AN EVALUATION OF THE ROLES OF PREDATION RATE AND PREDATION RISK AS SELECTIVE PRESSURES ON PRIMATE GROUPING BEHAVIOUR

by

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Summary

Establishing the importance of predation pressure in determining primate social structure has generated a great deal of discussion. However, the substantive issues in this debate have been obscured by a conflation of the respective roles of predation *risk* and predation *rate* as selective forces. In addition, the reported relationships between predation rate and both group size and body weight are likely to be confounded by the effects of reproductive rate and activity period. We propose that the level of sustainable predation rate for a species is determined by the rate at which it is able to reproduce, and that, within this constraint, a species adjusts its body weight and a population its group size so as to reduce predation rate to some tolerable level. In effect, the observed predation rate is the excess mortality from predation that animals are unable to control by adjusting their behaviour. This implies that there should be no relationship between predation rate and either group size or body weight, once the effects of reproductive rate and activity period are removed. We analyse data from the primate literature and show that reproductive rate is indeed the best predictor of a species' predation rate, and that the reported relationships with group size are entirely attributable to a combination of the inclusion of nocturnal species which do not use group size as an antipredator response and the confounding effects of reproductive rate. We discuss these findings in the light of current investigations on predation risk, and conclude that an understanding of the role of predation as a selective pressure on primates will only

be achieved by attempts to study the factors that are important in determining a primate's perceived risk of predation.

Introduction

The role of predation as a selective factor in the evolution of primate grouping patterns has been the subject of considerable debate (Alexander, 1974; Wrangham, 1980; van Schaik, 1983; Anderson, 1986; Cheney & Wrangham, 1987; Dunbar, 1988; Isbell, 1994; Hill & Lee, in press). Cheney & Wrangham (1987) compiled a data set of predation rates from a number of primate species but found no significant relationships with social structure. However, in a recent review, Isbell (1994) reanalysed these data, supplemented by an additional study on mouse lemurs (Goodman *et al.*, 1993), and found a negative relationship between group size and predation rate. Isbell (1994) concluded that since heavy predation should lead to the formation of large groups, these results indicated that predation represented an important selective factor favouring group-living in primates. In contrast, other studies have found a positive relationship between predation rate and group size (Anderson, 1986), while yet others have shown that a positive relationship exists between predation *risk* and group size, both within and across primate species (Dunbar, 1988; Hill & Lee, in press). Furthermore group composition has also been shown to be influenced by predation. Stanford (this volume) found a significant positive relationship between predation rate and male:female ratio, and Hill & Lee (in press) found a similar relationship using a habitat-specific index of predation risk.

A similar argument has been developed in respect of body size. Struhsaker (1968) suggested that small species of primate may be susceptible to more species of predators than large bodied ones, and this has been taken to imply a selection pressure in favour of increased body size under conditions of high predation (see Dunbar, 1988). Both Cheney & Wrangham (1987) and Isbell (1994) reported that body size showed a significant negative correlation with predation rate, and this was attributed to the relative lack of vulnerability of large-bodied primates (Isbell, 1994). However, body weight may also be an important confound underlying the relationship between group size and predation rate, since both body weight and

group size have been shown to be significantly associated (Clutton-Brock & Harvey, 1977).

One of the likely reasons for these apparently contradictory results is that most studies have failed to recognise the importance of distinguishing clearly between predation *risk* and predation *rate* (Vermeij, 1982; Dunbar, 1988; Hill & Lee, in press). *Predation rate* is the annual mortality within a population directly attributable to predation; it represents the level of successful predator attacks that the animals are unable to control after they have implemented their antipredation strategies. *Predation risk*, on the other hand, represents the animals' own perception of the likelihood of being subject to an attack by a predator, irrespective of whether or not the attack is successful; it reflects the animals' collective past historical experience of actual attacks by predators and is the basis on which the animals implement their antipredator strategies. It can be operationalised as the likelihood of an animal (or a group) encountering a predator. The animal's current behaviour is maintained by (and hence driven by) predation risk and not predation rate because the animals will be just as responsive to unsuccessful attacks as to successful ones.

We argue that animals seek to reduce their predation *risk* such that their predation rate is kept at some acceptable level. What defines an acceptable level should, however, vary between and within species according to two key considerations. One of these will be the habitat's characteristics. Animals may be willing to accept high levels of actual predation when they are unable to implement more effective antipredator strategies and the only alternative is not to live in that particular habitat. High predation levels may thus be a cost paid by some populations that have no choice about where they live. The second consideration is likely to be the species' (or population's) reproductive rate: animals may accept higher levels of predation rate if their potential reproductive rate is high enough to compensate for the losses incurred, especially when these losses are confined to immature animals.

