

A community-level evaluation of the impact of prey behavioural and ecological characteristics on predator diet composition

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Although predation avoidance is the most commonly invoked explanation for vertebrate social evolution, there is little evidence that individuals in larger groups experience lower predation rates than those in small groups. We compare the morphological and behavioural traits of mammal prey species in the Tai forest, Ivory Coast, with the diet preferences of three of their non-human predators: leopards, chimpanzees and African crowned eagles. Individual predators show marked differences in their predation rates on prey species of different body sizes, but clear patterns with prey behaviour were apparent only when differences in prey habitat use were incorporated into the analyses. Leopard predation rates are highest for terrestrial species living in smaller groups, whereas eagle predation rates are negatively correlated with group size only among arboreal prey. When prey predation rates are summed over all three predators, terrestrial species incur higher predation rates than arboreal species and, within both categories, predation rates decline with increasing prey group size and decreasing density of groups in the habitat. These results reveal that it is necessary to consider anti-predator strategies in the context of a dynamic behavioural interaction between predators and prey.

Keywords: predation risk; group size; comparative method; prey choice; primates; duiker

1. INTRODUCTION

Predation imposes two costs on prey individuals: the direct catastrophic costs of mortality and the chronic indirect costs of employing behaviours that reduce mortality risk. To quantify these indirect costs, it is possible to document behaviours that can be considered as fitness corollaries, such as an increase in vigilance or a reduction in feeding or reproductive activities under elevated predation risk (Lima 1998). These costly behaviours are maintained because of the reduced mortality risk experienced by the individual. Through measuring the investment in anti-predator behaviour we can assess the relative costs that individuals are willing to bear as a function of predation risk. However, to measure the efficacy of an anti-predator behaviour, the costs sustained by the prey need to be considered in the context of their impact on the actual predation rate.

Predation avoidance is presumed to be the primary advantage of group living among most social vertebrates, with the assumption that *per capita* predation rates decline with increasing group size owing to the benefits of dilution, confusion, early warning and coordinated defence (Pulliam 1973; Elgar 1989). Theoretical models have supported such anti-predator benefits for individuals living in groups (Vine 1971; Taylor 1976; Lima 1987), whereas empirical evidence is limited to documenting the

indirect costs of increased investment in anti-predator behaviour in small groups, or to observing changes in group size under high predation risk (e.g. Elgar 1989; Whitfield 1988). Unfortunately, very little evidence is available for how investment by prey in anti-predator behaviour affects the decisions made by foraging predators (Lima 2002). A few studies have documented predator attack rates on prey groups of different sizes in either natural or experimental systems, but the connection between attack and capture rates does not appear to be straightforward (Lindstrom 1989; Turchin & Karieva 1989; Creswell 1994; Krause & Godin 1995; Hebblewhite & Pletscher 2002).

An alternative approach to understanding the evolutionary function of sociality in terms of predator-prey interactions is to use a comparative approach. However, in several different taxonomic groups, comparative analyses have found support for sociality having functional roles besides predation avoidance, such as access to resources (Beauchamp 2002) or minimizing the energetic costs of foraging (Ebensperger & Cofré 2001). The use of a comparative approach to study the role of predation in the evolution of sociality is limited by the availability of accurate estimates of predation rates and by the difficulties in controlling for behavioural differences caused by underlying ecological variation in resource availability between sites. Although it is clear that sociality can serve functions other than reducing predation risk, there remains inadequate verification of how group size affects actual realized predation rates.

