

Predation risk as an influence on group size in cercopithecoïd primates: implications for social structure

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(Accepted 28 November 1997)

Abstract

Predation pressure has long been proposed as a determinant of mammalian social systems. Group size and composition were compared for 121 populations of cercopithecoïd primates, from 39 species of 13 genera, living under low, moderate or high predation risk. In confirmation of previous studies, predation risk was found to have a major effect on group size, with populations under high predation pressure living in significantly larger groups than those at lower risk. However, there were differences in social structure between the predation risk categories. Unimale groups were smaller, had fewer females than multimale groups and were infrequently found under conditions of high predation risk. Predation risk had marked effects on the composition of multimale groups. Under conditions of high predation risk there was a disproportionate increase in the number of adult males over that predicted by the number of females present or by group size. At low predation risk there were fewer males than predicted on the basis of female group size. Together, these results suggest that male strategies to monopolize females depend both on the females' grouping patterns and on the needs of both sexes to maximize group size under high predation pressure.

Key words: social evolution, group composition, primate mating systems

INTRODUCTION

Predation has long been considered as a major selective force favouring group living, with larger groups reducing the risk of predation through increased vigilance and flight distances, and by decreasing the probability that any particular individual will be killed during a predation event (Hamilton, 1971; Alexander, 1974). While the primary explanation for differences in social structure among non-human primates focuses on the separate grouping strategies of males and females (e.g. Wrangham, 1980; van Schaik & van Hooff, 1983), predation pressure has also been proposed as an important determinant of group composition and as a factor in the evolution of multimale groups (Crook, 1970; Busse, 1976; Hamilton, Buskirk & Buskirk, 1978).

When females live in groups, they are a defensible resource for males (Emlen & Oring, 1977) and thus the number of males in a bisexual group should be dependent on a male's potential to exclude others from mating opportunities (Clutton-Brock, 1989). His ability

to maintain exclusive access to females is a function of the number of breeding females. Andelman (1986) found a linear relationship between the mean number of males and females in groups of 18 species of cercopithecoïd monkeys, and Dunbar (1988) demonstrated similar intraspecific trends for both *Papio* and gelada (*Theropithecus gelada*) baboons. Female reproductive synchrony and mating seasonality (Rowell & Richards, 1979; Ridley, 1986; Caldecott, 1986; Dunbar, 1988) as well as group spread (van Schaik & van Hooff, 1983) are also linked to the number of males in a primate group. Mitani, Gros-Louis & Manson (1996) recently concluded that female group size was the best predictor of the number of males in a primate group.

Previous attempts to establish the relative importance of predation in determining primate group composition have reached conflicting conclusions. If males are more vigilant than females, multimale groups are predicted when predation risk is high (van Schaik & van Noordwijk, 1989; van Schaik & Hörstermann, 1994) especially if males participate in active defence (Busse, 1976; Hamilton *et al.*, 1978). Males appear to form a larger percentage of adult group members under high predation pressure, and they are more likely to defend conspecifics (Anderson, 1986). However, Cheney &

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Wrangham (1987) found no evidence that predation rate increased the number of males in populations of either vervet (*Cercopithecus aethiops*) or red colobus (*Procolobus badius*) monkeys. Since primate group size is proposed to increase with predation risk (Dunbar, 1988), an increase in the number of males may simply be a consequence of larger group size and more females. However, arboreal langurs under low or no predation live in groups with single adult males, whereas groups of colobus and howlers (*Alouatta* spp.) of comparable size and subject to eagle predation contained multiple males (van Schaik & Hörstermann, 1994).

This paper investigates the effect of predation risk on group structure using comparative analyses of group size and composition for 121 populations of cercopithecoid primates experiencing varying predation risks. In order to assess the effects of predation, a predation risk category has been estimated for each population (e.g. Anderson, 1986). Comparisons between populations are made on the assumption that predation risk is habitat-specific (due to attributes of the local environment such as predator type, density and refuge distribution) rather than a species characteristic.

METHODS

Data collection

Data were extracted from the available literature for 121 populations from 39 primate species of 13 genera, taken exclusively from the superfamily Cercopithecoidea in an attempt to minimize some confounding effects of phylogeny. Data were collected from wild or free-ranging populations, and precedence was given to long-term studies where estimates of predation risk and group composition data were likely to be more accurate. Multiple data points from the same site were only included if more than 10 years had elapsed between censuses (e.g. van Schaik & Hörstermann, 1994), or if environmental conditions had changed at the site resulting in changes in social structure. The minimum, mean and maximum group sizes of the censused groups within a population were determined. If only one group was counted, it was considered as a 'mean' for that population in the absence of other information. The number of sexually mature males and females in each group, or the mean for the groups within that population, was also determined. Data collection was restricted to populations where direct human influences on group size and composition were noted as minimal. Data used in the analyses are presented in Appendix 1.

For each population, reports of potential predators present in the habitat, predation attempts, and suspected causes of mortality were combined in order to assign a subjective 'predation risk' category. Three categories were assigned as high, medium and low, which were specific to the population or group analysed. The aim of using a relatively small number of categories was to explore the potential variation in predator

presence and contacts on group size and structure in those cases where data on actual predator offtake or rates of predator-prey interaction were limited or lacking. Categories were constructed on the basis of a) the presence of major and minor primate predators in the habitat of the population (large carnivores, some small carnivores known to take monkeys, raptors, pythons, and other predatory primate species); b) interactions between predators and the primates using reports of behavioural modification in the presence of predators; c) attempted predation events, and details of suspected or known predation of study animals. Populations were then assigned to one of the three predation risk categories on this basis. The categories and examples of populations in each are given below (see also Appendix 1).