Some evidence to support the second claim comes from a recent analysis by Lycett *et al.* (1998), who found a significant negative relationship between interbirth interval and predation *risk* for nine baboon populations. This suggests that a relationship exists between predation and reproductive rate, and that ultimately a population's 'acceptable' predation rate is

constrained by the rate at which it is able to reproduce. We propose that species who are able to maintain high reproductive rates will be able to tolerate higher levels of predation mortality, whereas those species that are constrained to reproduce more slowly will be forced to opt for antipredator strategies that allow them to reduce the rate of loss to a lower level. Since animals have some control over the rate of reproduction through the capacity to adjust their interbirth intervals (at least within species typical limits), we can expect this result to hold between species as well as between populations within species (see also Stanford, in press).

Previous analyses have predicted a negative relationship between predation rate and group size (or body weight) but we argue here that this prediction is in fact based on confusing predation *rate* with predation *risk*. In contrast to most previous analyses, we argue that so far from providing evidence for the importance of predation as a selective factor, a significant relationship between predation *rate* and group size or body size probably reflects the fact that some animals are willing to tolerate higher levels of predation than others. If predation is the principal factor influencing the grouping patterns (or body sizes) of primates, then there should be a positive correlation between predation *risk* and group size (or body size) and no correlation between predation *rate* and either of these variables. We would expect a negative relationship between group size and predation rate *only* when predation *rate* and predation *risk* are identical (something that could only happen if the animals have no anti-predator strategies and a predator killed every animal it encountered). We would, however, expect to find a significant positive correlation between predation *rate* and reproductive rate and this might give rise to a negative relationship between group size (or body size) and predation *rate*. We may therefore need to partial out the confounding effects of reproductive rate when examining the relationship between predation *rate* and either group size or body weight. If we still find a relationship between group size (or body weight) and predation *rate*, then this would be strong evidence *against* the hypothesis that predation acts as a selection factor favouring larger group sizes (or body weight): it would imply either that group size (or body weight) is *not* an effective antipredator strategy or that there are other sources of confound (*e.g.* correlated habitat differences in predator density). One likely source of confound in this respect is activity period: many noctur-

nal species rely on a different antipredator strategy (crypticity) to diurnal species. Since nocturnal species tend to be small-bodied, a spurious negative correlation between predation rate and both group size and body size may result.

Predation risk is likely to be a difficult variable to measure and therefore test. Frequency of predation attempts, whether successful or unsuccessful, is likely to be a reasonable index (Hill & Lee, in press), but quantitative data are almost never provided on this. Hence, pending the obtaining of such data from field sites, there is little to be gained in attempting to test this prediction at the moment. However, a direct test of the predictions for predation rate is possible with the existing data.

Methods

The data on estimated predation rates are primarily those compiled by Cheney & Wrangham (1987), supplemented with additional data from three further populations in the literature. However, we exclude six data points from Cheney & Wrangham (1987) because their predation rates are described as rough guesses. In addition, the *Presbytis entellus* data from Abu and Jodhpur are also excluded since these represent sites which experience large degrees of human interference, and this could significantly influence a number of the variables under investigation (the presence of humans is known to deter predators, for example: see Isbell & Young, 1993).

A number of the reported predation rates in Cheney & Wrangham (1987) were not specific, and in these instances the predation rate was taken to be the designated value (*i.e.* an estimated predation rate of > 15 was taken to represent a predation rate of 15). Where predation rates were expressed as a range, the mid-point of this range was taken to be the predation rate. Predation rates were expressed as the percentage of the population lost to predators each year and we have converted these values to proportions for analysis.

Group size data were taken from the literature for the sites from which the estimated predation rate data derived. Where female body weight and birth rate data were available for these sites, these were also recorded. In the absence of data from the actual sites, species average values for these variables were used, with preference given to estimates taken from wild populations. The data are given in Table 1.

Two forms of analysis are used. Initially we perform linear regression analysis on the predation rate data and the three independent variables to determine the relationships between these variables. We perform these analyses in order to facilitate comparisons with the findings of Cheney & Wrangham (1987) and Isbell (1994).

Secondly, we utilise the technique of independent contrasts (Pagel & Harvey, 1989; Harvey & Pagel, 1991), but without reference to branch lengths, to control for any potentially confounding effects of phylogeny within these relationships. This method relies on the use of a phylogenetic tree which reflects as accurately as possible the evolutionary relationships of the species under consideration. The following analyses employ a phylogeny taken from the composite tree derived by Purvis (1995) for all 203 species of primate, which is

