

Costs of group size: lower developmental and reproductive rates in larger groups of leaf monkeys

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Feeding competition is suggested as a major factor constraining group size in social foragers. It has, however, been challenging to demonstrate consequences of reduced energy gain in terms of fitness, possibly because social foragers may compensate negative effects of scramble competition via adjustments in time budgets. Herbivorous animals are particularly interesting in this context because their fibrous diet and slow digestion process may make it difficult to adjust time budgets. Here we investigate infant development and reproductive rates in Phayre's leaf monkeys (*Trachypithecus phayrei*) at Phu Khieo Wildlife Sanctuary, Thailand. The diet of the species consists of 39.0% leaves (maximum 81.2% per month). Our analysis is based on data for 3 groups (185 group months) of different sizes (mean 11.4, 18.3, and 25.8 individuals, respectively). Infant development was significantly slower in the large group, in which infants changed to the adult coat later than in the medium-sized group (20.3 vs. 26.3 weeks) and were older when weaned (18.3, 19.7, and 21.4 months, respectively). The interbirth interval after a surviving infant significantly increased with group size (21.3, 22.8, and 24.5 months) while rearing success did not differ (77.8%, 76.5%, and 82.4%, survival to 2 years). Thus, infants in the large group developed more slowly were weaned later and females reproduced more slowly. With similar infant survival rates, these different reproductive rates indicate fitness differences across groups. As in other herbivores, these group-specific differences may reflect scramble competition for food or differences in habitat quality. *Key words*: infant development, infant mortality, interbirth interval, reproductive costs, scramble competition, *Trachypithecus phayrei*. [*Behav Ecol* 19:1186–1191 (2008)]

INTRODUCTION

Social foraging is assumed to provide benefits but might also impose costs (Giraldeau and Caraco 2000) with the rate of food acquired by an individual dependent on the number of foragers (Pulliam and Caraco 1984; Clark and Mangel 1986; Beauchamp 1998). As their numbers increase so do aggression and interference thereby reducing the benefits (Caraco 1979; Krause and Ruxton 2002). When food resources are limited, they will be depleted faster (Caraco 1979; Pyke 1984), which may lead to more patch visits and otherwise increased foraging efforts (Janson and van Schaik 1988; Chapman et al. 1995; Janson and Goldsmith 1995). Consequently, individuals living in larger groups may experience reduced food intake rates, increased energy expenditure or both translating into lower net energy gain, an effect often referred to as scramble competition (Nicholson 1957; van Schaik 1989). A less favorable energy balance may lead to slower somatic growth, older age at maturation, reduced birth, or increased mortality rates (Borries et al. 2001; Altmann and Alberts 2003, 2005). Thus, competition for food may effectively constrain group size in gregarious foragers (Bradbury and Vehrencamp 1976; Giraldeau and Gillis 1985; Janson 1992; Parker 2000), resembling density-dependent effects on nutrition and reproduction (Stewart et al. 2005).

Although a straightforward concept, it has proved difficult to document scramble effects with regard to fitness. Among car-

nivores and nonhuman primates, for example, large group size may be associated with longer daily path length (Isbell 1991; Wrangham et al. 1993; Janson and Goldsmith 1995; Chapman CA and Chapman LJ 2000), larger home range size (e.g., Davidge 1978; Suzuki 1979; Takasaki 1981), or reduced foraging efficiency (e.g., Janson 1988a; van Schaik and van Noordwijk 1988). Despite these energetic effects of group size negative effects on somatic growth, birth, and survival rates are often moderate (van Noordwijk and van Schaik 1999; McComb et al. 2001; Altmann and Alberts 2003) or even reversed (Cheney and Seyfarth 1987; Robinson 1988; Suzuki et al. 1998; Packer et al. 2001). Such inconsistent findings likely result from at least 3 factors. First, species or populations that form long-term associations may reduce scramble competition by regularly fission and fusion (e.g., some cetaceans, proboscideans, and nonhuman primates), or they may permanently fission once group size becomes too large (Chapman et al. 1995; Henzi et al. 1997; Karczmarski et al. 2005; Wittemyer et al. 2005). Second, animals in larger groups may compensate for lower energy input via adjustments in time budgets (Caraco 1979; Janson 1988b; Janson and van Schaik 1988) until certain components of the time budget cannot be compressed further (Dunbar 1992). Thus, scramble effects on foraging may be counterbalanced (Janson 1988a). Third, benefits of grouping may lead to fitness functions that are humped or n-shaped rather than linearly negative (Dunbar 1988; discussion in Krause and Ruxton [2002]; see also Wrangham 1980; Sibly 1983; van Schaik 1983).