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Among primates, a taxon often used to address questions about the evolution of sociality, there are numerous behavioural studies that have documented increases in group cohesion, vigilance levels and mixed species associations with elevated predation risk (e.g. Noë & Bshary 1997; Cowlshaw 1997; Shultz *et al.* 2003). By contrast, attempts to relate documented predation rates to group size and composition have arrived at conflicting conclusions, with positive (Anderson 1986), negative (Isbell 1994; Hill & Dunbar 1998) and no relationships (Cheney & Wrangham 1987) between increasing group size and predation rates. The inconsistency in these patterns may be the result of a failure to distinguish between chronic (risk) and catastrophic (mortality) costs of predation across different populations (Hill & Dunbar 1998; Janson 1998). However, there are also several underlying problems with documenting predation rates in primates. Predation events are rare and unpredictable. If predation rates are calculated using observed predator encounters, they can be drastically underestimated if even a few events are missed. Additionally, human observers can dramatically affect predator behaviour; consequently, realized predation rates could be artificially reduced (Isbell & Young 1993). A feasible alternative to documenting all predation events in a population is to compare the relative composition of different prey species in the diets of their predators. These measures of prey preferences can then be compared with ecological and behavioural characteristics of the prey to identify those traits associated with high predation rates.

Most prey live in complex communities where multiple predator species feed on the same prey species. However, experimental studies of predator–prey interactions either focus on single predators or study the effects of one predator at a time (Sih *et al.* 1998). As predator behaviour and prey preferences vary, predators can have very different effects on the prey population; studying species in isolation can lead to incorrect inferences about how multiple predators interact with the prey community. Vertebrate communities in tropical forests are composed of complex webs of trophic interaction with multiple shared prey and predators. To understand the impact of predation on different prey species, it is necessary to document the pressure exerted by all predators as well as the interactions of individual predator–prey combinations.

We compare the diet compositions and predation pressures of the three non-human predators of medium-sized mammals in the Taï National Park, Côte d'Ivoire: leopards (*Panthera pardus*), African crowned eagles (*Stephanoaetus coronatus*) and chimpanzees (*Pan troglodytes*). We calculate total estimated predation rates by the three predators to assess the overall predation pressure exerted on the prey community by their main predators and make several predictions about how behavioural and ecological characteristics of the mammal prey species should relate to predator diet composition. First, if sociality is an effective anti-predator strategy, relative predation rates will be higher for prey species that occur in smaller groups. Second, predator diets should be biased towards the prey that are most accessible to them, such that the diets of terrestrial predators should be biased towards terrestrial prey and the diets of arboreal or aerial predators should be biased towards arboreal prey.

2. MATERIAL AND METHODS

This study was undertaken in the Taï National Park, which is located in southwestern Côte d'Ivoire and, with an area of 454 000 ha, is the largest protected lowland forest in West Africa. The Station de Recherche en Ecologie Tropicale, 20 km east of the town of Taï, has been the location of numerous long-term projects resulting in extensive ecological data on primates and other mammals. In the national park, there are only three main non-human predators of medium-sized mammals: the African crowned eagle, leopard and chimpanzee. All three predators are commonly found in the area around the research station, from where the diet estimates are based (chimpanzees, Herbingier *et al.* 2001; leopards, Jenny 1996; crowned eagles, Shultz 2001). Although poaching is a problem in some areas of the park, humans exert little hunting pressure in the area immediately surrounding the research station (Hoppe-Dominik 1997).

Diet compositions for chimpanzees and leopards were taken from published data (271 prey individuals for chimpanzees, Boesch & Boesch-Achermann 2000; 227 prey individuals for leopards, Zuberbühler & Jenny 2002). To determine the composition of eagle diets, prey remains were removed from underneath 12 crowned eagle nests near the research station between October 1998 and July 2001. The minimum number of individuals from each nest was determined for each prey species following the identification of all remains. Primate prey were identified using W. S. McGraw's skeletal collections from the park. Non-primate prey were identified using the collections held by the Muséum National d'Histoire Naturelle in Paris.

(a) Prey choice

The analyses of predator diet and prey characteristics were restricted to prey species for which accurate estimates were available for population density and average group size (Shultz & Noë 2002; Newing 1994; Goldman & Dunham 2004; table 1).