TABLE 1. *Data on predation rate, group size, body weight and birth rate*

Species/Study site	Predation rate (proportion of animals killed)	Mean group size	Female body weight (kg)	Birth rate (infants/female/year)	Sources
Alouatta seniculus: Hato Masaguaral, Venezuela	0.01	8.90	4.50	0.723	1, 2, 3
Callicebus moloch: Manu, Peru	0.04	4.5	0.875	1.000	1, 4, 5
Cebus apella: Manu, Peru	0.13	7.75	2.10	0.545	1, 5, 6, 7
Cebus olivaceus: Hato Masaguaral, Venezuela	0.03	17.38	3.2	0.462	1, 7, 8, 9
* *Aotus trivirgatus:* Manu, Peru	0	5.0	0.961	1.659	1, 4, 5
Cercopithecus aethiops: Amboseli, Kenya	0.15	21.7	–	0.787	1, 10, 11
C. aethiops: Samburu, Kenya	0.06	40.1	2.57	–	1, 12, 13
C. ascanius: Kibale, Uganda	0.02	35	2.90	0.674	1, 7, 17
C. mitis: Kibale, Uganda	0.02	18.7	4.40	0.571	1, 14
Colobus badius: Gombe, Tanzania	0.15	27.7	9.0	0.494	1, 15
C. badius: Kibale, Uganda	0.015	34.0	7.0	0.476	1, 7, 16
Erythrocebus patas: Laikipia, Kenya	0.10	31.2	5.60	0.869	1, 5, 17
* *Galago senegalensis:* Transvaal, South Africa	0.15	1	0.193	2.920	1, 5, 18
Macaca fascicularis: Ketambe, Sumatra	0.11	24.2	3.5	0.936	1, 19
Macaca sinica: Polonnaruwa, Sri Lanka	0.01	24.7	3.4	0.689	1, 5, 20
* *Microcebus murinus:* Beza Mahafally, Madagascar	0.25	1	0.08	2.223	5, 21
Pan troglodytes: Tai National Park, Ivory Coast	0.033	59.5	31.10	0.200	5, 22

TABLE 1. (*Continued*)

Species/Study site	Predation rate (proportion of animals killed)	Mean group size	Female body weight (kg)	Birth rate (infants/female/year)	Sources
Papio anubis: Gombe, Tanzania	0.01	38.3	13.6	0.370	1, 23, 24
P. anubis: Mara, Kenya	0.03	54	14.0	0.500	1, 25
Papio cynocephalus: Amboseli, Kenya	0.06	51.4	11.9	0.551	1, 26, 27
P. cynocephalus: Tana River, Kenya	0.15	76	–	–	28
Papio ursinus: Moremi, Botswana	0.09	69.5	14.63	0.488	1, 29, 30
Saguinus fuscicollis: Manu, Peru	0.15	5	0.4	2.262	1, 5, 31
Saguinus imperator: Manu, Peru	0.15	4	0.5	** 2.433	1, 31, 32
Theropithecus gelada: Sankaber, Ethiopia	0	75.6	13.95	0.467	1, 33, 34, 35

Sources: 1: Cheney & Wrangham, 1987; 2: Rudran, 1979; 3: Crocket & Sekulic, 1984; 4: Wright, 1984; 5: Harvey *et al.*, 1987; 6: Janson, 1988; 7: Robinson & Janson, 1987; 8: Robinson, 1988; 9: Mittermier, 1977; 10: Cheney, 1981; 11: Lee, 1987; 12: Melnick & Pearl, 1987; 13: Turner *et al.*, 1994; 14: Cords, 1987; 15: Stanford, 1995, pers. comm.; 16: Struhsaker & Leyland, 1987; 17: Chism & Rowell, 1988; 18: Bearder, 1987; 19: van Schaik *et al.*, 1983; 20: Dittus, 1977; 21: Goodman *et al.*, 1993; 22: Boesch, 1991; 23: Ransom, 1981; 24: Dunbar, 1990; 25: Popp, 1978, 1983; 26: Altmann & Altmann, 1970; 27: Altmann *et al.*, 1993; 28: Condit & Smith, 1994; 29: Bulger & Hamilton, 1987; 30: Hamilton *et al.*, 1976; 31: Terborgh, 1983; 32: Stevenson, 1986; 33: Dunbar, 1992; 34: Kawai *et al.*, 1983; 35: Dunbar, 1984.

* Nocturnal species.
** Based on an estimated mean litter size of 1.5.

currently the best phylogeny available. Since some of the species included in the data set were represented by more than one population, we calculated species averages for the four variables in order to perform the comparative analysis. Unresolved nodes (*i.e.* those from which more than two species derive) were analysed as successive pairs (A with B, B with C, but not A with C) to preserve statistical independence; the nodal value was then taken to be the mean of all the species derivative of that node. The statistical significance of any relationship is assessed by a linear regression set through the origin, as recommended by Harvey & Pagel (1991). Although comparative methods are dependent on the accuracy of the phylogenies they use, there are few (if any) cases where the phylogenetic relationships of the species in the present sample are ambiguous.

One possible confound in the data set is that three of the points represent nocturnal species. Since nocturnal species do not follow a 'safety-in-numbers' antipredation strategy but rather rely upon crypsis, inclusion of these species in certain analyses (particularly in respect to group size) may confound the results. As a consequence, the results of all analyses are given for both the entire data set and for a data set where the nocturnal species are excluded.