The relationship between costs and benefits seems even more complex in herbivores. In many ruminants and kangaroos, group size changes continually, is often density dependent, and is not necessarily constrained by energetic costs of social foraging (Gerard et al. 2002; Pepin and Gerard 2008;

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contra Jarman 1974). In other herbivores forming rather stable associations (e.g., red deer, elephants), group size may be associated with negative effects on foraging success, maternal condition, and fecundity (Clutton-Brock et al. 1982; McComb et al. 2001; Focardi and Pecchioli 2005; Wittemyer et al. 2005). In contrast, in folivorous nonhuman primates, daily path length is often unrelated to group size (Struhsaker and Leland 1987; Yeager and Kirkpatrick 1998). Previously, this result was interpreted as absence of scramble competition, a plausible argument given that leaves appear to be rather evenly distributed in space and time and leaf patches nondepletable (Isbell 1991; Sterck et al. 1997). Recent studies, however, have found evidence for scramble competition in several folivorous species (Koenig 2000; Saj and Sicotte 2007; overview in Snaith and Chapman 2007). In addition, because of a diet high in fiber and a slow digestion process including fermentation (Lambert 1998), gut capacity might limit food intake and might not allow for any further compensation (Stephens and Krebs 1986). Lastly, the diet of folivores may also provide low energy yield so that daily path length cannot be increased (Janson and Goldsmith 1995).

In light of these foraging constraints, folivorous nonhuman primate species provide an ideal opportunity to study the effects of group size on reproductive rates. An early analysis found a decline in the number of infants per female with increasing group size (van Schaik 1983). However, the analysis was based on rates that may be subject to high interannual fluctuations (Dunbar 1988; Janson and Goldsmith 1995). More recent data for folivorous species showed no or weak effects of group size on birth or survival rates (Steenbeck and van Schaik 2001; Stokes et al. 2003; Robbins et al. 2007). In these cases, scramble effects may have been reduced due to small group sizes or masked by other factors (predation, infanticide) that may affect mortality differently across groups and will accelerate birth rates (Crockett and Janson 2000). Thus, when attempting to understand group size effects on fitness functions, more than one vital demographic rate should be measured while controlling for mortality patterns.

Here we investigate group size effects on demographic rates in wild Phayre's leaf monkeys (*Trachypithecus phayrei*). This medium-sized Asian colobine monkey is characterized by a ruminant-like digestion (Bauchop and Martucci 1968) with a diet consisting of 39.0% leaves (monthly values: 9.6–81.2%) and 35.6% fruits (Koenig et al. 2004). Thus, Phayre's leaf monkeys fall within the range reported for other folivorous Asian primates (29–78% leaves, 11–62% fruits; Kirkpatrick 2007). Group size is variable in the study population (3–33 members) and despite several years of observations, neither male immigration nor infanticide has been witnessed or suspected. Based on detailed, individualized, demographic data spanning multiple years, we compare infant developmental rates, age

at weaning, interbirth intervals, and infant survival rates with the expectation that individuals in larger groups have slower developmental and reproductive rates.

MATERIALS AND METHODS

We studied wild, habituated Phayre's leaf monkeys at Phu Khieo Wildlife Sanctuary, northeastern Thailand (16°5'–35'N, 101°20'–55'E; 500–1,300 m above sea level, total area 1,573 km², annual mean temperature 21.5 °C, rainfall 1,450 mm). The study site consists of dry evergreen forest with patches of dry dipterocarp forest and has a diverse predator community (Borries et al. 2002). Three groups of different sizes (PS small, PA medium, and PB large) were observed for 5 or more consecutive days each month. All group members were known individually. Details of the observation periods and group sizes are summarized in Table 1. The number of animals per group fluctuated during the course of the study but relative sizes remained constant (i.e., the smallest group was always the smallest). Both, the large and the small group had only one adult male (and always multiple adult female) for most of the observation period (small: 58 out of 63 months, i.e., 92.1%, large: 43 out of 48 months, i.e., 89.5%), whereas the medium-sized group always had 2–4 adult males (and multiple adult females).