Low predation risk

Predators present in the habitat but no actual or attempted predation observed or suspected. Infrequent behaviour associated with contact of potential predators. For example, vervet monkeys (*Cercopithecus aethiops*) on Lolui Island co-existed with eagles and snakes, but there were no reports of contact between these potential predators and the primates (Hall & Gartlan, 1965).

Medium predation risk

Interactions between predators and study animals were observed, with behaviour by the primates to reduce or minimize risks of predator contact, and with occasional predation attempts but infrequent predation observed or suspected. Vervets in the Burman Bush nature reserve were confronted with dogs, pythons and humans, and exhibited anti-predator vocalizations and behaviour upon contact, with no predation losses reported (Henzi & Lucas, 1980).

High predation risk

Frequent predator-prey interactions with regular contact and actual or attempted predation observed or suspected. Vervet monkeys in Amboseli experienced high losses to predators, eagles, leopards, pythons, baboons and small carnivores, and showed intense anti-predator behaviour and vocalizations (e.g. Cheney, Lee & Seyfarth, 1981).

It should be emphasized that these categories, while partially constructed from information on predation rates, represent a subjective composite measure of risk within a specific population. This risk is based upon the potential for and frequency of predator-prey interaction regardless of whether such interactions resulted in successful capture by the predator. As such, we are assessing the capacity for individuals and groups to alter

Table 1. Results of stepwise regression analysis showing the amount of variance explained by each taxonomic level for the group size, number of males and number of females variables

Level of analysis	Subfamily	Genus	Species	Population
Mean group size	0.143	0.385	0.083	0.388
Minimum group size	0.152	0.276	0.143	0.428
Maximum group size	0.153	0.378	0.045	0.423
Number of males	0.160	0.237	0.193	0.411
Number of females	0.079	0.392	0.074	0.455

their behaviour, group size or structure in response to either potential or actual contact with predators. We have used predation risk rather than rate with the hypothesis that predation rates represent rates of loss after any possible adjustments to group size in response to risks of predation through contact. Categorical classification of predation risk rather than using rate measures may allow for greater insight into population responses at the level of social structure.

Data analysis

In comparative studies, confounding phylogenetic effects need careful consideration (Harvey & Pagel, 1991). However, since the aim of this study was to examine population-specific traits, conventional methods for assessing phylogenetic trends (e.g. independent contrasts, autocorrelation, phylogenetic subtraction) are reduced in their applicability. A nested ANOVA, which partitions the variance within a variable into that explained by each taxonomic level, could not be performed due to empty cells. Therefore, a multiple regression analysis (using dummy variables to assess the categorical data) was used to examine the change in the amount of variance explained at each level. While these tests examine different elements of variance, the regression analysis describes the general contribution of phylogeny without claiming significance for those contributions (Table 1).

The genus and population levels explain the largest amounts of the variance in the demographic variables, and population level consistently accounts for more variance. While some group characteristics do appear to be genera-specific, group size and composition appear to be strongly linked to local environment. Subsequent analyses were therefore conducted at the population level, although conclusions derived from these analyses are extrapolated to provide some explanation for the generic differences.

In analyses of group composition, the number of males per group was coded into two categories: unimale and multimale. Populations with groups containing an average of 1.2 males or less were coded as unimale, and populations having greater than 1.2 males per group were considered as multimale. The selection of 1.2 as the cut-off point, as opposed to 1.0, was to allow for the possibility of occasional second adult males occurring in a few groups, when the population as a whole was

primarily unimale. This was done for two reasons. Firstly, for some species, it is difficult to determine an operational sex ratio. Although many cercopithecoid species are typically unimale, during their highly synchronous breeding seasons there are large influxes of all male bands (Cords, 1984; Tsingalia & Rowell, 1984; Chism & Rowell, 1986; Struhsaker, 1988). As a result, group composition is variable.

Secondly, the loss of reproductive success to a resident male upon the addition of an extra adult male group member will potentially be much greater for a harem-holding male than for a male already residing in a multimale group. The proximate pressures required to surpass a threshold number of females and shift from a unimale to a multimale system are likely to be more intense than those which operate to determine the number of males in multimale groups. Thus, unimale and multimale populations should display different trends in group composition under increasing predation pressure.

All continuous data were natural log transformed to ensure normality for parametric analysis. Analyses were based on comparisons of continuous data on group size and composition and predation risk. Standard regression techniques, ANOVA and analysis of covariance were used. All analyses were made using SPSS version 6.1 for PC. We recognize the problem of performing repeated tests on the same data set, but repeated tests were limited to two and hypotheses were not replicated. All probability values are two-tailed.

