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Time allocation and the evolution of group size

KIMBERLY A. POLLARD & DANIEL T. BLUMSTEIN
Department of Ecology and Evolutionary Biology, University of California, Los Angeles

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Group size is a core trait defining social systems, social complexity and social structure, so understanding group-size evolution is critical to understanding the evolution of sociality. Traditional views of group-size evolution focus on ecological factors such as predation risk and physical resources, but the additional factor of time has remained largely unexplored. Time is a valuable limited resource for all animals, and its partitioning both is influenced by sociality and may constrain sociality. Time allocation may in fact be an important mechanism through which predation risk, resource needs and other factors influence the evolution of group size. Classic group-size and time-use hypotheses make no consistent evolutionary predictions, so comparative analyses are necessary to determine which of the predicted processes are active on broad evolutionary scales. To evaluate these predictions, we conducted a comparative study using 50 species of diurnal primates as a model taxon for cohesive group-living animals. The evolution of group size was correlated with time spent resting, even after controlling for life-history variables such as body mass and diet type. We suggest that constraints on time allocation should be better integrated into models of the causes and consequences of sociality and that these constraints may have implications for conservation.

Keywords: evolution of sociality; group size; independent contrast; phylogeny; primate; temporal constraint; time budget

Animals display a wide range of social systems, social complexities and social group sizes. Although there are many ways to describe sociality, it is social group size that delineates the state space in which social systems and social complexity can evolve (see Terborgh 1983; van Schaik & van Hooff 1983; Terborgh & Janson 1986; Janson 1992).

The many factors that influence, and are influenced by, group size include predation risk (Alexander 1974; S. A. Altmann 1974; van Schaik 1983; van Schaik & van Hooff 1983; Janson 1998), resource availability and competition (Wrangham 1980; van Schaik 1983; van Schaik & van Hooff 1983), foraging patch size and heterogeneity (S. A. Altmann 1974; Leighton & Leighton 1982; Johnson et al. 2002), disease/parasite risk (Freeland 1976; Altizer et al. 2003), body mass (Jorde & Spuhler 1974; Clutton-Brock & Harvey 1977; van Schaik 1983; Janson & Goldsmith 1995), diet (Clutton-Brock 1975; Clutton-Brock & Harvey 1977; Janson & Goldsmith 1995; Williamson & Dunbar 1999), phylogenetic inertia (Di Fiore & Rendall 1994), life history (Wittenberger 1980), mating opportunities (Lindenfors et al. 2004) and travel costs (Chapman & Chapman 2000; Sernland et al. 2003). Most of these factors can be subsumed under two major categories of selective pressures: predation risk and resource needs (see also Dunbar 1988; Krause & Ruxton 2002; Caro 2005). The classic view on the evolution of group size is that observed group sizes reflect these two major factors (Terborgh 1983; van Schaik & van Hooff 1983; Janson 1992). (For reviews see Clutton-Brock & Harvey 1977; Terborgh & Janson 1986; Rodman 1988; Janson 1992; Wrangham et al. 1993; Janson & Goldsmith 1995; Muller & Thalmann 2000.) However, one important factor affecting sociality (and affected by sociality) has received comparatively little attention: time.

That time allocation could constrain group size was first shown by Dunbar (1992b): when animals are

Correspondence: K. A. Pollard, Department of Ecology and Evolutionary Biology, University of California, 621 Charles E. Young Drive South, Los Angeles, CA 90095-1606, U.S.A. (email: kpollard@ucla.edu).

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forced to spend more time meeting basic needs, social time is sacrificed, causing group instability and limiting group size. Williamson & Dunbar (1999) later expanded this model, whereas subsequent work (Hill et al. 2003; Korstjens et al. 2006; Korstjens & Dunbar 2007) showed that time constraints can influence group size and, via group size, the geographic distribution of species.

These studies suggest time is an important factor that influences, and is influenced by, group size. However, their scope is limited to a single species or genus, and the questions are not asked in a phylogenetically controlled or broader evolutionary context. The broad-scale evolutionary relationship between time use and social group size remains unknown.

Sociality is described in myriad ways (e.g. number of individuals, Bekoff et al. 1981; Dunbar 1992a; Deaner et al. 2000; number of roles, Blumstein & Armitage 1998; Shultz & Dunbar 2006; strength of social bonds, Stanford 1998; Henzi et al. 2000; Silk et al. 2003; the complexity of relationships, Hinde 1975; Foley & Lee 1989; Colmenares 1992; Barrett & Henzi 2002; Wey et al. 2008; and combinations of these, Crook & Gartlan 1966; Eisenberg et al. 1972). Although group size alone does not fully describe sociality, it is a critical trait that defines boundaries in which other attributes of sociality may be manifested (Janson 1992).

The costs and benefits of sociality include costs and benefits in terms of time (Caraco 1979; Blumstein et al. 2001; Korstjens et al. 2006). Time itself is a finite resource that animals must manage and partition to maximize reproductive success (S.A. Altmann 1974; Dunbar 1992b), and time management strategies depend not only on an animal's habitat and life stage, but also on its social environment. We expect time allocation to be an important cause and consequence of differences in sociality among species.