To determine whether the predators' diets were biased towards or against particular prey species, we compared the relative diet composition of each predator with a null model that assumes random prey selection. If there is no bias, prey should appear in the diet at roughly the same relative abundance as they occur in the habitat. Manly *et al.* (1993) suggested the following test to determine whether the composition of prey in the diet differs from random:

$$\chi^2 = 2 \sum_{i=1}^n \left[u_i \ln \left(\frac{u_i}{U p_i} \right) \right],$$

where u represents the number of each prey item in the diet, p represents the proportion of each prey item in the environment, U is the total number of prey individuals recorded and n is the total number of prey species.

(b) Predation rates

Predator densities were taken from Shultz (2002), Jenny (1996) and Boesch & Boesch-Achermann (2000). Minimum prey requirements for eagles were based on the estimation of 430 kg per individual per year from Brown *et al.* (1982). The figure of 5555 kg per leopard per year was based on estimates provided by Carbone & Gittleman (2002), and for chimpanzees the estimated predation rate was based on the hunting observations for the Taï chimpanzee community reported by Boesch & Boesch-Achermann (2000).

Table 1. Prey species used in the analysis with their ecological characteristics.

species	population density (number km ⁻²)	group size	group density	body size (kg)	r_{\max}	habitat use
<i>Cercopithecus diana</i>	78	28	2.79	4.55	0.19	arboreal
<i>C. petaurista/campbelli</i>	60	9	5.38	3.6	—	arboreal
<i>Colobus polykomos</i>	45	16	2.81	9.1	0.15	arboreal
<i>Procolobus badius</i>	153	73	2.10	6.9	0.14	arboreal
<i>Colobus verus</i>	18	12	1.25	4.45	—	arboreal
<i>Perodicticus potto</i>	8	1	8.0	0.83	0.34	arboreal
<i>Cercocebus atys</i>	25	90	0.28	8.6	0.24	terrestrial
<i>Pan troglodytes</i>	1.87	10	0.19	44	0.05	terrestrial
<i>Cephalophus maxwelli</i>	63	1.57	40.10	9.1	0.49	terrestrial
<i>Cephalophus</i> spp. (other)	40	1	40.00	12	0.30	terrestrial
<i>Crossarchus obscurus</i>	13	12	1.63	0.81	0.57	terrestrial

The number of individuals removed per square kilometre by each predator species from the prey populations was calculated using the following formula:

$$N_i = \frac{\frac{(m_i \times n_i)}{\sum_{i=1}^n (m_i \times n_i)} \times K}{m_i},$$

where N_i is the number of individuals of prey species i removed per square kilometre, m_i is the average body mass of the species, n_i is the number of individuals of each species in the diet and K is the total prey offtake (in kg) for each predator per square kilometre per year, calculated by multiplying prey requirement per individual predator by their population density. This measure represents the proportion of diet biomass per prey species, multiplied by the offtake per square kilometre, yielding a total mass removed per square kilometre. This number is then divided by the body mass of the prey species to calculate the number of individuals removed. The predation rates (proportion of the population removed per year) for different populations were calculated by dividing the number of individuals removed by the population density.

Predation rates are additive between predators and it is therefore possible to estimate the total impact of predation on each prey population. As these values are proportional, the estimated predation rates for each individual predator and the total over all three predators were arcsine transformed. The arcsine-transformed estimates of predation rates were compared with the following behavioural and morphological characteristics of the different prey species: average recorded group size, body size, population density (individuals per square kilometre), group density (average number of groups per square kilometre), habitat use and diet. To assess the relative influence of the different independent variables, we used a general linear model (GLM) with the categorical variable habitat use (less than 50% of time spent on the ground was classified as arboreal) as a fixed factor and the continuous variables $\ln(\text{group size})$, or $\ln(\text{group density})$, and $\ln(\text{body size})$ as covariates. Non-significant factors and interactions were removed and the analyses rerun, until the most predictive model was identified. Transformed predation rates were also correlated with r_{\max} , or the maximum rate of population increase over a year, for each prey species. Values for r_{\max} (table 1) were taken from the literature (primates, Ross 1992; duikers: Fa *et al.* 1995) except for that of mongooses where r_{\max} was calculated with Cole's (1954) formula, using

estimates from Goldman & Dunham (2004) and Kingdon (1997), and corrected for the approximate number of breeding females per extended family group.

