent patterns across species? Are friendly and agonistic interactions independent of one another, and how does this relate to reconciliation? What are the costs and benefits to the interactants? Do cooperative behaviors actually involve a cost to the actor, or do both the actor and the interactant benefit?

We believe that, at present, none of these questions can be answered fully. Further, we will not attempt to answer them here. However, in order to illustrate the problem, we present and compare data on the basic questions asked above, i.e., how much time do diurnal, social-living primates spend in social interaction, and how much of this time is affiliative and agonistic? These data should be seen as just a small start in addressing the problem of understanding primate sociality rather than as an answer to any of the above questions.

METHODS

We reviewed much, but certainly not all, of the literature on the socioecology of wild diurnal primates in order to identify the percent time that group members spend in social activity, and the rates of agonistic, affiliative, and aggressive interactions. Not all information was available in all studies. However, we included a study in our sample unless the data were transformed mathematically in such a way that it was not possible to reconstruct the basic information or the sample size. In many cases, the studies cited (N = 21) are doctoral dissertations. These monographs provide a comprehensive year-long or longer database with detailed descriptions of methodology and definitions of behavioral categories. We also systematically reviewed articles published over the last 25 years in the *International Journal of Primatology* (*IJP*) and the *American Journal of Primatology* (*AJP*), and used these as a representative data set. We cite 23 papers published in *IJP* and 13 papers published in *AJP* on primate sociality that provide appropriate data for this study. Finally, we also included data from edited volumes and journals such as *Behaviour*, *Primates*, and the *American Journal of Physical Anthropology*, although these references were collected more opportunistically.

Our data set includes information on 28 genera, 60 species, and 81 studies (Table 1). In these studies, affiliative interactions include grooming, playing, food-sharing, huddling, and alliance formation of two or more individuals. Agonistic interactions include fighting, visual or vocal threats, submissive gestures, and evidence of displacement. When collecting data on activity cycles, investigators normally only include "active" social interactions. Interactions associated with what might be considered "passive" social interactions (such as resting in contact or coordinated activity) or social communication (such as vocal behavior or marking) are not included in these data. In some studies, mild agonistic interactions (which we will refer to as agonism), such as instantaneous spats and displacements, are not distinguished from more serious interactions (referred to here as aggression) such as biting, fighting, and extended chases.

It is important to highlight several limitations in our data set. In general, researchers used different definitions of common behavioral categories, and recorded data using different sampling procedures. Moreover, different species and different individuals within the same species are likely to vary considerably in the expression and conspicuousness of social interactions. Therefore, the frequency of social interactions in certain individuals may be overrepresented or underrepresented in the data. In addition, most individuals spend the vast majority of their day in peaceful and close proximity to conspecifics; however, time spent in spatial proximity is rarely included in data on activity cycles. Thus, only active social interactions are considered in these analyses, because "passive" interactions are often not reported, and because active affiliative interactions are more directly comparable to the kinds of agonistic interactions that are reported in the literature. It is important to note, however, that maintaining (or avoiding) proximity is not passive, and that social communication can be affiliative or aggressive depending on the context and individuals involved. With this in mind, we view published percentages and rates of social interactions as general values that are likely to have considerable variance. Nonetheless, in those species for which we have values from more than a single study group, the percent time engaged in social interaction is quite constant. Furthermore, the rates we found of cooperative and agonistic behavior are comparable from the different sampling methods and in a large subset of species. Thus, we believe that the patterns of this large