The literature divides published time budgets into four mutually exclusive and exhaustive behavioural categories: subsistence (foraging/feeding), locomotion (moving/travel), rest (inactivity) and 'other' (including active social and nonsocial behaviours). To uncover broad evolutionary relationships between time allocation and group size, we used these time categories to test eight hypotheses drawn from the literature. Table 1 lists these hypotheses along with their rationales and supporting studies. Hypotheses in the literature lack a consistent prediction as to how time allocation and group size should relate, and few studies have addressed the issue on a scale broader than a single species or single genus. Thus, it is essential to conduct formal comparative analyses to identify which hypotheses best describe the broad evolutionary patterns observed in nature.

We used diurnal primates (50 species) as a model taxon to evaluate these evolutionary hypotheses. Time-allocation and group-size constraints are expected to be most influential in species exhibiting semipermanent social grouping (e.g. Korstjens et al. 2006), such as diurnal primates, social carnivores, cetaceans, equines, elephants, social rodents and many birds. Semipermanent social groups are relatively stable over time and are exclusive in their membership (Freeland 1976; Di Fiore & Rendall 1994). Primates are well suited to testing comparative hypotheses; both group-size and time-allocation patterns are highly variable across species, and well-resolved phylogenies are available. Results from diurnal primates are likely to be relevant to other taxa that live in semipermanent social groups.

METHODS

Selection Criteria and Data Transformation

We took values for all variables from the published literature. We took group-size and time-budget data from original authors. We traced secondary sources, including previous compilations of group size and time budgets, back to their original sources, which we then examined and cited directly (see also Purvis & Webster 1999). This ensured that all data met our inclusion criteria and, in some cases, corrected errors that had been introduced into the secondary literature.

We included time budgets if behaviour was recorded via instantaneous sampling (using focal animals or group scans) or continuous focal sampling (J. Altmann 1974). These methods generally do not result in significantly different estimates of time allocation (Doran 1997), and when they do, estimates typically differ by <2% (Marsh 1981).

We discarded studies reporting time budgets for only a single sex, or for only a single season, unless an equal number of studies for the other sex or other season could be found for the same species. In these cases, we averaged the time allocation for both sexes, or for both seasons (winter versus summer or rainy versus dry), to represent the species' typical time budget.

We discarded time budgets and group sizes from captive populations or actively controlled populations. Similarly, we included time budgets and group sizes only for free-roaming animals whose diet included 2% or less of human food. In all studies in which the amount of human food was not specified or discussed, we assumed the amount to be negligible.

We included time budget estimates in our analysis only if the time samples could be divided into four mutually exclusive and exhaustive categories as defined: subsistence (feeding/foraging), locomotion (moving/travel), resting (inactive) and 'other' (including active social and nonsocial behaviours). We excluded sources whose time budget categories were insufficiently delineated or included only their time budget categories that were adequately defined. In several studies, the authors divided time samples into only the first three categories (subsistence, locomotion and resting). Because the amount of time devoted to 'other' in four-category studies was usually low (often less than 5%, also see Dunbar 1988), we included these three-category studies in the data set, setting the value of the 'other' category to zero. If the primary authors felt confident placing all time samples into three categories for a particular troop, the frequency of 'other' behaviours was likely to be quite low, and we deferred to their judgment. When more than one time

Table 1. Time allocation versus group size relationships suggested in the literature

Time budget category	Predicted relationship to group size	
	Positive	Negative
Subsistence time	Hypothesis 1a: Scramble competition[2; 23; 26; 33] Within-group competition can increase foraging time and effort. Insufficient available subsistence time could constrain group size to reduce competition.	Hypothesis 2a: Intergroup competition[29; 33; 41] Larger groups may outcompete smaller groups, securing better resources, which may reduce foraging time and effort. If subsistence time is limited, living in larger groups may allow best use of that limited time, owing to the better resources secured.
	Hypothesis 1b: Vigilance/group size effect[2; 4; 5; 8; 17; 28; 31] Antipredator benefits of larger groups may reduce time spent (per individual) in vigilance, freeing up time that may be employed as subsistence. Animals obliged to spend much time in subsistence may be subjected to evolutionary pressure to increase group size for its antipredator benefits, because they cannot devote as much individual effort to pure vigilance.	Hypothesis 2b: Group coordination[11; 20] Group feeding may allow animals to optimize patch-return rates and waste less time searching for food in already exploited areas, thus reducing subsistence time. As above, if subsistence time is limited, living in larger groups may allow the most efficient use of this time, because of group coordination.
	Supporting studies: 2–4; 6–8; 12; 22; 26	
Locomotion time	Hypothesis 3a: Resource depletion[9; 39; 42] Larger groups may deplete resources more quickly and thus spend more time travelling to meet their resource needs. Insufficient available time for travel could constrain group size so resources are depleted more gradually.	Hypothesis 4a: Travel between patches[35] Short travelling time favours formation of larger groups because it reduces the overall costs of sociality.
	Hypothesis 3b: Home-range size[10; 18; 24; 36] Larger groups have larger home ranges and may require more travel to utilize and defend these ranges. A larger range also allows large groups to dilute spatially the increased amount of waste they shed. Group size may be limited if travel time is insufficient to defend ranges or disperse waste pathogens.	Hypothesis 4b: Conspicuous travel[37] Large groups greatly increase their conspicuousness to predators while travelling. When crypsis is important, travel time and group size may limit one another.
	Supporting studies: 15; 27; 38 Supporting studies (via day journey length): 10; 12; 15; 21; 22; 24; 25; 30; 38; 39; 42	Supporting studies: 6; 19
Resting time	Hypothesis 5a: Vigilance/group size effect Antipredator benefits of larger groups may reduce time spent (per individual) in active vigilance, freeing up time that may be used to rest. Animals obliged to spend much time in nonvigilant rest may experience evolutionary pressure to increase group size for antipredator benefits, because they cannot devote as much time to active vigilance (e.g., patrolling).	Hypothesis 6a: Resting as reserve time[1; 15; 16; 21; 27] Resting may be the default activity or may act as reserve time from which subsistence, locomotion and active social time are drawn. Animals in large groups may be too 'busy' to spend much time resting.
		Hypothesis 6b: Rest as physical/ecological constraint[14; 23; 26; 27; 40] Animals may be obliged to spend a certain amount of time resting due to digestive, thermoregulatory or other physiological or ecological needs. Species with large resting requirements may be unable to meet other categorical time demands imposed by larger group size.
	Supporting studies: 6; 34	Supporting studies: 22; 26; 38
'Other' time	Hypothesis 7a: Vigilance/group size effect Antipredator benefits of larger groups may reduce the time spent (per individual) in vigilance, freeing up time that may be used for 'other' activities.	Hypothesis 8a: Group territoriality Large groups may spend less time in territorial conflicts and anti-intruder aggression. In turn, less time spent repelling intruders may result in larger typical group sizes.
	Hypothesis 7b: Social bonds and coordination[13; 15] Larger groups may require more time spent in active social behaviour to maintain social bonds and social organization and to coordinate movements and behaviour. Deficiency of such time may constrain group size.	Hypothesis 8b: 'Other' as reserve time[15; 16] Time for 'other' activities may act as reserve time that may be used for more urgent activities such as locomotion or subsistence. Animals in large groups may be too 'busy' to spend much time in 'other' activities.
	Supporting studies: 6; 8; 13; 15; 27	Supporting study: 32