During each contact day, we recorded the presence of every group member, as well as births and nipple contact. Interbirth intervals ($n = 32$) were calculated from the birth month of a surviving infant to the birth month of the subsequent infant (to control for the accelerating effect of premature infant loss). Weaning ages ($n = 34$) were calculated from the birth month until the last month (inclusively) when nipple contact was observed (for 7 of the infants, the birth month was estimated). Infant survival was calculated for infants who became or could have become one ($n = 53$) or 2 years ($n = 43$) of age during the study.

In Phayre's leaf monkeys, infants are born with a flamboyant orange coat and pale skin that gradually changes into adult coloration (gray fur and skin). Skin and fur color changes were documented (by Eileen Larney) for 13 infants born between 24 November 2004 and 3 February, 2006 into the medium ($n = 4$) and the large ($n = 9$) group. Due to logistical problems, this work did not cover the small group for which no data on color change are available. For the first 8 weeks, color distribution of skin and fur was documented weekly, thereafter biweekly, until full adult coloration was achieved (Larney E, Koenig A, unpublished data).

Descriptive statistics and tests were conducted in STATISTICA 6.1 at an alpha level of 0.05, and results are reported 1-tailed due to the directed predictions (lower rates, older ages, and longer intervals with increasing group size). Due to the overall small sample size (even if large for a wild, slow-growing species), statistical trends are not interpreted.

Table 1
Observation periods and group size information (until July 2007 inclusively)

Group	Data since	Contact			Group size			Group size (excluding infants)			Adult female group size		
		Months	Days	Hours	Mean	Median	Range	Mean	Median	Range	Mean	Median	Range
PS ^a	March 2002	63	418	3,904	11.4	10.0	6–19	8.0	7.0	5–15	4.3	4.0	3–7
PA ^b	January 2001	74	759	7,298	18.3	18.0	14–23	14.0	14.0	10–18	5.4	5.0	3–8
PB	August 2003	48	669	7,207	25.8	25.0	20–33	16.6	17.0	13–23	10.5	10.0	9–12
Total		185	1,846	18,409									

Groups arranged from top to bottom according to size.

^a No data for May and June 2002.

^b No data for September 2001 through January 2002.

RESULTS

Infants in the large group completed the color change more slowly than infants in the medium-sized group. On average, it took infants in the large group 26.3 weeks (median = 25.0, range = 21–39, $n = 9$) compared with 20.3 weeks in the medium-sized group (median = 19.5, range = 18–24, $n = 4$; Mann-Whitney U-test [MWU] test: $U = 5.50$, $n_1 = 4$, $n_2 = 9$, $z_{\text{adj}} = 1.94$, $P = 0.025$ [Siegel and Castellan 1988]; Figure 1). Excluding the outlier in the large group (39 weeks, Figure 1) lowers the significance level, although the general relationship holds (MWU test: $U = 5.50$, $n_1 = 4$, $n_2 = 8$, $z_{\text{adj}} = 1.79$, $P = 0.036$).

Similarly, weaning age significantly depended on group size (Jonckheere test for ordered alternatives $J^* = 2.238$, $P < 0.050$ [Siegel and Castellan 1988]). On cessation of nipple contact, infants of the small group were youngest (mean = 18.3 months, median = 19.0, range = 13–23, $n = 8$), intermediate in the medium-sized group (median = 19.7 months, median = 20.0, range = 16–23, $n = 11$) and oldest in the large group (mean = 21.4 months, median = 21.0, range = 15–29, $n = 15$; Figure 2) although the multiple comparisons between groups were not significant ($P < 0.075$).

Female reproductive rates declined with increasing group size (Jonckheere test for ordered alternatives $J^* = 2.056$, $P < 0.050$; Figure 3). In the small group, the interval after a surviving infant averaged 21.3 months (median = 21.5, range = 15–27, $n = 8$), in the medium-sized group 22.8 months (median = 23.0, range = 20–24, $n = 9$), and in the large group 24.5 months (median = 24.0, range = 16–34, $n = 15$). Multiple comparisons between groups did not yield a significant result ($P > 0.075$).