RESULTS

Group size

Overall, group size varied as a function of predation risk categories. The mean, minimum and maximum group sizes under different predation risks are shown in Fig. 1. There is a clear effect for group size to be larger

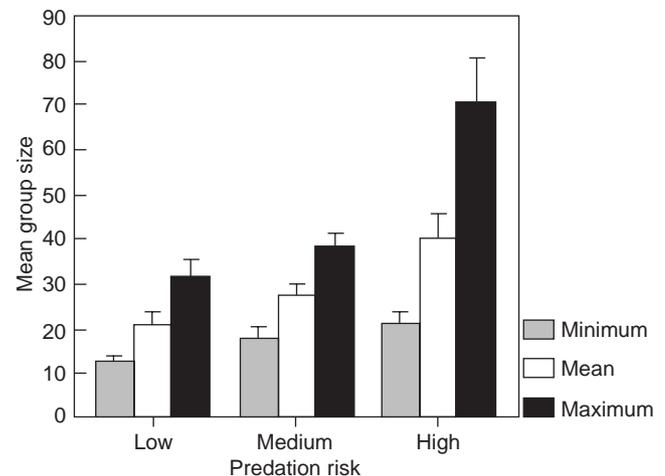


Fig. 1. Mean and standard error for the minimum, mean and maximum group sizes of populations under low, medium and high predation risk.

with increasing predation risk. Mean group sizes differ significantly between predation risk categories (ANOVA: $F_{2,118} = 6.68$, $P < 0.002$). *Post hoc* comparisons found significant differences between high predation risk and the low and medium categories (Scheffé, $P < 0.05$). Maximum group sizes also differ significantly between risk categories (ANOVA: $F_{2,87} = 7.35$, $P < 0.002$) with specific differences between the high and medium predation risk categories as well as between the high and low categories (both Scheffé, $P < 0.05$). Minimum group sizes tended to be larger under higher risk (ANOVA: $F_{2,87} = 2.54$, $P < 0.10$).

Group composition

General trends

The number of adult males was a positive linear function of the number of adult females present in the groups ($r^2 = 0.432$, $F_{1,96} = 74.63$, $P < 0.001$). Adding predation risk as a factor into the regression analysis increases the variance explained in the number of males by the model ($r^2 = 0.448$, $F_{2,95} = 27.24$, $P < 0.001$).

Unimale groups differ from multimale groups in having a smaller mean number of females ($t = -3.82$, $df = 96$, $P < 0.001$) and a smaller group size ($t = -5.18$, $df = 97$, $P < 0.001$). Multimale groups are larger and have more adult females, suggesting that predation risk should be assessed separately between these types of groups.

Unimale groups

Among unimale groups, similar trends to the total data set were found, with larger group size in the higher predation risk categories. Due to small sample sizes, the power of the effect was reduced (mean group size: $F_{2,23} = 3.13$, $P < 0.07$; maximum group sizes: $F_{2,16} = 4.53$, $P < 0.03$, Scheffé (high-medium, high-low), $P < 0.05$; minimum group size: ANOVA: $F_{2,16} = 0.97$, $P > 0.40$). By definition, unimale groups show no variance in the number of adult males as group size changes, and thus the observed increases in group size associated with predation risk must be mediated through an increase in the number of adult females (Fig. 2). Female group size among unimale groups differs significantly between the predation risk categories (ANOVA: $F_{2,23} = 3.79$, $P < 0.04$), and *post hoc* comparisons suggest that this is primarily due to differences between the high and low predation risk categories (Scheffé, $P < 0.05$). However, the possibility exists that this is an artefact of a small sample size (high predation risk: $n = 3$) rather than a realistic trend.

Multimale groups

The overall relationship between the number of adult males and females is also observed in multimale groups

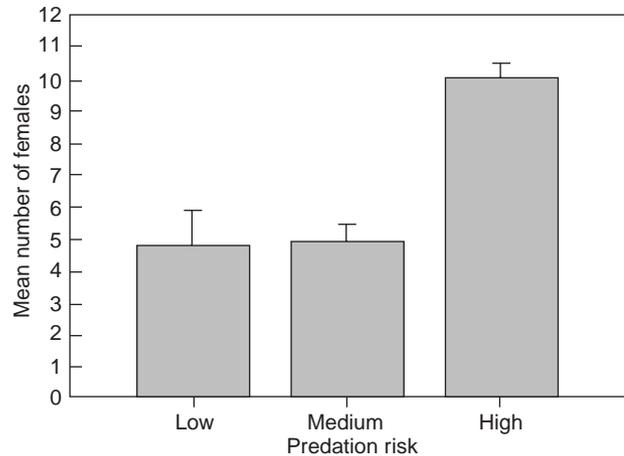


Fig. 2. Mean number of females in unimale groups under low, medium and high predation risk.

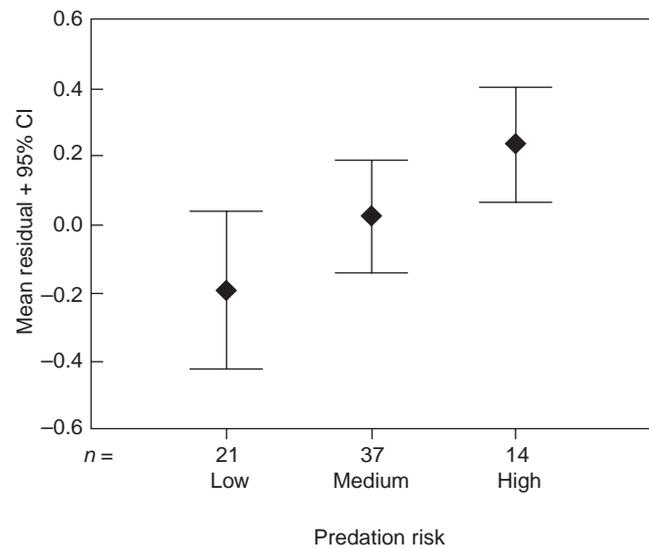


Fig. 3. Mean and confidence limits of residuals plotted from regression line of number of males on number of females for multimale groups in populations under low, medium and high predation risk.