All data were natural log transformed to ensure normality for parametric analysis. Since some of the estimated predation rates were reported as zero, the predation rate data were analysed as the natural logarithm of the value plus 1. All analyses were made using SPSS version 6.1 for the PC, with probability levels set at 0.05, and all tests are two-tailed.

Results

In confirmation of Isbell (1994) a significant negative relationship was found between predation rate and group size (Fig. 1a: $r^2 = 0.179$, $F_{1,23} = 6.245$, $p = 0.02$). Furthermore, the negative relationship between predation rate and female body weight reported by Cheney & Wrangham (1987) and Isbell (1994) persists within the extended data set (Fig. 1b: $r^2 = 0.347$, $F_{1,21} = 12.719$, $p < 0.002$). However, exclusion of the nocturnal species removes the significance of the relationship with group size ($r^2 = 0.029$, $F_{1,20} = 1.636$, $p > 0.20$); although the regression with body weight is still significant, its magnitude is greately reduced (Fig. 1b: $r^2 = 0.159$, $F_{1,18} = 4.602$, $p < 0.05$).

Independent contrast analyses confirm that the correlations between predation rate and both group size (Fig. 2a: $r^2 = 0.300$, $F_{1,22} = 9.060$, $p < 0.01$) and body weight (Fig. 2b: $r^2 = 0.284$, $F_{1,22} = 10.133$, $p < 0.005$) remain for the whole data set when the possible confounding effects of phylogeny are controlled for. However, exclusion of the nocturnal species removes the significance of both relationships (group
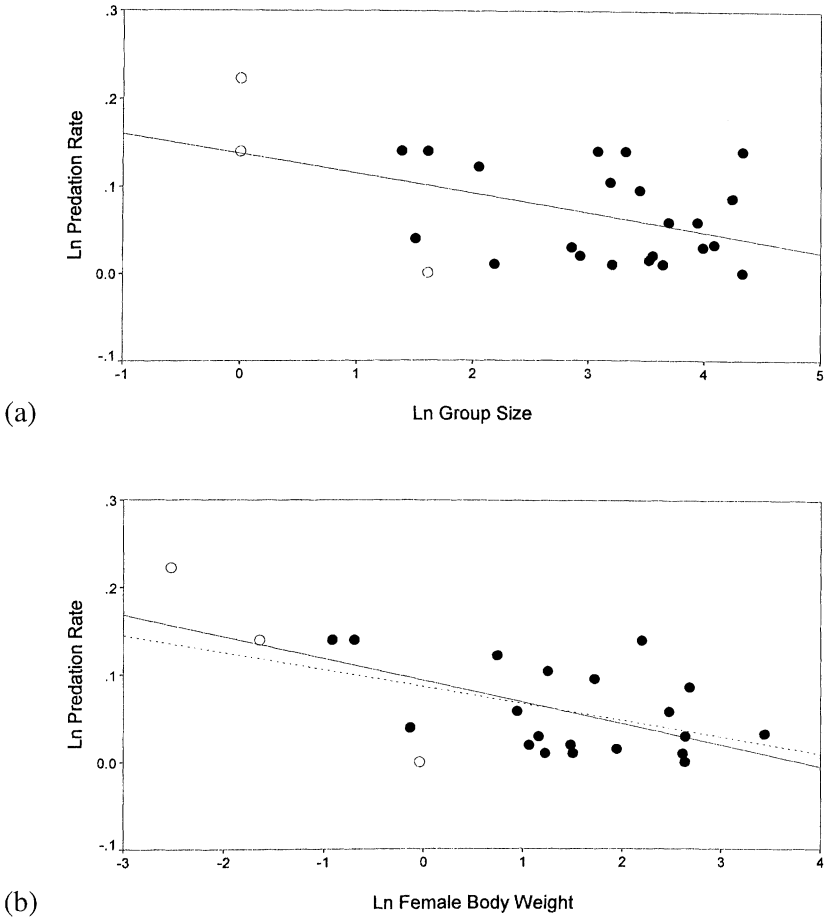
Fig. 1. Predation rate plotted against (a) group size and (b) female body weight. (●) Diurnal species; (○) nocturnal species; (——) all data; (.....) excluding nocturnal species.

size: Fig. 3a, $r^2 = 0.003$, $F_{1,16} = 0.938$, $p > 0.30$; body weight: Fig. 3b, $r^2 = 0.093$, $F_{1,16} = 2.746$, $p > 0.10$).