The relationships implicitly or explicitly suggested in the literature, along with rationales and supporting studies, are summarized. (1) Altmann & Muruthi (1988); (2) Beauchamp & Livoreil (1997); (3) Blumstein (1996); (4) Blumstein & Daniel (2003); (5) Blumstein et al. (2001); (6) Blumstein et al. (1999); (7) Bowyer et al. (2001); (8) Caraco (1979); (9) Chapman & Chapman (2000); (10) Clutton-Brock & Harvey (1977); (11) Cody (1971); (12) de Ruiter (1986); (13) Dunbar (1991); (14) Dunbar (1988); (15) Dunbar (1992b); (16) Dunbar & Dunbar (1988); (17) Elgar (1989); (18) Freeland (1976); (19) Hopewell et al. (2005); (20) Horn (1968); (21) Iwamoto & Dunbar (1983); (22) Janson (1988); (23) Janson (1998); (24) Janson & Goldsmith (1995); (25) Jorde & Spuhler (1974); (26) Korstjens & Dunbar (2007); (27) Korstjens et al. (2006); (28) Lima (1995); (29) Nishida & Hiraiwa-Hasegawa (1987); (30) Ostro et al. (1999); (31) Roberts (1996); (32) Robinson (1986); (33) Schoener (1971); (34) Semeniuk & Dill (2005); (35) Sernland et al. (2003); (36) Terborgh (1983); (37) Terborgh & Janson (1986); (38) van Schaik et al. (1983); (39) Waser (1977); (40) Williamson & (1999); (41) Wrangham (1980); (42) Wrangham et al. (1993).

budget was available for a given species, we averaged the values to calculate the 'species-typical' time budget (see Appendix 2 for details).

We compiled group-size values from original authors in the published literature, including only data from wild free-roaming troops. Whereas male group size closely tracks female group size and social structure is often considered female driven (see Lindenfors et al. 2004), whole group size is the standard sociality measure for time and resource studies (e.g. Janson & Goldsmith 1995; Williamson & Dunbar 1999; Chapman & Chapman 2000; Korstjens et al. 2006; Korstjens & Dunbar 2007). Using whole group size acknowledges the important contributions of males, as well as females, to competition, vigilance, conspicuousness, resource depletion and other time-related concerns (see Table 1). For fission−fusion species, the group size included here represents the size of the largest stable exclusive group (i.e. the 'community' for *Pan*, van Elsacker et al. 1995, and the 'band' for geladas, Kawai et al. 1983).

We took precautions to avoid double-counting group-size values recorded from the same study troop by different authors or at slightly different times. We did not allow any well-studied troop to contribute more than one group-size count to the species pool unless these values came from censuses that were at least 5 years apart or that occurred before and after a major group merging or splitting event. When an author reported group-size variations in a troop over multiyear studies, we extracted only the midpoint group-size value unless censuses were taken at least 5 years apart, in which case we extracted a group-size count from every fifth year. We pooled all group-size values for a given species and subsequently averaged them to calculate the species-typical value for use in the phylogenetic analysis (see also Eisenberg et al. 1972). Full time budgets and group-size data meeting our criteria were available for 50 diurnal primate species in the published literature.

We derived values for adult female body mass and for percentage folivory from both primary and secondary sources in the published literature. We subsequently averaged the data to derive species-typical values. To normalize distributions, we $\log_{10}$-transformed species-typical group-size and body-mass values. Time-budget distributions were normally distributed (all $P > 0.05$, Kolmogorov−Smirnov test) and so were not transformed. We multiplied all $\log_{10}$-transformed group-size and body-mass values by 100 to avoid digit truncation during the formal phylogenetic analysis.