(c) Phylogenetic comparative method

The non-independence of related taxa is an often-highlighted limitation of comparisons of characteristics between taxa. For this reason, a number of statistical methods, for example independent contrasts (Felsenstein 1985), have been developed to help control for the nested hierarchies of phylogenetic relationships. It is necessary to employ these statistical corrections only where there is an obvious expectation of, and evidence for, phylogenetic constraint and non-independence of data. Thus, the statistical independence of data should be tested both before and after phylogenetic comparative methodology is used (Abouheif 1999), and tests have been developed recently to test explicitly for non-independence in particular datasets (e.g. Reeve & Abouheif 2003).

As we have used a cross-taxa approach to look at predator preferences, it is likely that the prey species are non-independent in their behavioural and ecological traits. Comparative analyses assume a random walk or Brownian motion causing the divergence of traits (Pagel & Harvey 1989). Where this assumption is violated, for example in the adaptive radiation of a trait, standard comparative methods may not remove the non-independence of traits. In our data that were phylogenetically correlated, we calculated independent contrasts, reanalysed these data to determine whether the non-independence had been removed and reran the GLM analyses using the contrast nodes. Prey phylogeny was taken from Nowak (1991) and independent contrasts were calculated without incorporating branch lengths. We tested the independence of tip values and contrast nodes for prey traits using PHYLOGENETIC INDEPENDENCE 2.0 (Reeve & Abouheif 2003) with 1000 iterations.

3. RESULTS

(a) Predator diet composition

The prey spectra for these predators include 38 confirmed species of mammal varying in weight from 200 g to 80 kg. A minimum of 333 prey individuals were identified from the eagle prey remains (Shultz 2003). For eagles, the relative proportions of the major prey classes did not differ significantly between nest sites (goodness-of-fit test of the relative proportions of primates, duikers

Table 2. Pearson's correlation coefficients between arcsine-transformed predation rates for each predator and prey characteristics.

		ln(group size)	ln(group density)	ln(body size)	ln(population density)
eagle predation rate	<i>R</i>	-0.09	0.20	-0.82	0.14
	<i>p</i>	0.80	0.55	0.002	0.68
leopard predation rate	<i>R</i>	-0.27	0.24	0.77	0.02
	<i>p</i>	0.43	0.47	0.006	0.95
chimpanzee predation rate	<i>R</i>	0.38	-0.08	0.62	0.39
	<i>p</i>	0.25	0.81	0.17	0.24
total predation rate	<i>R</i>	-0.60	0.13	0.04	-0.09
	<i>p</i>	0.05	0.48	0.91	0.79

and others for nests with more than 10 prey individuals, corrected *G*-test: $\chi^2 = 18.01$, d.f. = 16, $p = 0.80$) and prey were summed over nest sites. The average prey weight (\pm s.d.) was 11.27 ± 13.6 kg for leopards, 5.67 ± 3.33 kg for eagles and 6.9 ± 1.28 kg for chimpanzees. Leopard prey were significantly heavier than those of eagles (*t*-test: $t = 22.77$, $p < 0.001$) and chimpanzees ($t = 18.14$, $p < 0.001$), and chimpanzee prey were heavier on average than eagle prey ($t = 10.13$, $p < 0.001$).