As predicted, predation rate shows a significant positive relationship with reproductive rate (Fig. 4a: $r^2 = 0.291$, $F_{1,21} = 10.034$, $p < 0.005$), and this relationship persists even when the nocturnal species are removed ($r^2 = 0.253$, $F_{1,18} = 7.438$, $p < 0.015$). When phylogenetic effects are accounted for through independent contrast analysis, the relationship remains significant, both for the entire data set (Fig. 4b: $r^2 = 0.209$,
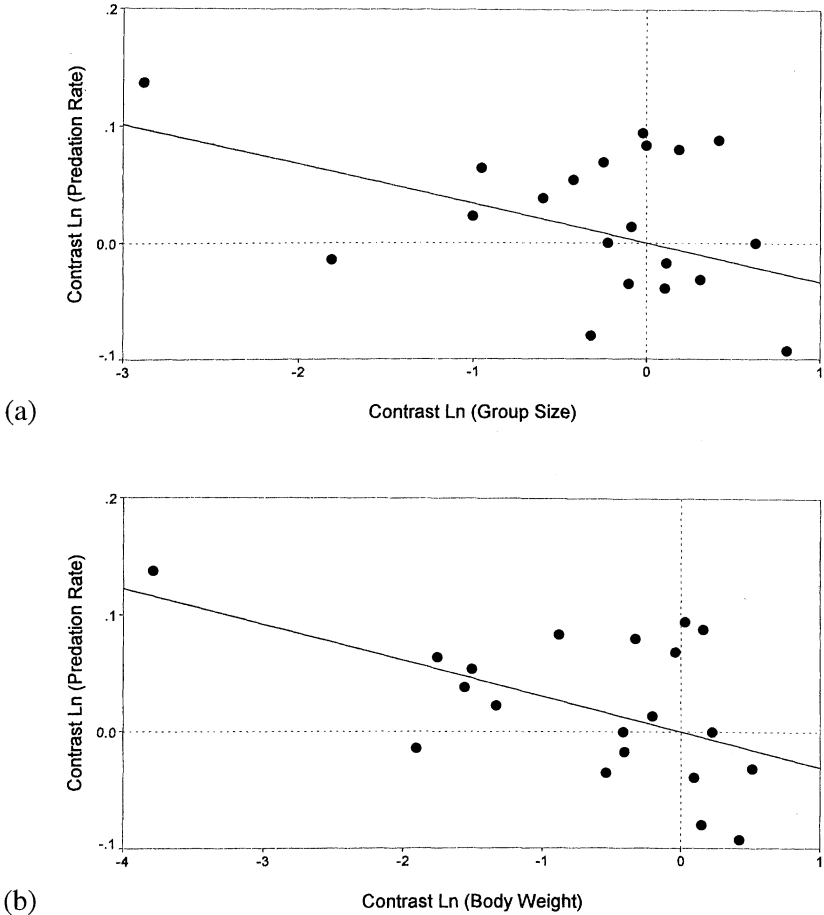
(a)

(b)

Fig. 2. Contrasts in predation rate plotted against (a) contrasts in group size and (b) contrasts in female body weight, for all species average data.

$F_{1,19} = 6.277$, $p < 0.022$) and when nocturnal species are excluded ($r^2 = 0.207$, $F_{1,16} = 5.431$, $p < 0.035$).

In order to control for the potentially confounding effects of reproductive rate on predation rate, the residuals from the reduced major axis regression of predation rate on reproductive rate were taken and regressed through the origin against the contrasts for the other two independent variables. With the effects of reproductive rate controlled for, neither of the relationships is significant, either for the entire data set (group size: Fig. 5a, $r^2 = 0.046$,
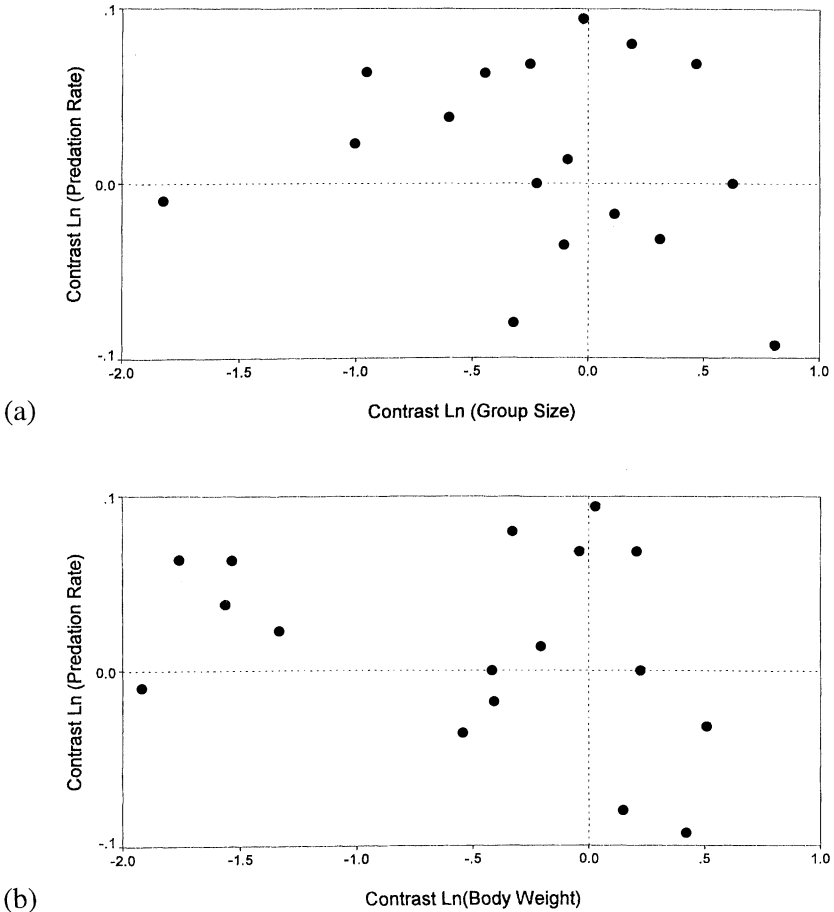
(a)