TABLE 1. Activity budget and rates of agonism in diurnal primates

Species	% time social	% affiliative	Agonistic	Reference
Diurnal prosimians				
Varecia variegata	<1.0	Rare	Rare	1
Eulemur fulvus	<1.0	Rare	Rare	1
Eulemur fulvus	1.0	1.0	Rare	2
Eulemur rubriventer	2.0	2.0	Rare	2
Lemur catta	2.6	2.1	0.5%	3
Lemur catta	2.6	1.9	0.7%	4
Eulemur fulvus	2.8	2.5	0.3%	4
Varecia variegata	3.1	3.1	0.02/hr male 0.17/hr female	5
Eulemur fulvus	3.5	3.5	Rare	6
Propithecus verreauxi	3.8	N.D.	0.35/hr	7
Eulemur mongoz	4.0	4.0	N.D.	8
Eulemur coronatus	4.3	4.0	0.3%	9
Propithecus diadema	5.0	4.5	0.12/hr	10
Eulemur fulvus	5.8	5.4	0.4%	9
Eulemur fulvus	8.5	7.7	0.8%	4
Lemur catta	8.6	7.1	1.4%	4
Overall mean prosimian	3.7 (±2.3) (mean weighted by species = 3.68)			
New World Monkeys				
Alouatta palliata	0.8			11
Alouatta palliata	0.9			12
Brachyteles arachnoides	0.9			13
Callicebus torguatus	0.9			14
Ateles paniscus	0.9			15
Alouatta palliata	1.0			16
Cebus olivaceus	1.3			17
Alouatta seniculus	1.7			18
Saguinus mystax	1.8	1.4	0.41%	19
Alouatta palliata	1.9		0.003/ind/hr agression	20
Callicebus torquatus	1.9		0.0006/ind/hr agression	21
Alouatta palliata	2.0			16
Cebus olivaceus	2.1			17
Saguinus fuscicollis	2.2	1.9	0.35%	19
Brachyteles arachnoides	2.7		0.0006/ind/hr agonism	22
Saguinus fuscicollis	2.8			23
Callithrix geoffroyi	2.8			24
Saimiri sciureus	2.9		0.0047/ind/hr agression	25
Leontopithcus rosalia	3.1			26
Saguinus mystax	3.1			23
Saguinus mystax	3.5		0.20% 0.0066/ind/hr agression	27
Alouatta pigra	3.9		0.10%	28
Lagothrix lagotricha	4.0	3.1	0.60%	29
Lagothrix lagotricha	4.8			30
Alouatta caraya	4.9		0.38% 0.019/ind/hr agression	31
Callithrix humeralifer	5.0	4.2		32
Leontopithcus rosalia	6.1			33
Leontopithcus rosalia	7.0			26
Leontopithcus chrysomelas	9.1	8.5		32
Cebus capucinus	9.9		0.016/ind/hr agression	34
Cebus apella	9.9			35
Cebus capucinus	12.5	7.7	0.034/ind/hr agression	36
Saimiri oerstedii	13.9		0.000009/ind/hr agression	37
Callithrix jacchus	14.0	11.1	0.051/ind/hr agonism	38
Ateles geoffroyi	17.0		0.18%	39
Ateles geoffroyi	22.0		0.92%	39
Alouatta palliata			0.007/ind/hr agression	40
Ateles geoffroyi			0.0043/ind/hr agression	41
Cebus apella			0.042/ind/hr agression	42
Cebus apella			0.007/ind/hr agression	42
Leontopithecus rosalia			0.0012/ind/hr agression	43
Saguinus fuscicollis			0.01/ind/hr agression	44
Saguinus nigricollis			0.20%	45
Overall mean New World Monkeys	5.1% (±5.1%) (mean weighted by species = 5.76)			
Old World Monkeys				
Cercopithecus diana	1.2			80
Colobus badius	1.9	1.8		46
Presbytis pontenziani	1.9			47
Colobus polykomos	2.0			79
Colobus vellerosus	2.0			79
Colobus vellerosus	2.0			79

(*continued*)

TABLE 1. (Continued)