The diet compositions of all three predators differed significantly from random (leopard: $\chi^2 = 46.83$, $p < 0.001$; eagle: $\chi^2 = 111.04$, $p < 0.001$; and chimpanzee: $\chi^2 = 112.95$, $p < 0.001$). Each predator responded differently to prey habitat use: leopard diets were biased towards terrestrial prey ($F_{1,9} = 7.13$, $p = 0.03$), and chimpanzee diets were biased towards arboreal prey ($F_{1,8} = 9.82$, $p = 0.01$), whereas eagle diets did not show a bias towards either terrestrial or arboreal prey ($F_{1,8} = 0.56$, $p = 0.48$). Eagle predation rates were negatively correlated, leopard predation rates positively correlated and chimpanzee predation rates uncorrelated with prey body size (table 2).

For each of the three predators, there was no clear overall relationship between prey group size and predation rate (table 2). However, when habitat use and group size were both incorporated into the analysis more interesting patterns emerged. For eagles, there was a strong negative relationship between predation rate and group size for arboreal prey (slope = -0.05 , $r^2 = 0.77$, $F_{1,4} = 13.50$, $p = 0.02$) but not for terrestrial prey (slope = 0.03 , $r^2 = 0.12$, $F_{1,3} = 2.68$, $p = 0.24$). There was a significant interaction between prey group size and habitat use because of the different directions of the relationship between group size and predation rate for arboreal and terrestrial prey ($F_{1,6} = 12.84$, $p = 0.012$). By contrast, for leopards, there was no significant relationship between prey group size and predation rate for either terrestrial (slope = -0.05 , $r^2 = 0.55$, $F_{1,4} = 3.65$, $p = 0.15$) or arboreal (slope = 0.03 , $r^2 = 0.42$, $F_{1,4} = 2.84$, $p = 0.17$) prey. However, as the directions of the relationships between group size and predation rate for arboreal and terrestrial prey were in opposite directions, there was a significant habitat by group-size interaction ($F_{1,7} = 6.55$, $p = 0.04$). There was no clear relationship between prey group size and predation rate for chimpanzees among either terrestrial or arboreal prey (arboreal: $F_{1,4} = 0.32$, $p = 0.61$; terrestrial: $F_{1,3} = 5.31$, $p = 0.15$) nor was there a habitat by group size interaction ($F_{1,6} = 0.01$, $p = 0.94$).

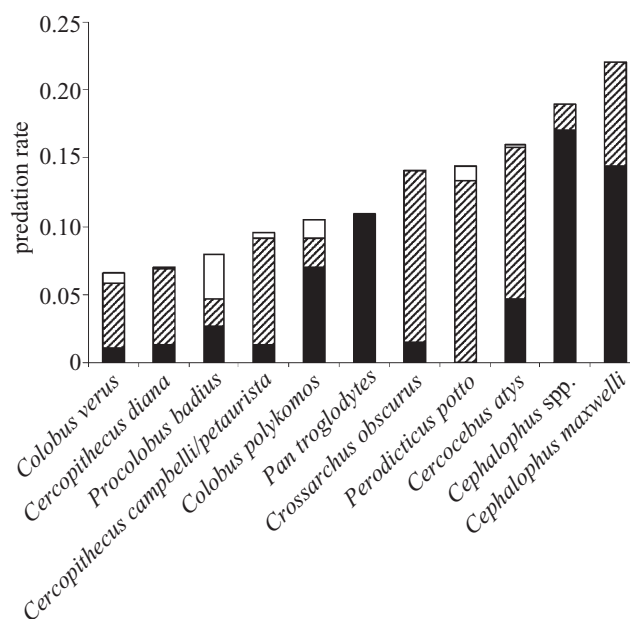


Figure 1. The total predation rate experienced by the different prey species in Taï National Park from leopard (filled), eagle (hatched) and chimpanzee (open).