(b)

Fig. 3. Contrasts in predation rate plotted against (a) contrasts in group size and (b) contrasts in female body weight, excluding nocturnal species.

$F_{1,19} = 0.126$, $p > 0.70$; body weight: Fig. 5b, $r^2 = 0.022$, $F_{1,19} = 0.568$, $p > 0.45$) or when the nocturnal species are excluded (group size: $r^2 = 0.043$, $F_{1,16} = 0.307$, $p > 0.55$; body weight: $r^2 = 0.057$, $F_{1,16} = 0.083$, $p > 0.75$).

We note that these results are unchanged if we include the eight sites given by Cheney & Wrangham (1987) which we excluded on grounds of either questionable data or human interference. With the full data set, the initially significant negative correlations with predation rate (group size:
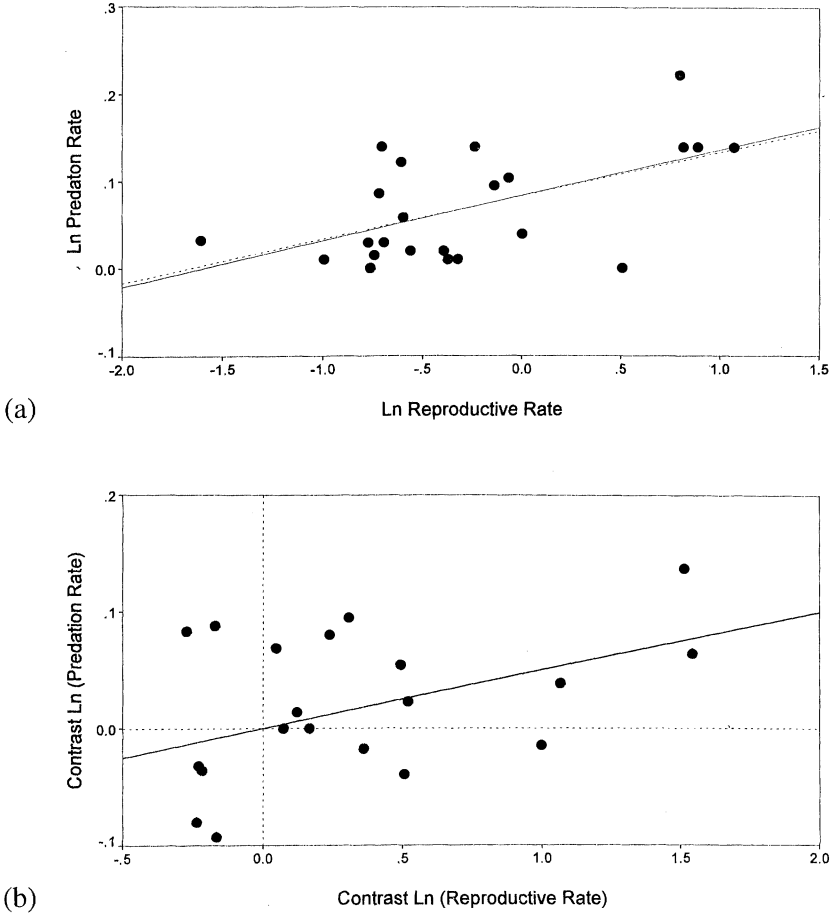
(a)

(b)

Fig. 4. (a) Linear regression of predation rate on reproductive rate; (———) all data; (.....) excluding nocturnal species. (b) Contrasts in predation rate plotted against contrasts in reproductive rate for all species (with data averaged for each species).