Infant survival did not depend on group size. For the small group, it was 81.8% ($n = 11$) after 1 year and 77.8% ($n = 9$) after 2 years; for the medium-sized group, 81.0% ($n = 21$) after 1 year and 76.5% ($n = 17$) after 2 years; and for the large group, 90.5% after 1 year ($n = 21$) and 82.4% ($n = 17$) after 2 years. Neither is significant (G -test of independence [Sokal and Rohlf 1995], degrees of freedom = 2, for 1 year $G = 0.890$, $P > 0.1$; for 2 years $G = 0.192$, $P > 0.1$).

DISCUSSION

In this study, Phayre's leaf monkey infants in the large group developed more slowly were weaned later and females repro-

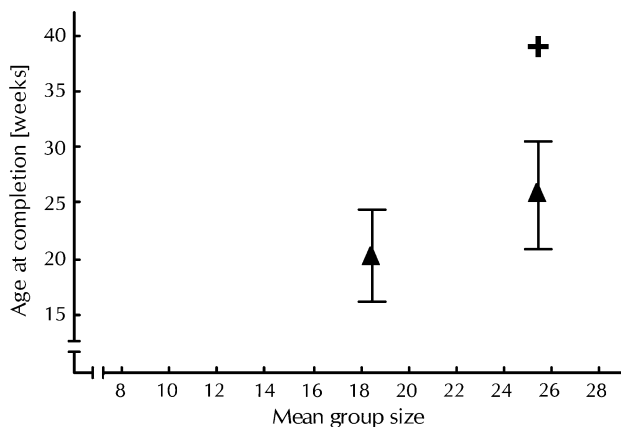


Figure 1

At the completion of fur color change (to adult pelage), infants of the large group were significantly older compared with the medium-sized group (no data available for the small group). Triangles represent mean values, whiskers the 95% confidence limits, the cross an outlier.

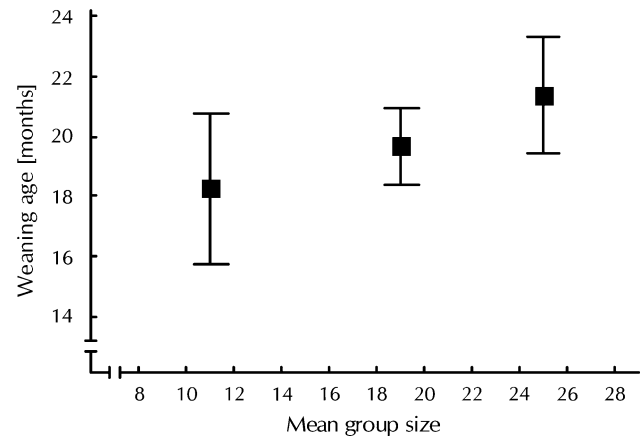


Figure 2

Weaning age ($n = 34$) increased with group size. Squares represent mean values, whiskers the 95% confidence limits.

duced more slowly. Because infant survival rates were similar, the differences found for reproductive rates should indicate real fitness differences across groups. However, sample sizes are small, and the results have to be treated with caution.

Group size, growth, and reproductive rates

The slower infant development during early infancy in larger groups (Figure 1) was most likely related to a lower energetic net gain of the mothers whose nutritional state might have negatively affected the developmental rates of the infants. Even though it is not entirely clear to what degree developmental measures reflect growth, it seems likely that early infancy is particularly sensitive to the energy available via the mother (Lee 1987; McCabe and Fedigan 2007). Similarly, during later infancy, nutrition might have influenced the speed of infant development because infants of the large group were weaned at a significantly older age (Figure 2). Although comparable measures have rarely been published for nonhuman primates (but see Altmann and Alberts 2005), the reported group size effects seem to resemble density dependence of infant development, infant body mass, or infant recruitment in other species including herbivores (Forchhammer et al. 2001;

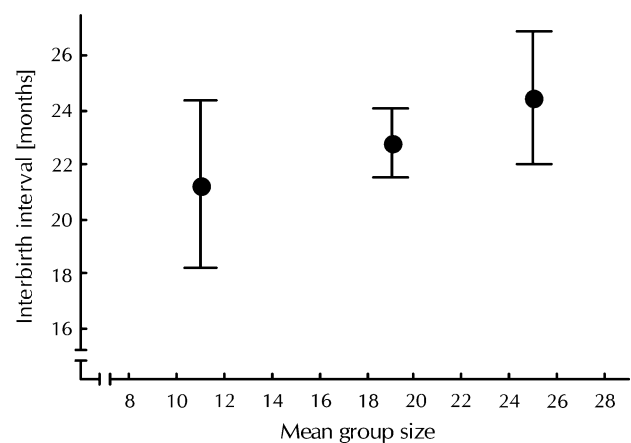


Figure 3

Interbirth interval after a surviving infant ($n = 32$) increased with group size. Circles represent mean values, whiskers the 95% confidence limits.