Phylogenetic Methods

Shared evolutionary history must be explicitly acknowledged when testing evolutionary hypotheses (Harvey & Pagel 1991; Di Fiore & Rendall 1994; Purvis & Webster 1999). We used Felsenstein's (1985) independent contrasts method to maximize degrees of freedom while ensuring the independence of data points. We used the Smith & Cheverud (2002) primate phylogeny and branch lengths, supplemented with data from Purvis (1995), Nagamachi et al. (1999), de Oliveira et al. (2002), Cortes-Ortiz et al. (2003) and de Lima et al. (2007). We added species missing from the Smith & Cheverud (2002) phylogeny at the midpoint of the branch leading to their sister taxon. We did this to avoid any introduced directional bias regarding time to divergence and it is unlikely to systematically bias the results.

Although the mammal phylogeny in Bininda-Emonds et al. (2007) is more recent, it is missing several of our target species and contains multiple polytomies (as a result of strict consensus methodology), so it is not ideal for running independent contrasts on our species pool. Running the analysis on the Bininda-Emonds et al. phylogeny with polytomies resolved supported the same hypotheses as with the Smith & Cheverud-based phylogeny, but with lower power.

Following Purvis & Rambaut (1995), we transformed phylogenetic branch lengths for some variables to better meet the assumptions of the independent contrasts model (see also Smith & Cheverud 2002). We transformed branch-length values within Mesquite (Maddison & Maddison 2004) via Grafen's (1989) rho method, with $\rho = 0.5$. For all regressions, we derived time budget, group size and folivory contrasts from the phylogeny with transformed branch lengths. We derived body-mass contrasts from the phylogeny with unaltered branch lengths.

We resolved taxonomic synonymies using the Smithsonian National Museum of Natural History's (1993) online index *Mammal Species of the World* and the World Conservation Union's (2006) online index *IUCN Red List of Threatened Species*. The final phylogeny, including raw branch lengths, is given in Appendix 1. We calculated independent contrasts with the PDAP module (Midford et al. 2003) in Mesquite version 1.04 (Maddison & Maddison 2004). We used SPSS version 10.0 (SPSS, Inc., Chicago, Illinois, U.S.A., 1999) for statistical analysis.

Statistical Considerations and Modelling

Using bivariate linear regressions and general linear models on contrasts values, we tested the eight hypotheses in Table 1. We asked whether variation in group size correlated with variation in (1) subsistence time, (2) moving time, (3) resting time, and/or (4) 'other' time. Our aim was not to test the direction of causality, but rather to assess whether correlations existed and to identify the nature (positive or negative) of the relationships. We simultaneously tested hypotheses (Table 1) that differ in their main direction of causal flow, including many that may be bidirectional (e.g. feedback processes).

We used the results from the bivariate regressions to decide which time variables to include in a general linear model. We used the general linear model to account for two potentially confounding life-history variables: body mass and diet type (degree of folivory). Body mass influences both predation risk and resource needs and may affect the evolution of group size or time allocation (Jorde

& Spuhler 1974; Clutton-Brock & Harvey 1977; van Schaik 1983; Dunbar 1992a; Ford & Davis 1992; Janson & Goldsmith 1995; Schmidt-Nielsen 1997; Nunn & van Schaik 2002). Similarly, diet type influences resource requirements, and it may affect time-allocation patterns or group size (Clutton-Brock 1975; Clutton-Brock & Harvey 1977; Janson & Goldsmith 1995; Williamson & Dunbar 1999; Nunn & van Schaik 2002). Body mass and diet type may affect group size or time allocation as main effects or as interactions with time variables or with one another, so we entered them into the general linear model along with time variables.

We fitted the general linear model using backwards elimination, starting from resting time, moving time, body mass and percentage folivory and all their two-way interactions. We chose resting time and moving time because they had the strongest time relationships with group size in bivariate regressions. The final four input variables (resting time, moving time, body mass, and percentage folivory) were not multicollinear: in no case were variance inflation factor values >2 or correlations between input variables >0.7 (Slinker & Glantz 1985). When fitting the general linear model, we removed predictor variables until all remaining variables were significant at the $\alpha = 0.05$ level.

RESULTS

The strongest bivariate relationship was between group size and rest time ($y = -0.603x$, $P = 0.050$, $N = 49$ independent contrasts), predicting nearly 8% of the variation ($R^2 = 0.078$). We found no significant bivariate relationship between group size and subsistence time ($R^2 = 0.011$, $y = 0.233x$, $P = 0.476$), moving time ($R^2 = 0.042$, $y = 0.749x$, $P = 0.152$) or 'other' time ($R^2 = 0.011$, $y = 0.423x$, $P = 0.464$).

The final linear model significantly ($P < 0.001$) explained 28.5% of the variation in the evolution of group size in diurnal primates and contained resting time and an interaction between body mass and percentage folivory as predictor variables (Table 2). Body mass and percentage folivory were not significant as main effects, with or without their interaction present in the model.

Using the Bininda-Emonds et al. (2007) phylogeny with polytomies resolved as in the Smith & Cheverud (2002)-based phylogeny yields the same main effects but loses power owing to missing species. Under both phylogenies, rest was the most important time category to group size, the relationship was negative, and rest was significant after controlling for body mass and folivory.