Species	% time social	% affiliative	Agonistic	Reference
Macaca silenus	2.4			48
Colobus badius	2.6	2.5		46
Cercopithecus campbelli	2.8			80
Macaca silenus	3.4			49
Colobus vellerosus	4.0			79
Cercopithecus petaurista	4.3			81
Colobus vellerosus	5.0			79
Colobus polykomos	5.3			80
Colobus guereza	5.9	5.7	0 agression event in 7,793 scans	50
Colobus badius	6.3			80
Colobus verus	6.7			80
Presbytis entellus	7.4	6.7		50
Cercebus atys	7.9			80
Colobus badius	8.0	7.6		46
Colobus badius	8.2	7.9		46
Colobus guereza	8.3	8.3	0 agression event in 8,917 scans	51
Macaca silenus	8.4			49
Colobus badius	8.5	8.5		46
Macaca sylvanus	10.0			52
Papio anubis	10.4	5.2		53
Cercopithecus mitis	10.4			54
Cercopithecus l'hoesti	11.4			54
Macaca sylvanus	11.5			52
Colobus satanas	13.0			79
Rinopithecus bieti	13.1	9.8		55
Macaca nigra	18.7			56
Macaca fuscata	21.7	18.9		57
Macaca nigra	23.1			56
Macaca nigra	23.5			56
Presbytis francois	27.9	27.5		58
Presbytis entellus			0.084/ind/hr females agonism	59
Presbytis entellus			0.01/ind/hr males agonism	60
Papio cynocephalus			0.14/ind/hr agonism males	61
Papio cynocephalus			0.11/ind/hr agonism males	62
Papio cynocephalus			0.079/ind/hr agonism males	62
Papio cynocephalus			0.14/ind/hr agonism males	62
Cercopithecus aethiops			0.0007/ind/hr agression	63
Erythrocebus patas			0.0007/ind/hr agression	63
Papio anubis			0.084/ind/hr agonism males	53
Papio cynocephalus			0.037/ind/hr agonism males	64
Overall mean Old World Monkeys	8.6% (±6.8%) (mean weighted by species = 9.38)			
Apes				
Pongo pygmaeus	1.6[2]			65
Hylobates lar	3.0			66
Gorilla gorilla	3.6			67
Hylobates muelleri	4.0			68
Pongo pygmaeus	5.4[2]			69
Gorilla gorilla	7.0	6.7	0.3%	70
Hylobates lar	11.0		0.009/hr	71
Hylobates syndactylus	15.0		0.15/hr	72
Pan troglodytes	22.0	9.0% (groom) (includes resting)	0.067/ind/hr agonism males	73
Pan troglodytes	24.9	16.8 (groom)		74
Gorilla gorilla		0.39/hr	0.20/hr	75
Pan troglodytes			0.03/hr	76
Pan troglodytes			0.05/hr	77
Pan troglodytes			0.016/hr males	78
			0.009/hr females	78
Overall mean apes	9.7% (±8.2%) (mean weighted by species = 9.7)			

[1] %, percent of total activity budget; N.D., no data provided. Rare, rarely observed. References: 1, Vasey, 1997; 2, Overdorff, 1991; 3, Gould, 1994; 4, Sussman, unpublished findings; 5, Morland, 1991; 6, Tattersall, 1977; 7, Richard, 1978; 8, Curtis, 1997; 9, Freed, 1996; 10, Hemingway, 1995; 11, Estrada *et al*., 1999; 12, Smith, 1977; 13, Milton, 1984; 14, Kinzey, 1981; 15, Symington, 1988, 16, Stoner, 1996; 17, Miller, 1992, 1996; 18, Gaulin and Gaulin, 1982; 19, Castro, 1991; 20, Larose, 1996; 21, Easley, 1982; 22, Strier, 1986, 1987; 23, Peres, 1991; 24, Passamani, 1998; 25, Mitchell, 1990; 26, Dietz *et al*., 1997; 27, Garber, 1997; 28, Silver *et al*., 1998; 29, Stevenson, 1998; 30, Defler, 1995; 31, Bicca-Marques, 1993; 32, Rylands, 1982; 33, Peres, 1986; 34, Mitchell, 1989; 35, Zhang, 1995; 36, Fedigan, 1993; 37, Boinski, 1986; 38, Digby, 1994; 39, Fedigan and Baxter, 1984; 40, Jones, 1980; 41, Klein and Klein, 1977; 42, Janson 1984, 1988; 43, Baker, 1991; 44, Goldizen *et al*., 1996; 45, de la Torre *et al*., 1995; 46, Decker, 1994; 47, Fuentes, 1996; 48, Kurup and Kumar, 1993; 49, Menon and Poirer, 1996; 50, Fashing, 2001; 51, Newton, 1992; 52, Menard and Vallet, 1997; 53, Harding, 1980; 54, Kaplin and Moermond, 2000; 55, Kirkpatrick *et al*., 1998; 56, O'Brien and Kinnaird, 1997; 57, Agetsuma, 1995; 58, Burton *et al*., 1995; 59, Borries *et al*., 1991; 60, Laws and Laws, 1984; 61, Strum, 1982; 62, Noe and Sluijter, 1995; 63, Pruetz, 1999; 64, Smuts, 1985; 65, Rodman, 1973; 66, Gittens and Raemaekers, 1980; 67, Watts, 1988; 68, Leighton, 1987; 69, Galdikas, 1985; 70, Olejniczak, unpublished findings; 71, Bartlett, 1999; 72, Chivers, 1974; 73, Boesch and Boesch-Achermann, 2000; 74, Teleki, 1981; 75, Schaller, 1963; 76, Bygott, 1974; 77, Ghigliari, 1984; 78, Goodall, 1986; 79, Teichroeb *et al*., 2003; 80, McGraw, 1998; 81, McGraw, 2000.