($r^2 = 0.483$, $F_{1,70} = 67.33$, $P < 0.001$). Predation risk again is a significant factor in the overall regression ($r^2 = 0.518$, $F_{2,69} = 26.48$, $P < 0.001$). Residuals from the overall regression line were compared between risk categories (Fig. 3), where residuals represent the difference between the observed number of males and that predicted for the number of females. Mean residuals in each predation risk category differed significantly (ANOVA: $F_{2,69} = 3.50$, $P < 0.05$), with marked differences between the high and low predation risk categories (Scheffé, $P < 0.05$). As predation risk increases, the number of males rises above that predicted on the basis of the number of females alone, whereas at low predation pressures there are fewer males than predicted. However, no differences in the mean number of females per group exist between the predation risk categories (ANOVA: $F_{2,69} = 0.085$, $P > 0.90$).

Table 2. The number of males predicted for specific female group sizes in the different predation risk categories. Predictions are based on the separate regression equations, as shown

Predation risk	Slope	Intercept	Female group size			
			5	10	15	20
Low	0.41124	0.23280	2.45	3.25	3.84	4.33
Medium	0.79349	-0.33977	2.55	4.43	6.10	7.67
High	1.06224	-0.68999	2.77	5.79	8.91	12.09

Trends in the relationships between number of males and females within the predation risk categories further support these findings. The slopes of the three regressions tended to be different (Fig. 4; ANCOVA: $F_{2,69} = 3.07$, $P = 0.053$), and predation risk makes a significant contribution to the variance in the overall relationship ($F_{2,69} = 3.46$, $P < 0.04$). The number of males predicted for female group sizes of 5, 10, 15 and 20 by each regression are compared in Table 2. For matched female group sizes, more males are found under medium predation risk than under low predation, with most males occurring under high predation risk.

Since total group size is highly correlated with the number of females per group ($r^2 = 0.880$, $F_{1,70} = 520.28$, $P < 0.001$), similar trends were observed in the regression of number of adult males on total group size. Thus as predation pressure increases there are again more males per group than predicted by size alone, with fewer males than predicted under low predation risk. While considering male numbers in relation to female group size alone has more explanatory value for understanding male distributions, the ratio of males to total group size could be an indication of male contributions to infant survival, as well as of reproductive rates.

DISCUSSION

Predation risk was found to have a major influence on group size among the cercopithecine primate populations examined here. Mean group size was largest under conditions of high predation risk, in confirmation of some previous studies (van Schaik, 1983; van Schaik & van Hooff, 1983; Dunbar, 1988). However, Isbell (1994) found a negative relationship between predation rate and group size in interspecific comparisons. This disparity may be partially explained by the fundamentally different aspect of predation assessed here; specifically the distinction between predation *risk* and predation *rate*. These two measures may predict different relationships, both within and between species.

Predation risk represents both a proximate and ultimate constraint with primates responding through antipredator strategies. Certain aspects of predation risk may be species- or genera-specific, such as body size, canine size and degree of arboreality or terrestriality (Harvey, Kavanagh & Clutton-Brock, 1978; Plavcan & van Schaik, 1992) and represent evolved strategies. In

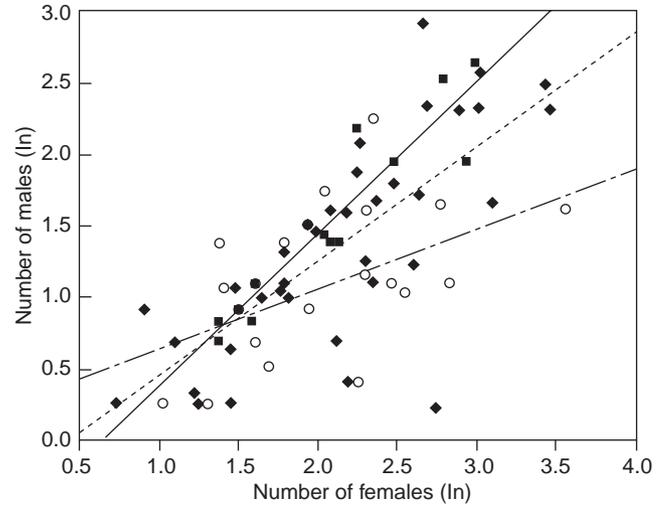


Fig. 4. Regression lines displaying the relationship between the number of adult males and number of adult females within the predation risk categories for multimale groups (○, --- low predation risk populations; ◆, medium predation risk populations; ■, _____ high predation risk populations).

these analyses, the generic level explained a considerable proportion of the variance in group composition. This suggests an evolutionary history of selection for group size in response to attributes of diet, physiology and energetics. Although resource abundance and distribution vary between habitats and populations, basic dietary preferences (e.g. folivory, frugivory) and adaptations to substrates (arboreal or terrestrial) may also contribute to explaining some of the generic level variance, determining the extent to which predation pressure influences group size and composition (but see Isbell, 1994).

However, predation risk is also closely related to the local environment and thus proximate responses are expected. The number and types of potential predators, predator density and the availability and distribution of refuges all are important in determining habitat-specific predation risk and behavioural antipredator strategies. Where strategies are based upon safety in numbers, increased predation risk favours the formation of larger groups. This is the trend observed across the populations in this study.