(b) Combined predation rates

Total estimated predation rates by all three predators for the different prey species ranged between 6.5% and 22% of the total population per year (figure 1) and were significantly correlated with the prey's maximum intrinsic growth rate ($r = 0.79$, $p = 0.02$). The relative impact of the different predators varied between the prey species, with some species preyed upon relatively evenly by all three predators, whereas others were found in the diet of only one predator. The proportions of the prey population removed by leopards (mean \pm s.d. = 0.27 ± 0.13) and eagles (mean \pm s.d. = 0.23 ± 0.12) did not differ significantly (paired *t*-test on arcsine-transformed values: $t = 0.197$, $p = 0.85$) but they did differ between chimpanzees (mean = 0.06 ± 0.06) and both leopards ($t = 3.08$, $p = 0.012$) and eagles ($t = 4.32$, $p = 0.002$). Overall estimated predation rates were higher for terrestrial than for arboreal prey species (means: terrestrial = 0.17 ± 0.4 s.d., arboreal = 0.09 ± 0.03 s.d.; $F_{1,8} = 26.54$, $p = 0.001$).

Total predation rates were correlated with prey group size (table 2). Thus, when group size and habitat were incorporated into a GLM, both variables had a significant effect on predation rate (table 3; figure 2a). Predation

Table 3. Results of GLM analysis of arcsine-transformed predation rates as a function of prey habitat use and different continuous traits (covariates).

	covariate				habitat			overall model			
	model ^a	F	d.f.	p	F	d.f.	p	r ²	d.f.	F	p
population density	1	0.70	2,8	0.43	11.11	2,8	0.01	0.59	2,8	5.64	0.03
	2	0.16	1,7	0.70	14.30	1,7	0.007	0.68	2,7	7.73	0.02
body size	1	0.89	1,8	0.37	11.68	1,8	0.01	0.59	2,8	5.85	0.03
	2	0.003	1,7	0.96	14.69	1,7	0.006	0.68	2,7	7.49	0.02
group size	1	11.46	1,8	0.01	25.12	1,8	0.001	0.81	2,8	17.56	0.001
	2	9.48	1,7	0.02	25.88	1,7	0.001	0.87	2,7	22.35	0.001
	3	3.28	1,6	0.12	1.54	1,6	0.25	0.38	2,6	1.87	0.23
	4	19.43	1,5	0.01	9.48	1,5	0.03	0.82	2,5	11.20	0.01
group density	1	6.78	1,8	0.03	12.90	1,8	0.007	0.76	2,8	12.37	0.004
	2	5.63	1,7	0.05	22.12	1,7	0.002	0.82	2,7	16.32	0.002

^a Model 1 includes chimpanzees as a prey species; model 2 excludes them. Models 3 and 4 for group size use independent contrasts with and without chimpanzees, respectively. Models in bold are the most explanatory.