[2] Orangutang data include any proximity between adults (76) or all individuals (77), not all of which would active social interaction.

sample are robust enough to absorb variance that might be introduced by sampling methods or subject focus. We have confidence that the data represent reasonable approximations of the true activity patterns of these primates. Furthermore, since these data were collected using widely different methods and trait definitions, we do not attempt to apply complex meta-analysis statistics to them, but rather use them simply for comparative and illustrative purposes. Finally, our main purpose is simply to show that group-living primates generally spend little time in active social interactions, and that extremely few of these interactions involve aggressive behavior. Some may question these conclusions because the data we used were collected with different methodologies. However, we hope that this will stimulate further research on these questions and the development of more comparable methods. Given the patterns we observe in our large data set, we predict that our general conclusions will stand.

RESULTS

Activity budget

In reviewing the literature, we found that diurnal prosimians spent an average of 3.7% (±2.3%) of their activity budget engaged in direct social interactions (Table 1). Studies in which lemurs were reported to engage in more frequent social interaction were conducted during the mating season, or involved cases in which observations of social interactions and "other" were lumped in a single category. In all studies but one, agonistic interaction accounted for less than 1% of the activity budget of diurnal lemurs (Table 1).

Similarly, most species of New World monkeys spent only a small fraction of their day involved in overt social interaction. Over 72% of the groups studied (26/36) devoted 5% or less of their activity budget to social interactions (Table 1). Mean percent of activity budget devoted to social interaction was 5.1% (±5.1%). Only four species of New World monkeys were found to devote more than 10% of their daily activity budget to social activities. In these, the primary social activity was grooming. Overall, the vast majority of overt social interactions reported were affiliative. There were no significant differences in the frequency of social interactions between diurnal prosimians and New World monkeys (t = 1.0, df = 50, P = 0.29 for all studies, and t = 1.1, df = 27, P = 0.27 for mean frequency of social interactions per species).

The frequency of social interactions among Old World monkeys was found to be relatively similar to those of neotropical forms. In 31 of 36 studies reviewed (86%), social interactions accounted for between 2–13% of the daily activity budget. In the remaining 5 studies, social interactions accounted for between 18–28% (3 of which were of groups of the same species, *Macaca nigra*). The mean value for our Old World monkey sample was 8.6% (±6.8%). This was higher than the frequency of social interactions among New World monkeys (t = 2.4, df = 70, P = 0.016 for all studies, and t = 1.89, df = 40, P = 0.064 for mean frequency of social interactions per species) and prosimians (t = 2.8, df = 50, P = 0.007 for all studies, and t = 2.2, df = 27, P = 0.03 for mean frequency of social interactions per species). Old World monkeys groom more frequently than do lemurs and New World monkeys, and allogrooming alone accounted for most of the differences in the frequency of social interactions among these taxa. For example, in a study of Japanese macaques (Agetsuma, 1995), social interaction accounted for 21.7% of the activity budget, 87% of which was grooming. In these macaques, nongrooming social interactions accounted for only 2.8% of the activity budget. Similarly, *Colobus guereza* was observed to engage in within-group social interactions during 8.3% of its activity budget, 81% of which was devoted to grooming. When grooming is omitted from the analysis, other forms of social interaction accounted for only 4.4% (±5.1%) of the activity budget of Old World monkeys (N = 12 studies). This value is comparable to that found in New World monkeys (t = 0.98, df = 15, P = 0.33) and diurnal lemurs (t = 0.50, df = 27, P = 0.061). Thus, allogrooming appears to take on added significance among Old World monkeys.

The data on ape social interactions are quite variable because each genus exhibits a very different type of social structure. Social interactions ranged from 3.6% of the activity budget of the mountain gorilla, to 4–15% in gibbons, to 22–25% in chimpanzees (Table 1). As in Old World monkeys, most ape social interactions take the form of grooming or bouts of play. Among our sample of lesser and great apes, 9.7% of the mean daily activity budget was devoted to within-group social interactions.