Table 2. Results from the general linear model explaining variation in group size

	B	P	Partial η^2
Model		<0.001	0.285
Rest	−0.678	0.015	0.120
Body mass*percentage folivory	−0.074	0.001	0.225

The rest and folivory variables in the model represent the standardized contrasts of the raw values, and the group-size and body-mass variables represent the standardized contrasts of 100 times the log of the raw values.

DISCUSSION

For our semipermanent social group species, the evolution of group size correlated with evolutionary change in time allocated to resting. Multivariate models revealed that, together, resting time (partial $\eta^2 = 0.120$) and an interaction between body mass and percentage folivory (partial $\eta^2 = 0.225$) explained significant variation in the evolution of group size. Evidence for the relationship between rest time and group size was thus stronger after the data were adjusted for the effects of two potentially confounding life-history variables, diet and body mass. The observed evolutionary relationship between group size and resting time is consistent only with hypotheses 6a and 6b (see Table 1). These hypotheses differ in their main direction of causality and mechanism of action, but they need not be mutually exclusive and may work together (see also Korstjens & Dunbar 2007).

Does Resting Act as Reserve Time (Hypothesis 6a)?

Because rest is the least energetically intensive activity, and the least conspicuous, it serves as a default behaviour (Iwamoto & Dunbar 1983; Altmann & Muruthi 1988; Dunbar & Dunbar 1988; Dunbar 1992b; Korstjens et al. 2006). Any active-time demands imposed by increased sociality (e.g. travel time, foraging time and/or active social time) would reduce the time available for resting, leading to the negative correlation observed.

Could Resting Time Constrain Group Size (Hypothesis 6b)?

Increases in group size may increase the need for activity while reducing opportunities to rest or 'be lazy'. For primates and other animals living in semipermanent social groups, this suggests an upper limit to group size, partly dictated by the amount of resting time that individuals are able to sacrifice (Williamson & Dunbar 1999; Korstjens & Dunbar 2007). A physiological or ecological need for rest, resulting from digestion constraints, heat dissipation/conservation, bodily repair, crypsis or other factors, may render a species unable to meet other categorical time demands imposed by sociality (Dunbar 1988; Janson 1998; Williamson & Dunbar 1999; Korstjens et al. 2006) and may constrain the evolution of larger group size.

Digestion constraints are one physiological cause for needed rest (see Dasilva 1992; Korstjens & Dunbar 2007) and are a particular concern for species with leafy diets.

Folivory is significantly and positively related to resting time ($R^2 = 0.092$, $P = 0.032$), and digestive resting time constraints have been shown to limit group size in certain taxa (e.g. colobus monkeys, Korstjens & Dunbar 2007). Our results suggest that folivory is not the only contributing factor to resting time requirements or their effect on group size, however. Evolutionary changes in resting time occur frequently in contrasts in which folivory remains constant, and after controlling for dietary folivory in the general linear model, resting time still explained a significant portion of the variation in social group size across diurnal primates.

Another physiological need for rest is thermoregulation. In hot climates or those with little cover, certain species may be forced to spend the warmest hours of their day sitting in the shade or otherwise resting to avoid overheating (Dunbar 1988, 1992b; Stelzner 1988). In cooler climates or during cold seasons, the converse may be true: resting may be vital for conserving heat (e.g. 'sunning' behaviour, Morland 1993). For any habitat in which animals frequently experience temperatures outside their thermoneutral zone, resting time may be essential. The relative importance of thermoregulation to resting time and group size remains to be explored.

Animals constrained to rest may be unable to meet the elevated time or energy demands of increased sociality, including active social interaction itself (see also Dunbar 1988). Although primates in general do not allocate much of their time budgets to social behaviours, the time they do allocate is critical. Social interaction reduces aggression and assists exchanges of help and resources among group members (Seyfarth & Cheney 1984; de Waal 1989; Baker & Aureli 2000), thus facilitating social cohesion. If social interaction is necessary to bind individuals into a social group (Dunbar 1988; Williamson & Dunbar 1999; Korstjens et al. 2006), large resting time requirements could force animals to interact socially with fewer individuals. This has been demonstrated in geladas: when females are forced to allocate extra time to feeding, and when they use up much of their resting time for this purpose, their social interactions subsequently become restricted to a smaller number of social partners (Dunbar & Dunbar 1988). Resting time cannot drop below a certain threshold, and after that, social time is sacrificed. Any species with steep physiological/ecological resting requirements could face this constraint. When rest time cannot be forfeited to accommodate the need for increased foraging or travel, social time and social relationships may be sacrificed, rendering the species unable to maintain large group sizes.

Significance and Implications

Traditional discussions of the causes and consequences of sociality have generally paid little attention to the limited resource of time. Our results suggest that a broad-scale evolutionary relationship exists between time allocation and social group size. Time allocation therefore deserves a place among the many ecological and life-history variables already considered in models of social evolution. By including time-allocation patterns in future models, alongside other life-history and ecological variables, biologists may better predict social group sizes and geographical distributions of different species. Furthermore, our results reveal a consistent, unified evolutionary influence of time, thus sorting out which of the many time–group-size predictions in the literature are operating on a broad evolutionary level.