Clutton-Brock and Coulson 2002; Dahle et al. 2006). At present, it is not clear whether these effects on growth and development will also influence offspring fitness as reported for other animals (Albon et al. 1987; Saether 1997; Lindstroem 1999; Gaillard et al. 2000; Metcalfe and Monaghan 2001; Descamps et al. 2008).

Overall, females in larger groups reproduced at a slower pace compared with smaller groups (Figure 3), whereas infant mortality did not differ. Similar group size effects on reproductive rates have been found in some nonhuman primates and African elephants (Kumar 1995; Sterck et al. 1997; Takahata et al. 1998; van Noordwijk and van Schaik 1999; McComb et al. 2001; Altmann and Alberts 2003).

In contrast, studies of mountain gorillas found no influence of group size on birth rates (Robbins et al. 2007; see also Stokes et al. 2003). Rather, female reproductive success was related to social organization with higher survival rates in groups with multiple males. The reverse situation has been found in feral horses, in which reproduction was also independent of group size but mares reproduced most successfully in single-stallion bands (Linklater et al. 1999). Although our sample comprises only 3 groups, there is no indication that the number of adult males influenced infant survival. The extreme values refer to the smallest and the largest group that both contained only one male and intermediate values for the medium-sized multimale group.

Overall, it seems that females in larger groups pay a price in that they reproduce significantly more slowly. The actual shape of the fitness function for the study population is, however, still unclear because data for extreme group sizes are not available. The smallest group in our sample contained 4 adult females on average. Unfortunately, the smallest bisexual group known to us with 1–2 adult females was not stable. This could indicate an n-shaped fitness function and groups should be commonly above optimal size (Sibly 1983), but other scenarios are possible as well (Giraldeau and Gillis 1985; discussion in Krause and Ruxton [2002]).

Group size and food availability

Questions remain as to what may have caused the observed effects on female reproductive success? Clearly, reduced birth rates can result from food stress experienced year round or during particular seasons (Pride 2005). But what might have caused the lower food availability for individuals in the larger groups? In social foragers with rather fixed home ranges such as in the study species, food intake and energy expenditure could depend on home range quality, scramble competition, or both (Snaith and Chapman 2007). If the amount of food available per independent forager would covary with group size, the reported effects could be due to habitat quality. Such habitat effects have been found in some ungulates (McLoughlin et al. 2006, 2007) and were suspected for another folivorous primate (Dunbar 1987; Harris and Chapman 2007). In the current study, variation in home range quality remains a potential explanation because the habitat is patchy and varies in structure and composition. The required data to answer this question are currently being collected, but results are not yet available.

In addition (or instead), the lower reproductive rates may have been caused by scramble competition. In contrast to species with a high amount of herbs and leaves in the diet such as mountain gorillas (Doran and McNeilage 1998), Phayre's leaf monkeys incorporate considerable amounts of fruits (and young leaves) that are more clumped in time and space (see discussions in Koenig et al. [1998]; Snaith and Chapman [2007]). Such patches will deplete faster, making scramble competition more likely (Snaith and Chapman 2005). In support of this, we found that in the study population, larger groups had more leaves in the diet (Koenig et al. 2004),

and feeding rates declined and movement rates increased over patch residence time indicating scramble competition (Koenig et al. 2008). In addition, the study groups may fission for several hours particularly when food is scarce, a response often interpreted as increasing costs of grouping due to scramble competition (e.g., Wrangham 2000).

In general, it appears that Phayre's leaf monkeys exhibit a pattern similar to other herbivorous species forming more permanent associations (red deer) or multilayered societies (elephants), in which habitat quality or group size or both may affect food intake and fecundity (Clutton-Brock et al. 1982; Wittemyer et al. 2005; McLoughlin et al. 2006). Whether these short-term consequences for fecundity and infant survival translate into differences in lifetime reproductive success remains to be seen.

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