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Costs and benefits of group living in primates: group size effects on behaviour and demography

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Socioecological models aim to predict the effect of environmental variables on species' ecology and social behaviour. Larger groups should face more within-group food competition than smaller groups but benefit from a reduction in predation pressure and/or between-group food competition. The balance between benefits and costs of living in larger groups may vary between populations and species. Moreover, sample size is usually relatively small in field studies and this increases variation in the results. We used meta-analytical techniques to analyse the effect of group size on behaviour and fitness in an attempt to measure the benefits and costs related to group size differences in primates. Meta-analysis allows the presence of an overall effect to be determined across different studies and taxa while controlling for sample size. We selected published papers from the PrimateLit database (http://primatelit.library.wisc.edu). Larger groups travelled further per day and spent more time feeding than smaller groups. Time spent on social behaviour and resting was not affected by group size differences. We found partial support for a decrease in female fecundity in larger groups whereas no significant difference was found for juvenile survival. These results were relatively unaffected by habitat characteristics, by species' ecology and social structure, and by indirect measures of predation risk. Our findings indicate that folivores and frugivores face similar ecological pressures and suggest that the costs of living in larger groups balance or outweigh the benefits.

Keywords: fitness; food competition; group living; predation; socioecology

Among vertebrates, permanent group living is a taxonomically widespread social system (Krause & Ruxton 2002). Although the costs and benefits of group life may be broadly similar in a variety of taxa (e.g. Trivers 1985; Mann et al. 2000), these have been more thoroughly investigated in primates.

Primate socioecological models consider group size to be an important factor modulating behaviour and individual fitness (Wrangham 1980; van Schaik 1983; Janson & Goldsmith 1995; Sterck et al. 1997; Koenig 2002). Group size differences are expected to be associated with various benefits and costs for group members primarily in relation to two factors: food and predators. Other things being equal (e.g. habitat quality), larger groups should be freer to gain access to and better able to monopolize rich food sources than smaller groups, that is, larger groups should experience less between-group contest food competition (Wrangham 1980; Janson & van Schaik 1988). Larger groups should also experience a lower predation pressure as predator detection through vigilance and/or defence from predators (e.g. mobbing) are expected to be more efficient than in smaller groups (van Schaik 1983; Sterck et al. 1997). The main expected cost for larger groups, however, is an increase in the level of within-group food competition (both contest and scramble) with increasing group size (Janson & van Schaik 1988; Isbell 1991).

The behaviour and fitness of group members depend on the balance between the various benefits and costs associated with group size differences (van Noordwijk & van Schaik 1987; van Schaik 1989; Isbell 1991; Janson &

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Goldsmith 1995). For example, when the benefit of reduced between-group competition outweighs the cost of higher within-group competition, we may expect foraging effort to be greater and energy intake lower for animals in smaller groups. This would result in significant differences in individual fitness between groups of different size (Whitten 1983; van Schaik 1989; Koenig 2002). This scenario would go in exactly the opposite direction when the balance between within- and between-group competition is reversed. Indeed, estimating the balance between benefits and costs associated with different group sizes is instrumental to testing socioecological models and for functional interpretations of the evolution of group living. This type of test, however, is difficult to conduct as several key variables are often difficult to estimate. For example, reliable measures of predation pressure are difficult to collect and, indeed, frequently unavailable (Cheney & Wrangham 1987; Hill & Dunbar 1998). Similarly, assessing the level of between- and within-group food competition and its consequences for individual fitness may be difficult, it may vary depending on a number of species-specific characteristics (e.g. diet or social system), and it requires long-term data on reproductive success and survival of group members. Local ecological conditions may have a significant effect on group size differences (Janson 1988) so that comparative studies have to be conducted within the same population and in groups living in habitats of the same quality. Sample size is an additional factor that determines the degree of variation, inconsistency and 'noise' in the results of field studies, as data on wild animals are often available on a small number of groups and are collected in a relatively short period of time.

We tackled these theoretical and empirical challenges by analysing the effect of group size differences on behaviour and fitness across primate species, using meta-analytical techniques. Meta-analysis is a particularly beneficial statistical approach in this respect, as it allows the presence of an overall effect to be determined across different studies and taxa while taking into account differences in sample size and precision of estimates (Gates 2002). Our aims were twofold. First, we aimed to estimate the balance between benefits and costs associated with living in groups of different sizes. We hypothesized that the presence and direction of a difference in behaviour and fitness between groups of different size may tell us whether the benefits of living in large groups (i.e. reduced between-group competition and predation risk) outweigh the cost (i.e. increased within-group competition) or whether the reverse is true. Second, we aimed to analyse the consistency of group size effects across primate species by determining the importance of species' ecology, social structure and habitat characteristics. In particular, we aimed to test whether group size differences have less effect in folivores than in frugivores, as predicted by socioecological models (e.g. Wrangham 1980), given that this prediction has been recently challenged (Snaith & Chapman 2007). Our approach is new in the use of meta-analysis and in the advantages that this technique gives when analysing studies with different sample sizes and/or contrasting results. More importantly, to our knowledge this is the first attempt to analyse comprehensively the possible effects of group size differences in primates. Ecological variables produce 'cascade effects' on behaviour and fitness so that a comprehensive approach, such as ours, is essential for testing the predictions of socioecological models. For example, a high predation risk will force animals to forage and move close together: a strategy that should increase food depletion rate per unit area. This will have direct consequences for travel time and foraging effort and consequently also for time to be devoted to other activities (e.g. resting), physical condition and individual fitness.

We extracted data from the literature and tested whether animals in groups of different sizes differ in their foraging effort, in the level of between- and within-group food competition they experience, and in the extent to which foraging effort and food competition affect other aspects of activity budgets (i.e. time available for resting and for social behaviour). Moreover, to analyse the fitness consequences of group size differences we used data on female fecundity and juvenile survival. In mammals, female fecundity is a direct consequence of female physical condition that, in turn, depends on daily energy intake (Cuthill & Houston 1997). Juveniles are the age class category most at risk of predation in primates and other animal species (Cheney & Wrangham 1987; Krause & Ruxton 2002). Juvenile survival is thus expected to be related to predation pressure (van Schaik 1983; Dunbar 1987) given that, in primates, juveniles very rarely disperse before adulthood (Pusey & Packer 1987). Therefore, female fecundity and juvenile survival are reliable measures for testing whether behavioural differences between groups of different sizes translate into differences in reproductive success (van Schaik 1983; Whitten 1983).

METHODS

Data Collection

We reviewed the primatological literature using PrimateLit (available online at http://primatelit.library.wisc.edu), a comprehensive database containing all the published studies in primatology since 1940. Our data collection was restricted to the period from 1940 to March 2007, with the exception of Carpenter's (1934) study. We also reviewed various books on primatology as an additional source of data. To be included in our data set, a study had to contain data on the size of at least two groups. We selected studies containing data on one or more of the following behaviours: daily distance travelled, time spent feeding, resting or on social behaviour, frequency of within-group aggression, and proportion of between-group encounters won. Moreover, we selected studies reporting the composition of each group and derived demographic data from this information. Following van Schaik (1983), we calculated female fecundity as the ratio between the number of infants and the number of mature females, and juvenile survival as the ratio between the number of juveniles and the number of mature females. Although these are relatively crude measures, they offer unbiased estimates when groups belonging to the same species and population are compared.