Agonism and aggression

Incidences of agonistic and aggressive interactions are normally presented as a rate, i.e., the number of events per observation hour. In addition, it is common for the data to be reported as a single category "agonism," and therefore it is impossible to separate mild spats, displacements, stares, and avoidance from more intense forms of agonistic interactions such as chasing, fighting, and biting which can result in severe injury, death, and social disruption.

In our search of the literature on prosimians, the mean rate of agonism was 0.16 events per hour (N = 4; Table 2). Both New World and Old World monkeys averaged approximately 0.6 agonistic events per hour. Among apes, rates of agonism were extremely low, averaging 0.09 events per hour (Table 2). Our data on Old World monkeys

TABLE 2. Summary of agonistic and affiliative social interactions in primates[1]

	Prosimians	New World Monkeys	Old World Monkeys	Apes
Agonism (events per hour)	0.16	0.60	0.58	0.09
Events per individual per week	0.002	3.6	6.3	0.0001
% social interactions (only 1 species) that are affiliative	93.2 ± 7.3	86.1 ± 10.5	84.8 ± 17.5	95.7

[1] Data are calculated from information presented in Table 1. Events/per hour represent studies using all occurrence data (recorded any time it is observed) on number of agonistic social interactions recorded per observation hour. Data on events per individuals per week are presented to account for the fact that by chance alone, individuals in larger groups are more likely to vie for food or space more frequently than individuals in smaller groups. We assumed that animals are active 12–14 hr per day. Therefore, events per individuals per week represent 14 hr × 7 days or approximately 98 hr of observation. Data on % social interactions that are affiliative were calculated using mean values for each species. For Apes, data are available for only 1 species and 1 study (*Gorilla gorilla*).

indicate that rates of agonistic behavior ranged from 0.067 events per hour among male vervet monkeys to 1.19 events per hour among male cynocephalus baboons (N = 13 studies). In the five studies of *Papio cynocephalus* we examined, rates of agonism among males ranged from 0.67–1.19 events per hour (mean, 0.92).

Based on the expectation that within-group feeding and reproductive competition increase with increasing group size, we corrected, where possible, the rate of agonism by the number of potential interactants in the group. In Tables 1 and 2, we present data on rates of agonism per adult group member per hour and per week (assuming a 12–14-hr period of daily activity). The mean values ranged from 6.3 times per individual per week in Old World monkeys to 3.6 times per individual per week in New World monkeys to extremely rare in apes and prosimians (Table 2). The highest frequency of agonism per individual group member per week was 10–11 times in *Papio cynocephalus*.

We found a small number of studies in which severe forms of agonism (defined as aggression here) were recorded separately from mild agonism. In 12 of 14 studies (85.7%) in New World monkeys, the average group member was involved in less than two aggressive interactions per week. Species characterized by the greatest rates of aggressive interactions were *Cebus capucinus* and *C. apella* (3.5 and 4.2 aggressive interactions per individual per week, respectively). In Old World monkeys, there are three studies in which aggression (fighting and chasing) was separated from milder forms of agonistic interactions (2 of *Cercopithecus aethiops* and 1 of *Erythrocebus patas*). In these three studies (all focusing on adult females), rates of aggression averaged 0.007 per hour per group (range = 0.008–0.014), or 1 aggressive event every 142 hr for the entire group. How closely these values reflect levels of aggression in other species remains unclear. However, our values for apes (Table 2) support these very low rates of within-group aggressive interactions.

With respect to feeding competition, it was hypothesized that due to their reproductive requirements, adult females, especially those species that form a linear despotic dominance hierarchy, are expected to engage in frequent food-related agonistic contests (Sterck et al., 1997). However, in our review of the literature, this was not the case. In Table 3, we present published data on food conflicts in five primate species. The data represent food conflicts per female per hour of feeding, and indicate extremely low rates of contests, even among species forming linear dominance hierarchies. Taken together, these data indicate that the frequency of food-related agonism among females occurred at a rate of once per 17 hr of feeding (once every 3–5 days) in mangabeys, to once per 143 hr of feeding (once every 1–2 months) in chimps and vervet monkeys. Thus, in the cases reviewed, rates of agonism are extremely low and do not relate to type of female hierarchy.

TABLE 3. Female food conflicts per hour of feeding

Species	Conflict rate	Dominance regime
Cercocebus torquatus[1]	0.058/female/hr	Linear
Erythrocebus patas[2]	0.004/female dyad/hr	Egalitarian
Cercopithecus aethiops[2]	0.007/female dyad/hr	Linear
Saimiri sciureus[3]	0.013/female/hr	Linear
Pan troglodytes[4]	0.007/female/hr	Linear

[1] Range and Noe, 2002.
[2] Pruetz and Isbell, 2000.
[3] Mitchell, 1990.
[4] Witting and Boesch, 2003.