A time-allocation perspective may also prove useful for wildlife conservation and management. If resting time constrains social group size in species living in semi-permanent social groups, anything that disrupts resting time (e.g. anthropogenic disturbance) may have longer-term ramifications on social stability. If resting time is a hardwired physiological constraint for some species, any lost resting time will have to be made up by extracting time from a behavioural category that is more immediately expendable. Social time might serve as the emergency reserve category of time, if resting is constrained (Dunbar & Dunbar 1988).

In sensitive populations, anthropogenic disturbance could set off a chain of temporally mediated events that ultimately reduces the amount of time animals have available to spend in social behaviours or otherwise maintain social cohesion (see Lusseau 2004). This loss of resting and social time could decrease social cohesion and subsequently reduce group size below optimal levels, which may have repercussions for population viability. Assessments of anthropogenic disturbance already account for changes in physical resources, but it may be prudent to account for temporal resources as well.

Implications may extend beyond direct disturbance. Time has been shown to be an important factor influencing not just social group size but also the distribution of species: when combined with climactic variables, time allocation data help predict the observed group size and geographic distribution of colobus monkeys (*Colobus* spp. and *Procolobus* spp., Korstjens & Dunbar 2007), spider monkeys (*Ateles* spp., Korstjens et al. 2006) and baboons (*Papio* spp., Dunbar 1992b). If ecological and time constraints prevent a species from maintaining a sufficiently large group size in a given habitat, that species will be absent from that habitat (Dunbar 1992b). Therefore, anthropogenic climate change could, among other things, alter animals' time allocation needs and ultimately may have detrimental effects on social group size. Changes in social group size could affect both population viability and overall geographic range. Identifying the time constraints and group-size needs of a given species may help researchers mitigate anticipated negative effects.

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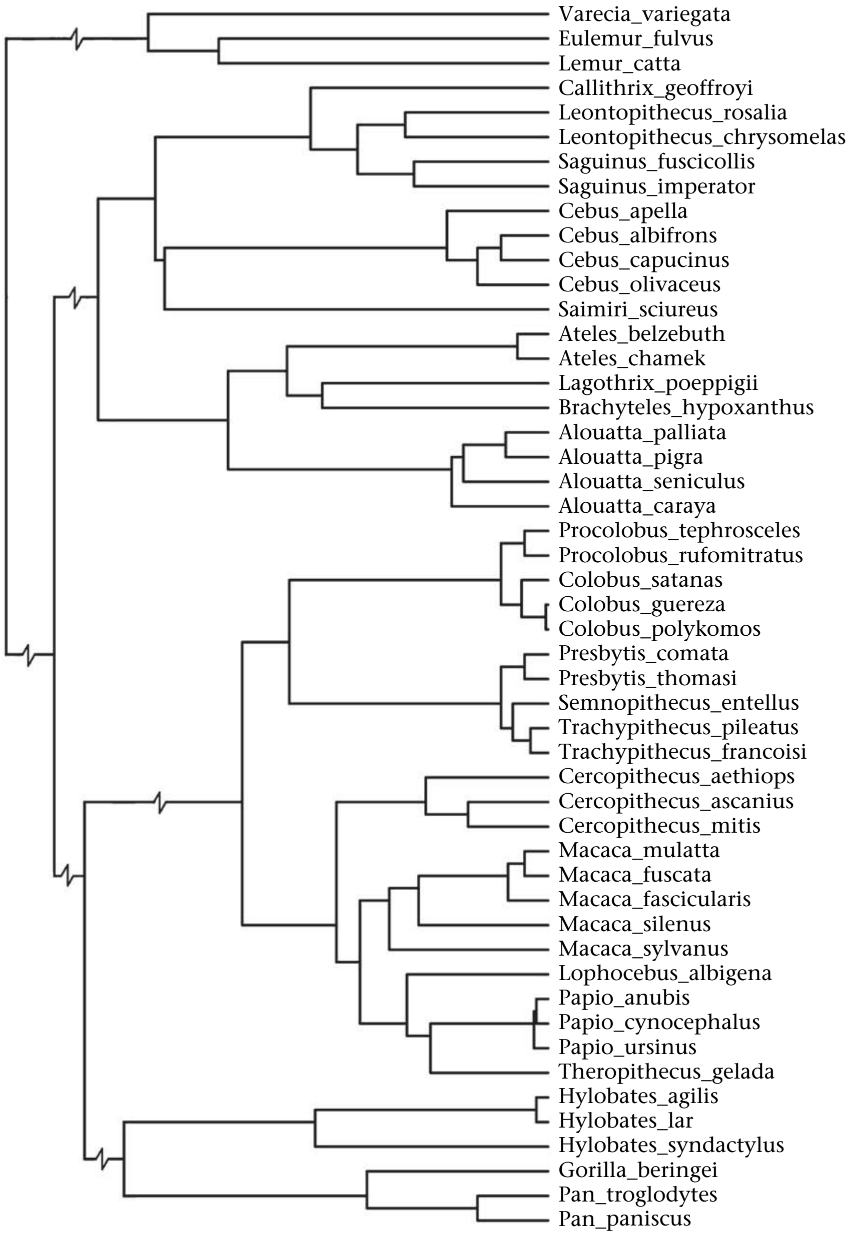
Appendix 1