$r^2 = 0.167$, $F_{1,31} = 7.426$, $p \leqslant 0.02$, independent contrasts: $r^2 = 0.257$, $F_{1,22} = 8.957$, $p = 0.01$; body weight: $r^2 = 0.311$, $F_{1,27} = 13.623$, $p = 0.001$, independent contrasts: $r^2 = 0.291$, $F_{1,22} = 10.429$, $p < 0.005$) are lost when the effects of reproductive rate are partialled out, even when nocturnal species are included in the analysis (group size: $r^2 = 0.020$, $F_{1,22} = 1.478$, $p > 0.20$; body size: $r^2 = 0.007$, $F_{1,22} = 0.849$, $p > 0.35$).
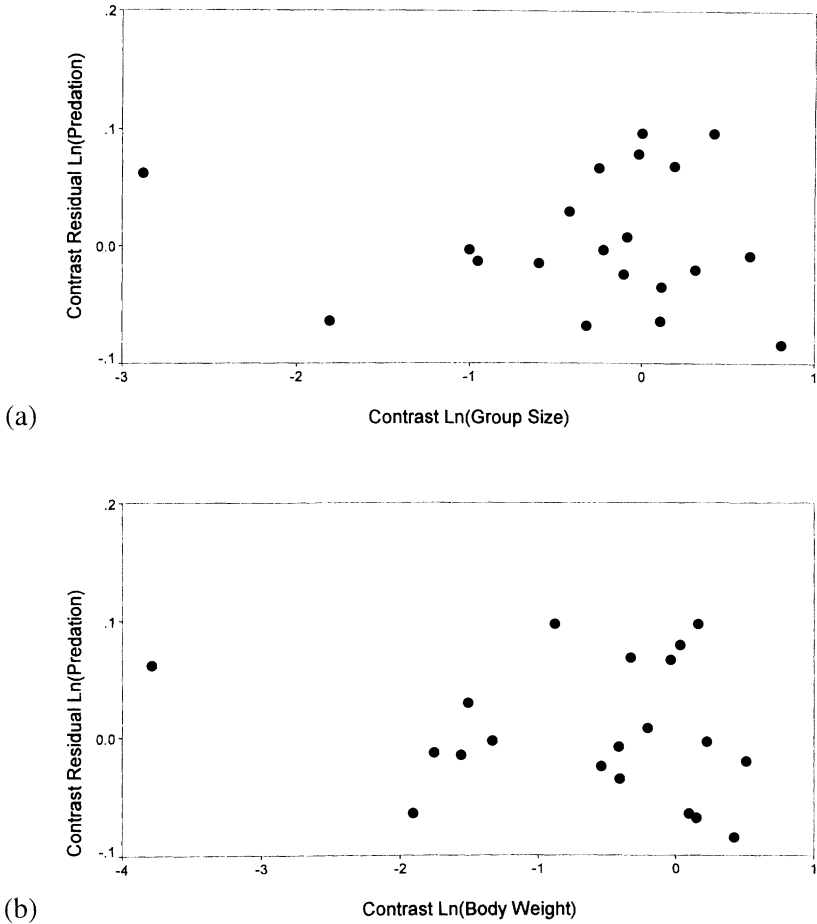
(a)

(b)

Fig. 5. Contrasts in residual predation rate (partialling out the influence of reproductive rate) plotted against (a) contrasts in group size and (b) contrasts in body weight for all species. See text for details.

Discussion

The use of predation rate as an index of predation pressure has introduced considerable confusion into the debate over the importance of predation as a selective force on primates. This has resulted in some studies reporting negative correlations between predation rate and group size (Isbell, 1994) while others have found positive relationships (Anderson, 1986). Furthermore, it seems likely these relationships are confounded by the effects of

body weight (Cheney & Wrangham, 1987; Isbell, 1994). However, we have shown that although the reported relationships with group size persist within this refined data set, even when confounding phylogenetic effects are controlled for, the significance of this relationship is entirely due to the inclusion of nocturnal species. Since nocturnal species rely upon crypsis rather than safety-in-numbers as their antipredator strategy, they introduce a confounding factor into the analysis for the effects of group size. With the three nocturnal populations in the sample excluded, no relationship exists between predation rate and group size.

Body weight was also found to be significantly correlated with predation rate even after phylogenetic effects had been accounted for, confirming the findings of previous studies (Cheney & Wrangham, 1987; Isbell, 1994). However, when the nocturnal species were excluded, the relationship was lost with an independent contrasts analysis. Although there is no intuitive reason why nocturnal species should be excluded from correlations with body weight, the fact that the relationship does not hold for diurnal species suggests that this relationship is not as strong as that with reproductive rate. Indeed, rather than providing evidence for a direct link between predation rate and body size, it probably reflects the strong interrelationship between body weight and reproductive rate ($r^2 = 0.826$, $F_{1,20} = 100.568$, $p < 0.0001$; independent contrasts: $r^2 = 0.747$, $F_{1,19} = 60.039$, $p < 0.0001$).

As predicted, reproductive rate was shown to be the best predictor of a species' predation rate, and this relationship persists even after the potentially confounding effects of phylogeny have been removed. Furthermore these correlations are maintained if the nocturnal species are excluded, indicating that this relationship is consistent across species regardless of their antipredation strategy. In effect, predation rate represents the acceptable level of mortality that can be accommodated within a species' life history strategy.