Predation rate may represent mortality even after primates have implemented their anti-predation strategies. There is no *a priori* reason that a level of predation should be consistent across species; it is likely to vary as a function of species life-history traits and potential reproductive rates. As a consequence, few relationships between predation rate and group size would be expected within species (e.g. vervets; Isbell, 1994), or between species when confounding effects of reproductive rate and phylogeny are removed (Hill & Dunbar, in press).

Maximum group size varied with predation risk, with maximum sizes for groups under high predation risk almost double those of low or medium risk. If maximum permissible group size is set by ecological

conditions (Dunbar, 1992, 1996; Wrangham, Gittleman & Chapman, 1994; Chapman, Wrangham & Chapman, 1995; Janson & Goldsmith, 1995), then groups should fission when intra-group feeding competition is intense. Risk of predation may promote groups that are larger than the maximum ecologically tolerable size when the fissioned groups must themselves be sufficiently large to counteract risks of predation.

Minimum group size showed only a trend to be larger with increasing predation risk. When ecological conditions permit large maximum group sizes, few groups of the minimum permissible size are expected since fissioned troops should be able to exceed this minimum level. Thus, while predation risk could influence minimum permissible group size in a given habitat, observed trends are likely to be confounded by ecological conditions permitting larger groups.

Group structure varied between predation risk categories. In part, this is a consequence of higher predation pressures favouring larger group sizes. Unimale groups occurred when mean group size was small consisting of <11 individuals and <5 females. Multimale groups occurred when group size was large; in this case >25 and with >12 females. Intermediate group sizes or numbers of females were associated with both uni- or multimale groups, as originally found by Andelman (1986). Since unimale groups are small, few unimale populations should be found under conditions of high predation pressure which favour large group sizes. Of the 26 unimale groups, 10 (34.5% of all groups, $n=98$) were under low predation risk, 13 (25% of all) under medium predation risk, but only 3 (17.6% of all) were at high risk. If this distribution represents reality rather than sampling error, then unimale systems may simply be less viable under high predation risk (e.g. van Schaik & van Noordwijk, 1989; van Schaik & Hörstermann, 1994). Unimale groups could enter into polyspecific associations in response to predation risk, thereby increasing effective group size and allowing them to persist in medium and high predation risk habitats (e.g. Gautier-Hion, Quris & Gautier, 1983; Cords, 1990; Struhsaker & Leakey, 1990; Noë & Bshary, 1997). While unimale groups may be able to modify group size in response to predation pressure, either through increasing the number of adult females or through polyspecific associations, ultimately such groups may only be able to increase in size by switching to a multimale mating system.

Within multimale groups, predation risk was a significant factor determining group composition. Under conditions of high predation risk, there was a disproportionately large number of adult males in relation to the number of females. At low predation risk, there were fewer males than predicted by both the number of females and overall group size. It thus appears that an increased group size in response to predation may only be achieved by adding more males than predicted by the number of females, due to the constraints of inter-female feeding competition.

Resident males may not resist immigration attempts if the loss in number of offspring sired is outweighed by increased infant survival (van Schaik & Hörstermann, 1994), particularly when dominance hierarchies limit the mating access of additional males (*Cebus apella*: Janson, 1984) or when additional males are subadults delaying dispersal. Females also may manipulate group composition by soliciting males to join a group even when residents resist immigration attempts (Smuts, 1987). A further possibility is that the additional males found under conditions of high predation risk are parasitic and confer little benefit to the troops to which they attach themselves (Baldellou & Henzi, 1992) but do so because the costs of being solitary are prohibitively high.

The final question, which can only partially be addressed by this analysis, is whether predation is a causal factor in primate social evolution. The comparative analyses above provide strong additional support for a proximate role of predation pressure in determining group sizes of cercopithecoid primates. Whether predation pressure determines group structure independently of group size is less clear. The number of females in a group does not appear to respond directly to predation risk among cercopithecoids, and resource base remains the primary factor determining female distributions (Wrangham, 1980). Since males map onto female distribution, the ultimate determinants of primate group composition are resource characteristics. However, predation pressure serves to modify group size by favouring larger groups as predation risk increases, and this results in associated changes in both group composition and structure. Whether the relative increase in the number of males as group size increases is due to males being favoured because of their higher vigilance levels, or whether it is simply the most economical way of increasing group size considering the constraints imposed by intra-group feeding competition, cannot be addressed by this analysis. These results suggest that male strategies to monopolize females depend both on the females' resource acquisition strategies, which determine female distribution, and on the need to maximize group size under high predation pressure.

Acknowledgements

We are grateful to Louise Barrett, Robin Dunbar, John Lycett and Carel van Schaik and other referees for helpful comments on earlier drafts of this manuscript.

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Appendix 1. Data on estimated predation risk (PR), group size and group composition for the populations included in the study.
(List of source references available on written request from the authors).