Cooperation and affiliation

Quantitative data on social cooperation and affiliative behaviors other than grooming, playing, and huddling are not commonly reported in the literature, although qualitative accounts of these behaviors are available. Notable examples of cooperative and affiliative behaviors in primates include cooperative infant care and food sharing (e.g., Sussman and Kinzey, 1984; Goldizen, 1989; Garber, 1997; Mitani and Watts, 2001), male vigilance, and protection and defense of neonates (Boinski, 1987; Rose and Fedigan, 1995; Savage et al., 1996; Gould et al., 1997; Treves, 1998, 2000), alliance and friendship formation (e.g., Altmann, 1980; Strum, 1982; Smuts, 1985; Strier, 1993; Cords, 2002; Silk, 2002a), coordinated hunting (e.g., Rose, 1997; Boesch and Boesch-Achermann, 2000), and coordinated range and resource defense (e.g., relevant papers cited in Boinski and Garber, 2000).

In our sample, among diurnal prosimians (N = 7), 93.2% (range, 78.5–99%) of all social interactions represented affiliative interactions (Table 2). In New World monkeys (N = 10), affiliative social interactions accounted for 86.1% (range, 61.6–97.3%) of all social interactions. The percentage of affiliative social interactions in our Old World monkey sample (N = 7) was almost identical to that found in New World monkeys (84.8%; range, 50–98.5%; Table 2). We found only one study on apes in which the percentage of time engaged in affiliative behavior was reported. This was a study of *Gorilla gorilla* by Olijniczak (unpublished findings). In this research, affiliative behaviors accounted for 95.7% of all social interactions in lowland gorillas. Clearly affiliative interactions represent the overwhelming majority of primate social interactions, and form the basis of individual social bonds.

DISCUSSION

> "Within societies all across the planet, be they small nomadic groups of kin wandering through the grasslands or millions of unrelated individuals living in a metropolis, whether modern or prehistoric, cooperation is the glue that binds us together. It is difficult to even imagine a society in which cooperation, at some level or another, has not been integral" (Dugaktin, 1999, p. 2).

Published data on diurnal prosimians, New World monkeys, Old World monkeys, and apes indicate that most species devote between 3–10% of their activity budget to active social interactions, and are characterized by infrequent bouts of agonism and aggression. Clearly affiliative interactions represent the overwhelming majority of primate social interactions, and form the basis of individual social bonds. Given rates of aggression per individual ranging from once or twice per week to once or twice per month, we question whether social affiliation and cooperation in primates are best understood mainly as means of facilitating coalitionary competition or as reconciliatory behaviors. Qualitatively, we suggest that friendly, peaceful, coordinated, and cooperative interactions serve a greater role in alliance formation, friendships, social cohesion, and obtaining access to resources, and have utility outside of combating or ameliorating aggression.

We fully recognize that rarely occurring behaviors may be extremely important to an animal's survival, and that the frequency of an activity may not accurately measure its importance. Certainly a fight causing the injury or death of an individual will affect its life trajectory just as a rare predatory event can be disastrous to an individual or group. Periodic harassment of an individual also can seriously affect its health and severely disrupt group cohesion. However, evolution does not operate on individuals but on populations over time. We must not confuse variation in fitness with selection. Antipredator tactics, for example, are already in place when we are making our observations. Certainly, being eaten by a predator affects the fitness of the victim, but whether it effects evolutionary change in the population is a much more complex matter. If predators capture prey that have a random distribution of phenotypes, no selection occurs. However, if the predator captures prey representing only a subset of the population, such as the smaller animals, this would represent selection. This selection will then result in evolution to the extent that variation in the phenotype is heritable (passed from parents to offspring). It is possible, if the predator and prey populations have evolved in concert over many millennia without change in this relationship, that we witness the proximate consequences of a predatory event, but its evolutionary consequences may be insignificant or nonexistent. The same would be true of the results of infrequent aggressive interactions.