Given that predation rate represents the residual rate of mortality once an animal has implemented its antipredation strategy, and that the level of acceptable predation mortality is constrained by the species' reproductive rate, one implication is that, all else equal, predation rates within species should be consistent across habitats. However, under certain conditions animals may be prepared to trade up predation against other variables in order to survive at all, and thus some variance in species' predation rates

may be anticipated. Evidence for such a trade-off comes from a recent study by Lycett *et al.* (1998). This study found a significant negative correlation between interbirth interval and predation *risk* (estimated using the categorical index developed by Hill & Lee, in press) for nine baboon populations. These results suggest that baboon mothers are responding to their perceived risk of care-independent mortality (*i.e.* factors such as predation that are not influenced by parental input: see Pennington & Harpending, 1988) by manipulating their degree of parental investment in each offspring. Where mothers perceive that the probability of their offspring succumbing to a predator before reaching reproductive age is high, they concentrate on producing offspring at a maximal rate. In contrast, when the chances of care-independent offspring mortality are perceived as low, mothers increase the investment in each individual offspring. However, the degree to which females can trade predation off against reproductive rate is not unlimited, and they are ultimately constrained by their species-specific maximum reproductive rate.

The level of predation rate is thus determined by the antipredator strategy employed by an individual in response to predation risk. Predation rate is, in effect, the probability that an individual will succumb to a predator within a given time period, relative to the state of predator and prey behaviour. Over sufficient timescales, current predation risk will tend to be linearly related to the observed predation rate. However, since current predation rate reflects the risk of predation at the current state of antipredator behaviour, it does not reflect predation risk as a selective force (unless the animal is exercising no antipredation strategy). Predation risk as a selective force can be defined as the probability that an animal living on its own and exercising no behavioural antipredator strategies (*e.g.* vigilance) will succumb to a predator during any given time period. Since this will be difficult to measure in practice, an adequate operational definition might be the frequency with which groups (or individuals) are subjected to predator attacks (regardless of whether or not these are successful). The frequency with which observers encounter predators may also be a reasonable approximation of predation risk. Alternatively, predator encounter rates may be estimated theoretically by using the gas model (see Lowen & Dunbar, 1994) to calculate the frequencies with which randomly moving prey will

encounter randomly searching predators, given the observed densities of predators and prey in the habitat.

An individuals' perceived predation risk has a number of different components, many of which are closely related to the local environment (e.g. density of predators, visibility within the habitat, distribution of refuges). Cowlishaw (1997) showed that for a desert baboon population, habitat choice did not occur simply on the basis of food availability. Rather, the baboons trade-off predation risk (evaluated through estimates of attack risk [based on habitat visibility and predator ambush distances] and capture probability [based on predator attack velocities, prey escape velocities and refuge density]) against food availability such that they spent less time feeding in high-risk/food-rich habitat and more time feeding in low-risk/food-poor habitat. This indicates that baboons are acutely aware of the relative predation risk of each sector of their habitat and adjust their behaviour accordingly.

Similar responses to environmental factors determining predation risk have also been shown to occur between populations. Dunbar (1996a) found that, for a sample of 33 baboon populations, the population minimum group size (in this study, taken as a surrogate for predation risk) was positively correlated with the density of low level (bush layer) cover from which a predator could ambush, but negatively related to the density of large trees that can act as refuges. Baboons appear to respond to the perceived likelihood of predator attack by increasing the minimum group size in which they are prepared to live, but seem to be willing to compromise on this if refuges are easily accessible.

Demographic factors are also an important component in an individual's risk of predation, if for no other reason than the fact that the larger an individual's group, the lower the probability that any one individual will be taken during a predation event (the selfish herd effect: Hamilton, 1971). Thus, if group size is the response to predation *risk*, then within habitats, where many aspects of predation risk are held constant, we should see the commonly predicted negative correlation between group size and predation *rate* for individual species. Isbell (1994) tested this prediction using data from vervet groups at Amboseli, but did not find the predicted trend. However, Isbell's (1994) results need to be interpreted cautiously since the relationship between group size and predation rate is likely to have

been confounded both by between territory differences in refuge density (Dunbar, 1996b) and by the effect that variation in proximity to human settlement can be expected to have on predator densities (see Isbell & Young, 1993). More care will be needed to ensure that confounding variables are held constant if we are to test any of these predictions satisfactorily.

Although measures of predation rate may thus prove useful in conducting certain analyses, it is clearly evident that they have little value when considering the role of predation as a selective pressure on primates. Previous authors have suggested that significant progress in understanding the importance of predation on primates will only come from studies of the predators themselves (Anderson, 1986; Cheney & Wrangham, 1987; Isbell, 1994; Boinski & Chapman, 1995). While a precise knowledge of predator hunting strategies is undoubtedly essential to understanding primate antipredator behaviour (*e.g.* Cowlishaw, 1997), we argue that in itself this cannot provide a comprehensive explanation as to the importance of predation in determining primate social structure. Rather, it is research aimed at identifying the factors that *primates* perceive as important about predator behaviour that will prove to be the most fruitful avenue for future research.

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