Species	Study site	PR	<i>n</i>	Mean group size	Range	<i>n</i> Ad. males	<i>n</i> Ad. females	Sources
Cercopithecinae:								
<i>Cercoebus albigena</i>	Bujuko	L	1	17	-	-	-	Chalmers, 1968
<i>C. albigena</i>	Kanyawara	M	5	14.1	6–28	2.9	4.4	Struhsaker, 1975; Waser, 1974 (in Ham, 1994)
<i>C. albigena</i>	Lope Reserve	M	2	19.8	18–23	2.0	8.3	Ham, 1994
<i>C. albigena</i>	Nagojje	L	1	25	-	-	-	Chalmers, 1968
<i>C. albigena</i>	Ngogo	M	7	17.0	10–28	2.9	5.9	Barrett, unpublished data
<i>C. aterrimus</i>	Lake Tumba	H	4	17.3	14–19	3.0	5.0	Horn, 1987
<i>C. galeritus</i>	Tana Forest	L	3	26	17–36	-	-	Marsh, 1979; Homewood, 1978
<i>C. torquatus</i>	Campo Reserve	M	9	21.1	-	-	-	Mitani, 1989
<i>Cercopithecus aethiops</i>	Amboseli (<1987)	H	3	21.7	11–28	4.2	7.7	Cheney, 1981; Cheney <i>et al.</i> , 1981
<i>C. aethiops</i>	Amboseli (>1987)	H	3	10.7	8–13	2.3	4.0	Isbell, 1990; Isbell <i>et al.</i> , 1990
<i>C. aethiops</i>	Badi	M	5	11.8	8–16	2.5	2.5	Dunbar, 1974
<i>C. aethiops</i>	Bakossi	H	2	14.5	11–18	2.5	4.5	Kavanagh, 1981
<i>C. aethiops</i>	Barbados	M	?	15.3	12–19	1.3	4.3	Horrocks, 1986; Horrocks & Hunte, 1986
<i>C. aethiops</i>	Bole Valley	M	4	18.8	13–29	-	-	Dunbar & Dunbar, 1974a
<i>C. aethiops</i>	Buffle Noir	M	1	18	-	3	6	Kavanagh, 1981
<i>C. aethiops</i>	Burman Bush	M	3	24.7	8–37	-	-	Henzi & Lucas, 1980
<i>C. aethiops</i>	Diani Beach Forest	M	1	14	-	-	-	Moreno-Black & Maples, 1977
<i>C. aethiops</i>	Kamaloue	M	1	76	-	10	18	Kavanagh, 1978, 1981
<i>C. aethiops</i>	Lolui Island	L	18	12.7	7–20	2.9	4.1	Hall & Gartlan, 1965
<i>C. aethiops</i>	Masai-Amboseli	H	9	24.1	7–53	2.3	4.9	Struhsaker, 1967a,b,c
<i>C. aethiops</i>	Mt. Assirik	M	9	19.2	-	4.5	7.0	Dunbar, 1974; Harrison, 1983a,b
<i>C. aethiops</i>	St. Kitts (1969–70)	H	18	20.0	8–30	2.0	4.0	Poirier, 1972; Fedigan <i>et al.</i> , 1984
<i>C. aethiops</i>	St. Kitts (1981–82)	M	4	45.2	-	10.3	14.8	Fedigan <i>et al.</i> , 1984
<i>C. aethiops</i>	Windy Ridge	H	1	23	-	4	8	Baldellou & Henzi, 1992
<i>C. ascanius</i>	Ngogo	M	1	35	-	1	10	Struhsaker, 1975, 1977
<i>C. cephus</i>	Makokou	M	1	8	-	1	3	Gautier-Hion & Gautier, 1974; Gautier-Hion <i>et al.</i> , 1983
<i>C. diana</i>	Tiwai Island	L	2	24.0	21–27	1.0	7.0	Oates & Whitesides, 1990
<i>C. nictitans</i>	Makokou	M	1	13	-	1	5	Gautier-Hion & Gautier, 1974; Gautier-Hion <i>et al.</i> , 1983
<i>C. pogonias</i>	Makokou	M	1	13	-	1	5	Gautier-Hion & Gautier, 1974; Gautier-Hion <i>et al.</i> , 1983
<i>Miopithecus talapoin</i>	Ivindo River	M	6	66.5	-	10.2	20.4	Gautier-Hion, 1973
<i>Erythrocebus patas</i>	Abuko	L	2	20.0	-	-	-	Starin, 1981, 1993
<i>E. patas</i>	Laikipia District	H	10	31.2	13–56	1.0	10.8	Chism <i>et al.</i> , 1983; Chism & Rowell, 1988
<i>E. patas</i>	Murchison Falls	M	12	19.0	5–31	0.9	7.2	Hall, 1965
<i>E. patas</i>	Waza Reserve	H	8	21.0	7–34	1.0	10.0	Struhsaker & Gartlan, 1970
<i>Macaca fascicularis</i>	Gunung Leuser	M	2	37.5	22–53	6.5	9.5	Vos <i>et al.</i> , 1992; Rijksen, 1978
<i>M. fascicularis</i>	Ketambe	M	5	24.2	11–34	4.3	7.4	van Schaik <i>et al.</i> , 1983; Rijksen, 1978
<i>M. fascicularis</i>	Kuala Lompat	L	2	23.0	23	2.5	7.0	Aldrich-Blake, 1980; Raemaekers & Chivers, 1980
<i>M. fascicularis</i>	Kutai Nature Reserve	L	4	27.0	22–30	3.2	9.9	Wheatly, 1980; Fittinghoff & Lindburg, 1980
<i>M. fascicularis</i>	Mentoko	L	1	17	-	3	5	Palombit, 1992
<i>M. fascicularis</i>	Sungai Tekam	L	2	23.0	-	-	8.5	Johns, 1983
<i>M. mulatta</i>	Rara Lake	L	1	39	-	3	17	Teas <i>et al.</i> , 1980
<i>M. mulatta</i>	Siwalik Hills	H	2	58.8	35–85	-	-	Lindburg, 1977
<i>M. radiata</i>	Dharwar	M	12	30.0	16–44	8.0	9.7	Sugiyama, 1971; Yoshida, 1968