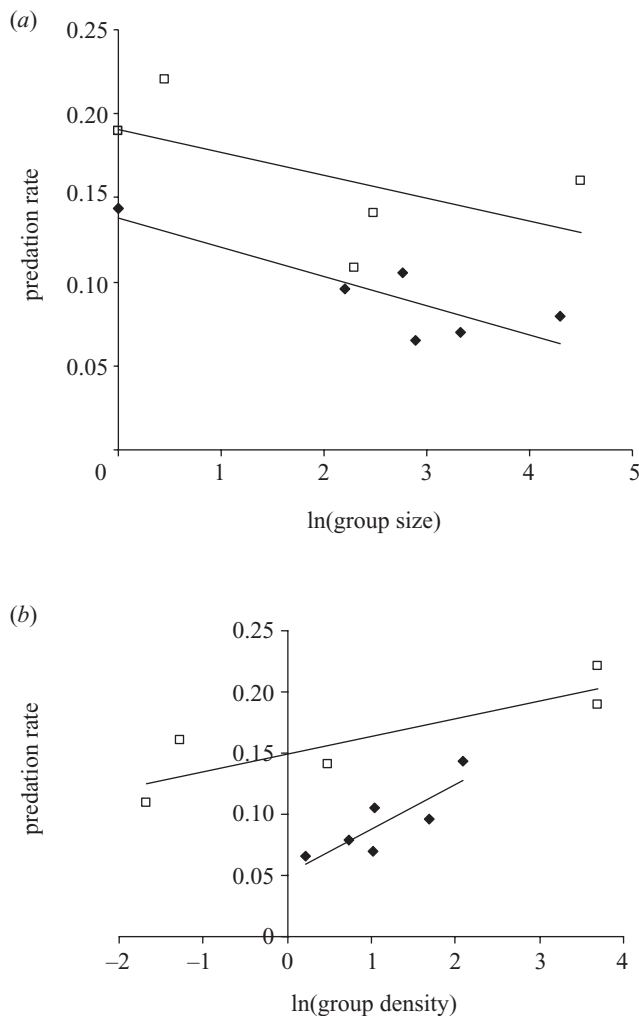


Figure 2. The relations between overall predation rate and (a) group size and (b) group density for terrestrial (open squares) and arboreal (filled diamonds) prey species. Overall predation rates are calculated by summing the estimated predation rates for leopards, eagles and chimpanzees for each prey species.

rates were also significantly related to group density when habitat was incorporated into the models (figure 2b). Neither body size nor prey population density were significantly associated with predation rates even when habitat use was included (table 3). Prey group density and group size were significantly correlated (both ln-transformed: $n = 11$, $r = -0.73$, $p = 0.01$), potentially obscuring causal relationships between the two factors and prey preferences.

Only a single chimpanzee was found in the leopard diet and this occurred during a disease epidemic in the chimpanzee population. In a similar study of leopard diets from across the park (Hoppe-Dominik 1984), there were no chimpanzees in a total sample of 258 identified prey individuals. Zuberbühler & Jenny (2002) report that radio-collared leopards tend to avoid chimpanzee groups. Thus, GLM analyses were run both with and without chimpanzees as a prey species, but the significance of the results does not change according to whether or not chimpanzees are included (table 3).

(c) Incorporating phylogenetic relationships

There was significant phylogenetic autocorrelation in group size and predation rate, but not group density (table 4). Independent contrasts were calculated for group size and predation rate for terrestrial and arboreal prey and were incorporated into the GLM model (table 3). The relationship between group size and predation rate remains significant when chimpanzees are excluded, but not when they are included in the model. We also tested the independence of these contrast nodes and found that the non-independence between contrast nodes is removed for predation rate and for group size (table 4). Thus, there appears to be a phylogenetic non-independence in respect of group size but not group density. Independent-contrast analysis removed the non-independence, and the relationship between group size and predation rate remains significant if chimpanzees are excluded from the model.

4. DISCUSSION

To understand the evolutionary significance of sociality and group size, we present relationships between

Table 4. Test for phylogenetic independence.

(Tip and node averages are calculated using PHYLOGENETIC INDEPENDENCE, following Reeve & Abouheif (2003); *p*-values are the proportions of iterations (*n* = 1000) with mean values above the observed value for the topology. Where this figure is less than 0.05 (one-tailed) there is significant phylogenetic autocorrelation.)

	observed tips average	<i>p</i>	observed contrast node average	<i>p</i>
predation rate	0.49	0.02	0.19	0.25
group size	0.38	0.01	−0.63	0.99
group density	0.28	0.10	−0.30	0.12

predator-diet composition and prey ecology and behaviour. By estimating total predation rates for each major non-human predator of medium-sized mammals, we were able to analyse predation risk in terms of prey characteristics on a predator-by-predator basis and as a function of the overall predation pressure exerted by the predator community. The relationship between diet composition and prey ecology is not straightforward when prey habitat use is not considered. The importance of prey habitat use may be partly explained by the predators' hunting style. Eagles are sit-and-wait ambush predators that drop onto unsuspecting prey from within the canopy (Shultz 2001); arboreal prey in large groups will benefit from increased vigilance levels and are more likely to detect an eagle before it attacks (Shultz & Noë 2002). Leopards use a similar ambush strategy on the ground (Zuberbühler *et al.* 1997), and large groups of terrestrial prey are more likely to detect them, mount a communal defence once a leopard is detected and benefit from the effects of dilution if the leopard attacks. By contrast, chimpanzees use a pursuit strategy where neither early warning nor dilution appear to compensate for their preference for colobine monkeys (Boesch & Boesch-Achermann 2000), which are the heaviest and slowest moving arboreal species (McGraw 1998).