Variance in fitness provides the opportunity for selection, but evolution by both selection and genetic drift occurs through differential reproductive success. For evolution to occur, natural selection must act upon underlying genetic variation. The problem is that most measurements of natural selection are limited to phenotypes. The underlying assumption behind many selection analyses is that there is a causal connection between fitness and the trait in question. However, environmental variables can independently affect fitness. Kruuk et al. (2003) found that nearly 25% of selection gradients were biased by environmental covariance, making selection seem a stronger force for evolution than it actually is. Kruuk et al. (2003, p. 209) concluded that:

> "Recent studies underline the need for more caution in describing the forces of natural selection. They provide strong evidence that environmental covariances can bias our estimates of selection: in doing so, the results highlight the benefits to be gained by considering genetic, rather than simply phenotypic, measures when trying to understand the evolution of quantitative traits. They also provide a potential explanation for the widespread lack of correspondence between predicted and observed evolutionary trajectories in natural populations (Merilä et al., 2001)."

Most primate social interactions are affiliative. If an individual's survival is enhanced by the collective advantages of living in a cohesive, socially integrated behavioral unit, then an understanding of an individual's abilities to maintain affiliative and coordinated behaviors and to minimize agonistic interactions is likely to provide critical insights into the evolution of sociality and group-living in primates. After all, the easiest way to minimize agonistic interactions is by avoidance. If this is so, why do most primates spend so much time together? Here, we argue for a change in emphasis and perspective. We hypothesize that affiliation, coordinated behaviors, and proximity to conspecifics, rather than aggression and competition, are the major governing principles of primate sociality.[2]

Clutton-Brock (2002) recently provided evidence that the benefits of cooperation in vertebrate societies, generally, may show parallels to those in human societies, where cooperation between unrelated individuals is frequent and social institutions are often maintained by generalized cooperation and reciprocity. Cooperation and affiliation represent behavioral tactics that can be used by group members to obtain resources, provide comfort, maintain or enhance their social position, or increase reproductive opportunities (Brown, 1983; Sapolsky et al., 1997; Taylor et al., 2000; Clutton-Brock et al., 2001; Clutton-Brock, 2002; Cheverud, 2004).

Many affiliative or cooperative behaviors among group-living animals can be explained by individual actions that may benefit several individuals. In acts of cooperation, both participants may receive immediate benefits from the interaction. Coordinated behaviors such as joint resource defense, range defense, cooperative hunting, alliance formation, cooperative food searching and harvesting, mutual grooming, huddling, spatial proximity, and predator vigilance can be explained in terms of immediate benefits to participating individuals. Acts that appear to benefit recipients may also benefit actors. These benefits need not be equal for each individual. If the cost to the actors of affiliative behavior is low, even if the rewards are low and/or variable, we should expect affilation and cooperation to be common. This intraspecific mutualism may help explain why nonhuman primates and other social mammals live in relatively stable social groups and solve the problems of everyday life in a generally cooperative fashion.

Brown (1983, p. 30) described a type of cooperative behavior that occurs when "each animal must perform a necessary minimum itself that may benefit another individual as a by-product." This has been referred to as "by-product mutualism." This is typically characterized by behaviors that a solitary individual must do regardless of the presence of others, such as hunting for food. In many species, these activities are more profitable in groups than alone. Dugatkin (1997, p. 31–32) stated:

> "This category might be thought of as the simplest type of cooperation in that no kinship need be involved, nor are the cognitive mechanisms that require scorekeeping ... necessary for byproduct mutualism to evolve. As such byproduct mutualism is "simple" in the sense of what is needed for cooperation to evolve, and this in turn might make it the most common category of cooperation, when all is said and done."

We now speculate on mechanisms that might lead to cooperative behavior among related and nonrelated individuals that do not necessitate selfish genes, complex calculations of kin recognition or relationships, or complicated predictions of future reciprocity. In experiments using MRI scans, mutual cooperation was associated with consistent activation in two broad brain areas that have been linked with reward processing (the anteroventral striatum and the orbitofrontal cortex). It was proposed that activation of this neural network positively reinforces cooperative social interactions (Rilling et al., 2002). This results from the fact that both of these brain areas are rich in neurons that respond to dopamine, the neurotransmitter known for its role in addictive behaviors. The dopamine system evaluates rewards: both those that flow from the environment, and those conjured up in the brain. When the stimulus is positive, dopamine is released, which makes the individual take some action. "The dopamine system works unconsciously and globally, providing guidance for making decisions when there is not time to think things through" (Blakesee, 1999, p. 347). In experiments with rats, for example, in which electrodes are placed in the striatum, the animals continue to press a bar to stimulate the electrodes, apparently receiving such pleasurable feedback that they will starve to death rather than stop pressing the bar. With these systems, investigators believe they have identified a pattern of neural activation "that may be involved in sustaining cooperative social relationships, perhaps by labeling cooperative social interactions as rewarding" (Rilling et al., 2002, p. 403).