<i>M. radiata</i>	Somanathapur	M	2	52.0	46–58	18.5	14.5	Simons, 1965
<i>M. sinica</i>	Polonnaruwa	M	18	24.7	8–43	2.7	6.2	Dittus, 1977
<i>M. sylvanus</i>	Atlas Mountains	M	6	18.3	12–25	2.7	5.2	Deag & Crook, 1971
<i>Papio anubis</i>	Awash River	M	4	55.0	38–71	-	-	Nagel, 1973
<i>P. anubis</i>	Awash Valley	L	8	44.0	14–87	-	-	Aldrich-Blake <i>et al.</i> , 1971
<i>P. anubis</i>	Bole Valley	M	7	20.0	15–24	-	-	Dunbar & Dunbar, 1974a
<i>P. anubis</i>	Chololo	M	3	43.3	29–69	5.3	10.7	Kenyatta, 1995
<i>P. anubis</i>	Gombe	H	10	38.3	18–70	8.8	9.5	Ransom, 1981
<i>P. anubis</i>	Gilgil	M	7	65.0	35–121	5.2	22.1	Harding, 1976
<i>P. anubis</i>	Laikipia District	H	7	101.0	52–179	-	-	Berger, 1972; Chism <i>et al.</i> , 1983
<i>P. anubis</i>	Q. E. National Park	L	2	45.0	32–58	9.5	10.5	Rowell, 1966
<i>P. cynocephalus</i>	Amboseli (<1970)	H	51	51.4	16–198	12.5	16.5	Altmann & Altmann, 1970
<i>P. cynocephalus</i>	Amboseli (>1970)	H	11	39.0	17–77	7.0	12.0	Samuels & Altmann, 1991
<i>P. cynocephalus</i>	Mikumi	H	3	52.3	17–71	-	-	Rhine & Westlund, 1981; Norton <i>et al.</i> , 1987
<i>P. cynocephalus</i>	Ruaha	H	1	72	25–150	7	19	Lee & Oliver, unpublished data
<i>P. cynocephalus</i>	Tana River	H	1	76	-	-	-	Condit & Smith, 1994
<i>P. ursinus</i>	Cape of Good Hope	L	4	31.8	20–53	2.8	12.8	Hall, 1962
<i>P. ursinus</i>	Drakensberg	L	61	22.5	4–41	-	-	Whiten <i>et al.</i> , 1987; Henzi & Lycett, 1995
<i>P. ursinus</i>	Honnet	M	6	47.2	30–77	13.0	20.5	Stoltz & Saayman, 1970
<i>P. ursinus</i>	Moremi	H	2	69.5	69–70	14.0	20.0	Bulger & Hamilton, 1987
<i>P. ursinus</i>	Mkuzi	H	2	38.5	34–43	4.0	8.5	Ron, 1994; Ron <i>et al.</i> , 1994
<i>P. ursinus</i>	Namib Desert	L	3	28.0	20–35	5.7	7.7	Hamilton, 1985; Brain, 1992
<i>P. ursinus</i>	Tsaobis Leopard Park	M	4	34.3	22–55	3.0	11.8	Cowlshaw, 1994, 1995
<i>P. hamadryas</i>	Awash River	M	2	54.0	51–57	-	-	Nagel, 1973
<i>P. papio</i>	Badi	M	1	83	40–83	12	31	Dunbar, 1974; Dunbar & Nathan, 1972
Colobinae;								
<i>Colobus angolensis</i>	Diani Beach Forest	M	2	9.0	8–10	2.0	3.0	Moreno-Black & Maples, 1977
<i>C. guereza</i>	Bigodi	M	1	6	-	1	3	Struhsaker, 1975; Clutton-Brock, 1975
<i>C. guereza</i>	Bole Valley	M	10	7.1	3–11	1.3	2.1	Dunbar & Dunbar, 1974b
<i>C. guereza</i>	Budongo Forest	M	25	6.9	2–13	1.1	2.2	Reynolds & Reynolds, 1965; Suzuki, 1979
<i>C. guereza</i>	Chobe	M	2	6.0	5–7	1.0	3.0	Oates, 1977
<i>C. guereza</i>	Kanyawara	M	7	11.4	9–15	1.4	3.4	Struhsaker, 1975; Oates, 1977
<i>C. guereza</i>	Lake Shalla	L	6	7.8	6–10	1.0	2.0	Dunbar, 1987
<i>C. guereza</i>	Murchison Falls	M	1	12	-	2	3	Hall, 1965; Leskes & Acheson, 1971
<i>C. guereza</i>	Q. E. National Park	L	4	6.3	3–9	1.3	2.8	Rowell, 1966; Marler, 1972
<i>C. polykomos</i>	Tiwai Island	L	1	11	-	4	4	DaSilva, 1989; Oates & Whitesides, 1990
<i>Procolobus badius</i>	Abuko (<1980)	M	3	34.0	24–40	3.0	10.5	Gunderson, 1977
<i>P. badius</i>	Abuko (>1980)	L	5	26.0	-	-	-	Starin, 1981, 1993
<i>P. badius</i>	Bigodi	M	1	64	-	10	32	Struhsaker, 1975; Clutton-Brock, 1975
<i>P. badius</i>	Gombe	H	20	27.7	12–44	4.5	7.0	Stanford, 1995
<i>P. badius</i>	Jozani Forest	M	7	33.6	25–46	4.9	8.9	Silkiluwasha, 1981
<i>P. badius</i>	Kibale Forest	M	14	34.0	9–68	3.5	10.0	Struhsaker, 1975; Struhsaker & Leyand, 1987
<i>P. badius</i>	Mahali Mountains	M	?	40.0	30–50	-	-	Nishida, 1972
<i>P. badius</i>	Tana River (1975)	L	13	18.0	12–30	1.5	9.6	Marsh, 1979
<i>P. badius</i>	Tana River (1987)	L	9	10.8	4–25	1.0	5.3	Marsh, 1979; Decker & Kinnard, 1992
<i>P. badius</i>	Tiwai Island	M	1	35	-	6	12	Oates <i>et al.</i> , 1990; Oates & Whitesides, 1990
<i>P. badius</i>	Uroa Forest	L	2	9.5	9–10	2.5	4.5	Silkiluwasha, 1981
<i>P. verus</i>	Tiwai Island	L	1	10	-	2	5	Oates & Whitesides, 1990
<i>Pygathrix nemaus</i>	Mt. Sontra	L	3	9.3	8–11	1.3	3.7	Lippold, 1977