Phylogeny with untransformed branch lengths, in drawn tree and Newick formats
Branches are drawn proportional to lengths except where indicated.



```
((Varecia_variegata:17.0,(Eulem
ur_fulvus:14.0,Lemur_catta:14.0)
:3.0):46.0,((((Callithrix_geoffroyi:
10.1,((Leontopithecus_rosalia:6.
075,Leontopithecus_chrysomela
s:6.075):2.025,(Saguinus_fuscic
ollis:5.7,Saguinus_imperator:5.7)
:2.4):2.0):6.6,((Cebus_apella:4.3,
((Cebus_albifrons:2.0,Cebus_ca
pucinus:2.0):1.0,Cebus_olivaceu
s:3.0):1.3):12.0,Saimiri_sciureus:
16.3):0.4):3.4,(((Ateles_belzebut
h:1.3,Ateles_chamek:1.3):9.8,(La
gothrix_poeppigii:9.6,Brachyteles
_hypoxanthus:9.6):1.5):2.5,(((Alo
uatta_palliata:1.8,Alouatta_pigra:
1.8):1.8,Alouatta_seniculus:3.6):
0.5,Alouatta_caraya:4.1):9.5):6.5
):14.9,(((((Procolobus_tephroscel
es:1.0,Procolobus_rufomitratus:1
.0):1.0,(Colobus_satanas:1.125,(
Colobus_guereza:0.1,Colobus_p
olykomos:0.1):1.025):0.875):9.0,(
(Presbytis_comata:1.0,Presbytis
_thomasi:1.0):1.0,(Semnopithecu
s_entellus:1.5,(Trachypithecus_p
ileatus:0.75,Trachypithecus_fran
coisi:0.75):0.75):0.5):9.0):2.0,((C
ercopithecus_aethiops:5.2,(Cerc
opithecus_ascanius:3.4,Cercopit
hecus_mitis:3.4):1.8):3.8,(((((Ma
caca_mulatta:1.0,Macaca_fusca
a:1.0):0.7,Macaca_fascicularis:1.7
):3.8,Macaca_silenus:5.5):1.25,
Macaca_sylvanus:6.75):1.25,(Lo
phocebus_albigena:6.0,(((Papio_
anubis:0.5,Papio_cynocephalus:
0.5):0.1,Papio_ursinus:0.6):4.4,T
heropithecus_gelada:5.0):1.0):2.
0):1.0):4.0):12.0,(((Hylobates_agi
lis:0.5,Hylobates_lar:0.5):9.4,Hyl
obates_syndactylus:9.9):9.1,(Gor
illa_beringei:7.7,(Pan_troglodyte
s:3.0,Pan_paniscus:3.0):4.7):11.
3):6.0):10.0):28.0);
```