Another physiological mechanism related to affiliation and nurturing is the neuroendocrine circuitry associated with maternal responses in mammals. Orchestrating the broad suite of these biobehavioral responses is the hormone called oxytocin. Oxytocin has been related to every type of animal bonding: parental, fraternal, sexual, and even the capacity to sooth oneself (Carter, 1999; Carter and Cushing, 2004; Angier, 1999; Taylor et al., 2000). It was suggested that, although its primary role may have been in forging the mother-infant bond, oxytocin's ability to influence brain circuitry may have been co-opted to serve other affiliative purposes that allowed the formation of alliances and partnerships, thus facilitating the evolution of cooperative behaviors (Carter, 1999; Taylor et al., 2000).

If cooperation and spatial proximity among group-living animals is rewarding in a variety of environmental and social circumstances, and if physiological and neurological feedback systems reinforce social tolerance and cooperative behavior, then

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[2] We say this in light of such statements as: "Feeding competition is considered to be the driving force behind group-life" (Wrangham, 1980, p. 288), or the sentiments expressed by Sterck et al. (1997), van Schaik and Aureli (2000), and Silk (2004) on pages 1, 2, and 3 in this manuscript.

social group-living can persist in the absence of any conscious recognition that material gains might also flow from mutual cooperation. Social animals appear to be wired to cooperate and to reduce stress by seeking each others' company (Carter, 1999; Carter and Cushing, 2004; Taylor et al., 2000; Rilling et al., 2002). Social affiliation and cooperative behaviors provide psychological, physiological, and ecological benefits to social primates that are reinforced by hormonal and neurological systems and serve as a positive reward in their own right. Recently, data from a 16-year study in Kenya provided direct evidence that sociality enhances the fitness of female *Papio cynocephalus*. Females who had more social contact with other group members and were more fully socially integrated into their groups were more likely to rear infants successfully than other females. These effects were independent of dominance rank and variation in ecological conditions (Silk et al., 2003). Interestingly, this species has the highest rates of agonism in our sample. As discussed above, however, whether this relates to long-term evolutionary change in the baboon population remains to be seen.

Sociality has evolved independently in many diverse groups of animals. Among primates, sociality may have its origin in the general benefits of mutual cooperation, strong maternal-infant bonds, and the evolution of an extended juvenile period. Specifically, neurological and ocytocin and endogenous opioid mechanisms may be at the core of innate cooperative social responses (Carter, 1999; Taylor et al., 2000). This could explain the evolution not only of cooperation among nonrelatives but also of "nonselfish" altruistic behavior. Again, we acknowledge the important role of aggression and competition in understanding primate social interactions. Our perspective, however, is that affiliation, cooperation, and social tolerance associated with the long-term benefits of mutualism form the core of social group-living. In most instances, aggression and competition are better understood as social tactics and individual adjustments to the immediate and ephemeral conditions of particular social situations.

Finally, we highlight the importance of collecting data on the frequency and context of social behavior to better understand the mechanisms that govern everyday interactions within social groups. We must better understand who does what to whom, how often, and when. As emphasized by Silk (2002b, p. 440), "We need to pay more attention to methodological details, such as how we should interpret information about the content, frequency, quality and patterns of social interactions." Furthermore, since active social behavior generally takes up such a small proportion of an individual's time, social interactions must be understood within a wider context, such as general activity pattern, life history of the individual, group and population demography, and potential recent perturbations to the ecosystem that may affect the group or population. Until we have a better understanding of these mechanisms, hypotheses concerning evolutionary explanations of cooperation, agonism, and sociality may be misleading. We agree with Clutton-Brock (2002, p. 72) that "if mutualism proves to be important in maintaining cooperative animal societies, the benefits of cooperation in animals may be more similar to those of cooperation in humans than has been previously supposed. In humans, unrelated individuals commonly assist each other ... [and] generalized reciprocity appears to be important in maintaining many social institutions ... [these] trends appear to have close parallels in other cooperative animals."

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