Appendix 1 (continued)

Species	Study site	PR	<i>n</i>	Mean group size	Range	<i>n</i> Ad. males	<i>n</i> Ad. females	Sources
<i>Nasalis larvatus</i>	Tanjung Puting	M	7	12.4	3–23	1.0	4.7	Yeager, 1990; 1991
<i>Presbytis comata</i>	Kawah Kamojang	M	6	7.5	6–12	1.0	3.0	Ruhayat, 1983
<i>P. comata</i>	Petenggang	L	6	6.0	3–10	1.2	1.4	Ruhayat, 1983
<i>P. melalophos</i>	Kuala Lompat	L	3	15.0	12–18	1.0	7.7	Bennett, 1983
<i>P. melalophos</i>	Sungai Tekam	L	2	14.0	-	1.0	4.3	Johns, 1983
<i>P. rubicunda</i>	Tanjung Puting	L	9	4.9	3–8	1.0	2.6	Suprianta <i>et al.</i> , 1986
<i>P. thomasi</i>	Bohorok District	M	8	7.5	3–17	1.3	3.5	Kunkun, 1986
<i>Semnopithecus entellus</i>	Dharwar	M	6	21.5	15–27	1.0	7.5	Yoshiba, 1968
<i>S. entellus</i>	Gir Forest	M	2	28.0	25–31	1.5	9.0	Starin, 1978
<i>S. entellus</i>	Hatto	L	1	83	-	5	35	Sugiyama, 1976
<i>S. entellus</i>	Junbesi-Ringmo	M	5	12.3	4–19	1.9	4.3	Bogges, 1980
<i>S. entellus</i>	Kanha Tiger Reserve	H	14	21.7	11–34	1.1	9.1	Newton, 1987
<i>S. entellus</i>	Karnali-Bardia	L	?	26.2	12–40	-	-	Teas <i>et al.</i> , 1980
<i>S. entellus</i>	Kumaon Hills	M	?	23.0	15–30	-	-	Vogel, 1971
<i>S. entellus</i>	Melemchi	M	1	32	-	5	8	Bishop, 1979; Bishop <i>et al.</i> , 1981
<i>S. entellus</i>	Mundanthurai	M	5	37.0	16–63	5.5	14.0	Ross, 1993
<i>S. entellus</i>	Nadi District	L	2	21.5	11–32	1.0	10.5	Das-Chaudhuri & Roy, 1989
<i>S. entellus</i>	Orcha	M	3	18.7	10–28	3.7	6.0	Jay, 1965
<i>S. entellus</i>	Polonnaruwa	M	4	24.8	12–42	3.8	-	Ripley, 1967; Dittus, 1977
<i>S. entellus</i>	Rajaji	M	4	46.3	25–85	3.4	13.5	Laws & Vonder Haar Laws, 1984
<i>S. entellus</i>	Sariska	H	?	64.0	30–125	-	-	Vogel, 1971
<i>S. entellus</i>	Simla Region	L	5	47.6	23–98	5.2	16.0	Sugiyama, 1976
<i>S. entellus</i>	Singur	M	?	12.8	10–14	1.0	5.0	Oppenheimer, 1977; Bishop <i>et al.</i> , 1981
<i>S. entellus</i>	Tara Devi	L	2	26.5	19–34	1.5	9.5	Sugiyama, 1976
<i>Trachypithecus cristatus</i>	Kuala Selangor	M	4	30.6	20–51	1.3	15.6	Bernstein, 1968
<i>T. geei</i>	Assam	L	9	13.3	10–18	1.7	5.4	Mukherjee & Saha, 1974
<i>T. obscura</i>	Sungai Tekam	L	7	14.0	-	-	5.5	Johns, 1983
<i>T. pileatus</i>	Assam	L	16	10.3	3–16	1.1	4.1	Mukherjee, 1978
<i>T. pileatus</i>	Madhupur	L	25	5.4	3–13	1.0	3.0	Islam & Hussain, 1982
<i>T. vetulus</i>	Polonnaruwa	M	29	8.6	-	1.2	4.7	Ripley, 1967; Rudran, 1973; Dittus, 1977