Appendix 2

Raw data values used in this analysis

Species	Group size	Subsistence (%)	Locomotion (%)	Rest (%)	Other (%)	Adult female body mass (kg)	Folivory (%)	Sources (group size and time budgets)	Sources (body mass and folivory)
Alouatta caraya	9.0	14.1	17.7	62.6	5.6	5.4	62.6	10; 132; 158	10; 111; 132; 158
Alouatta palliata	13.8	27.5	16.2	50.2	6.1	5.6	52.6	6; 22; 47; 51; 64; 98; 99; 100; 139	17; 30; 47; 58; 100; 111; 125; 139
Alouatta pigra	5.4	21.9	9.9	65.7	2.5	6.3	51.9	11; 115; 118; 135; 138	111; 118; 138
Alouatta seniculus	7.9	17.3	11.4	70.3	1.0	5.9	43.3	12; 29; 37; 54; 73; 107	30; 54; 80; 111; 141
Ateles belzebuth	22.7	22.2	14.8	63.0	0.0	7.3	7.0	82; 136	17; 80; 82; 140
Ateles chamek	38.5	29.0	26.0	45.0	0.0	7.2*	7.9*	154	17; 80; 130
Brachyteles hypoxanthus	27.2	18.8	29.4	49.3	2.5	7.9	67.1*	32; 144; 145	87; 101
Callithrix geoffroyi	4.0	47.7	20.4	29.0	2.9	0.3	0.0*	117	21; 117; 80
Cebus albifrons	21.9	61.0	21.0	18.0	0.0	2.2	0.0	36; 157	17; 80; 157
Cebus apella	10.2	66.0	21.0	12.0	1.0	2.4	0.0	74; 75; 141; 157	17; 80; 140; 157
Cebus capucinus	16.7	34.4	41.9	17.4	6.2	2.5	15.0	16; 51; 52; 98	17; 52; 58
Cebus olivaceus	17.6	45.1	22.9	18.2	13.9	2.3	12.2	33; 50; 127; 128	17; 50; 80
Cercopithecus aethiops	24.9	31.8	27.1	31.6	9.5	3.2	18.7	18; 44; 85; 103; 129; 146; 153	17; 44; 80; 111; 146; 160
Cercopithecus ascanius	27.8	37.4	29.7	26.9	6.0	2.9	11.7	28; 148; 149; 153	28; 55; 148
Cercopithecus mitis	26.7	43.8	13.1	40.1	3.0	3.8	12.6	28; 79; 103; 149; 153	27; 28; 55; 79; 149
Colobus guereza	7.8	23.4	4.0	62.6	10.0	8.2	79.0	25; 43; 45; 48; 91; 112; 129; 134; 153	17; 80; 111; 112; 113; 140; 149
Colobus polykomos	14.5	27.3	13.1	57.1	2.5	8.1	53.1	31; 53; 114; 156	31; 53; 114; 130
Colobus satanas	15.6	23.8	3.8	57.3	15.0	9.5	38.6	95	17; 80; 113
Eulemur fulvus	9.5	16.6	20.0	49.7	13.7	2.2	70.6	152	17; 111; 152
Gorilla berengei	11.1	25.7	14.4	52.4	7.6	87.0	85.8	49	7; 49
Hylobates agilis	3.7	36.0	30.0	29.0	5.0	5.7	39.0	46; 57; 102	17; 57; 80; 111
Hylobates lar	3.7	35.7	39.7	12.6	12.0	5.3	32.9	15; 19; 46; 57; 90	17; 19; 57; 80; 90; 111
Hylobates syndactylus	4.0	51.3	16.3	27.0	5.4	10.6	50.1	19; 46; 57; 90	17; 19; 20; 57; 90; 111
Lagothrix poeppigii	23.7	36.2	34.5	23.2	6.1	6.2*	7.5	40	17; 39; 40; 80; 140
Lemur catta	15.4	31.1	13.2	38.6	17.0	2.6	34.0	67; 83; 152	17; 111; 152
Leontopithecus chrysomelas	4.6	31.5	34.2	22.5	11.8	0.5	0.0	122; 133	80; 81
Leontopithecus rosalia	4.6	24.9	20.8	50.8	3.5	0.6	0.0	81; 97	41; 81; 130
Lophocebus albigena	15.3	51.9	26.2	11.8	10.1	6.2	5.3	121; 165	55; 149; 165
Macaca fascicularis	21.6	47.5	19.1	33.4	0.0	3.6	14.8	9; 90; 163	17; 90; 111; 166
Macaca fuscata	20.4	37.5	21.4	21.2	19.9	9.1	32.0	1; 2; 63	1; 2; 63; 65; 80
Macaca mulatta	40.9	17.5	23.2	30.5	28.7	4.2	32.0*	142; 155; 159	1; 2; 63; 65; 80; 111
Macaca silenus	22.0	54.5	15.0	27.0	3.5	5.0	26.3*	84	1; 2; 63; 65; 80; 90; 166
Macaca sylvanus	24.5	29.7	21.2	38.5	10.8	10.0	40.0	34; 96; 169	80; 130
Pan paniscus	57.8	42.7	17.0	33.7	6.7	33.0	20.1	5; 69; 77; 162; 167	7; 78; 119; 167
Pan troglodytes	46.7	45.0	17.7	32.0	5.3	35.1	14.5	42; 71; 86; 94; 109; 110; 124; 126; 153; 161; 170	7; 17; 80; 124; 130; 170
Papio anubis	41.8	28.1	25.7	30.9	15.3	13.1	32.9	3; 38; 44; 106; 123; 150; 153	44; 80; 111; 140
Papio cynocephalus	50.1	46.7	24.0	21.9	7.4	13.6	7.8	3; 26; 103; 120; 137	17; 111; 130; 140
Papio ursinus	42.2	50.0	23.5	14.8	11.7	15.4	21.2	4; 14; 61; 62; 66; 168	14; 17; 111; 168
Presbytis comata	6.8	29.3	4.7	63.9	2.1	6.7	64.7	131	131; 111
Presbytis thomasi	7.5	28.6	9.0	62.4	0.0	6.0	36.5	60; 143	60; 80
Procolobus rufomitratus	14.9	26.9	14.0	50.1	9.0	5.4	64.1	35; 92; 93	53; 55; 113

(*continued on next page*)

Appendix 2 (*continued*)

Species	Group size	Subsistence (%)	Locomotion (%)	Rest (%)	Other (%)	Adult female body mass (kg)	Folivory (%)	Sources (group size and time budgets)	Sources (body mass and folivory)
Procolobus tephrosceles	41.9	37.3	8.1	46.5	8.1	6.4	74.8	23; 24; 56; 147	17; 148
Saguinus fuscicollis	5.0	31.7	19.8	43.6	5.0	0.4	0.0	59; 157	80; 111; 157
Saguinus imperator	4.0	50.5	20.8	24.8	4.0	0.5	0.0	157	17; 111; 157
Saimiri sciureus	38.8	60.4	26.7	10.9	2.0	0.7	0.0	73; 157	17; 80; 130
Semnopithecus entellus	19.1	28.6	14.6	46.5	10.2	11.7	49.8	76; 108	17; 80; 108; 151
Theropithecus gelada	101.9	38.5	18.3	22.4	20.8	12.7	83.0	44; 72	17; 44; 72; 111
Trachypithecus francoisi	8.9	13.4	12.1	65.1	9.4	8.7	55.9*	68; 89	8; 21; 70; 88; 142
Trachypithecus pileatus	7.1	33.5	15.6	44.5	6.4	9.5	66.9	70; 142; 159	21; 70; 142
Varecia variegata	19.4	26.2	19.2	54.6	0.0	3.4	5.5	13; 104; 105; 164	13; 111; 116; 164

For each species, the time-budget values were averaged first within a source and then between multiple sources. Each complete time budget was scaled so that the combined categories summed to exactly 100.0 (to compensate for authors' rounding). When including time-budget data from studies that did not report exact values for all distinct categories (i.e. the authors lumped two or more categories), each distinct category was averaged separately between sources, and then the averages were scaled such that the final four categories summed to exactly 100.0.
*Includes data from congeners.

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