One unexpected result of this analysis is that the terrestrial prey species of these three predators incur higher overall levels of predation than do arboreal species. Over all prey species, predation rates were lowest among arboreal primates living in large groups; even in terrestrial species, those living in larger groups experience lower predation rates than those in smaller groups or those that are solitary. Nevertheless, group density and group size were highly correlated and both are equally predictive of realized predation rates. This indicates that predator foraging success for different prey could be a function of either their attack success on small groups or their encounter rates with prey groups (i.e. group density).

The importance and validity of controlling for phylogenetic relationships in these analyses is debatable. It is more difficult to detect phylogenetic signatures in small datasets, and behavioural traits tend to be more labile than morphological ones (Blomberg *et al.* 2003). There is no evidence of phylogenetic non-independence in group density, although there is significant autocorrelation in group size. However, there remains a strong relationship between group size and predation risk even using independent-contrast nodes. If sociality is an adaptive trait, as seems to be the case in terms of realized predation rates, then we would expect selection for large group sizes where species have the behavioural flexibility and social systems to allow them.

Other studies on the relative composition of primate prey in predator diets have arrived at different conclusions from those presented here. The several studies of crowned eagle diet composition in Kibale (Skorupa 1989; Struhsaker & Leakey 1990; Mitani *et al.* 2001) have not directly addressed group size as a factor in predation rates, though a separate reanalysis of their data arrives at similar conclusions to those of this study (Shultz 2003). Zuberbühler & Jenny (2002) examined leopard diet composition in Tai with the same data used here and found that prey species occurring at high population densities were found most frequently in leopard diets. However, since even random prey selection will result in the most abundant prey being taken most often, it is necessary to control for prey abundance. The reanalysis of these data, controlling for abundance, indicates that there is no relationship between prey abundance and leopard predation rates.

The findings reported here may explain an unusual feature of primate biogeography, namely the complete absence of terrestrial primates in South America. In the Neotropics, there are several species of large cat and forest raptor but no terrestrial primate species. By contrast, in Southeast Asia, where there are no large forest raptors and cats occur at low density, there are several sympatric species of semi-terrestrial macaque. In African forests, with one species of large diurnal raptor and up to two species of large cat, the terrestrial forest primates either occur in very large groups (e.g. mandrills, *Mandrillus sphinx*, drills, *M. leucophaeus*, and mangabeys *Cercocebus torquatus* and *C. atys*) or are very large bodied (e.g. chimpanzees and gorillas, *Gorilla gorilla*).

Prey generally face more than one natural enemy and they are expected to employ anti-predator strategies that best confront the hunting strategies of their predators. Therefore, it is necessary to consider prey behavioural decisions as part of a dynamic interaction between predators, their prey and the habitat (Lima 2002). Out of the previously published studies of multiple predator effects on prey risk or mortality, none focuses specifically on the role of prey group size as an effective anti-predator strategy (Sih *et al.* 1998). Within social primate species, individuals in larger groups generally suffer higher levels of resource competition (Janson & Goldsmith 1995), and the observed group size is a trade-off between predation risk (a direct cost of predation) and feeding competition (an indirect cost) (Dunbar 1996). However, across species, the amount of intra-group competition varies spatially and temporally depending on diet and resource distribution. Contrary to conventional assumptions, large groups do not themselves guarantee lower levels of individual predation risk from all potential predators. Yet, when predation risk for individual species is considered as the

accumulation of predation pressure over all predators, increasing group size does appear to have a negative impact on realized predation rates. This emergent pattern is best seen by identifying those particular predators that a prey species is vulnerable to rather than assuming a general relationship between group size and predation risk over all predator–prey combinations.

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