Large body and small brain and group sizes are associated with predator preferences for mammalian prey

Susanne Shultz\textsuperscript{a,b} and Laura V. Finlayson\textsuperscript{b}

\textsuperscript{a}Institute of Cognitive and Evolutionary Anthropology, University of Oxford, 64 Banbury Road, Oxford OX2 6PN, UK and \textsuperscript{b}School of Biological Sciences, University of Liverpool, Liverpool L69 7ZB, UK

Predation is a major force in shaping biological communities, both over ecological and evolutionary timescales. In response to predation pressure, prey have evolved characteristics designed to mitigate predation pressure. We evaluated predator foraging biases in relation to prey characteristics across 16 vertebrate communities. We show that although predator biases vary, some prey traits are consistently associated with predator diet composition. Within their acceptable prey size range, predators show positive bias toward larger bodied prey, small-brained prey (controlling for body size), small group size, and terrestriality. Thus, whether predator foraging decisions are passive or active, predator choice exerts differential pressure on prey species according to prey characteristics. Predator biases also were positively associated with early age at maturity, supporting the role of mortality in driving life-history characteristics. These results support several theoretical models of predation including its role as a selective force driving evolutionary changes in life history, brain size and sociality, optimal diet theory, and antiapostatic predation. Key words: encephalization, foraging ratio, predation, sociality, selectivity, wild dogs. [Behav Ecol 21:1073–1079 (2010)]

Predation is a key driver of biological systems over both ecological and evolutionary time. Over ecological timescales, predation plays roles in regulating population dynamics (e.g., Krebs et al. 1995; Korpimäki and Norrdahl 1998) and community richness and composition (Haitson et al. 1960; Paine 1980). Over evolutionary timescales, predation pressure selects for major morphological and behavioral adaptations (Dawkins and Krebs 1979; Caro 2005). Thus, prey characteristics associated with differential predation pressure should both be important in shaping community structure as well as ultimately influencing long-term evolutionary trends in prey morphology and behavior. Apart from selection for anti-predator traits, extrinsic mortality drives life-history strategies, such that high mortality rates are associated with early maturity and high reproductive rates (Charnov 1993). Thus, behavioral and morphological characteristics that impact on realized mortality will have knock on consequences for species life-history strategies.

Prey employ a wide arsenal of morphological, chemical, life-history and behavioral traits in response to predation, which are assumed to effectively reduce mortality rates. Behavioral strategies that prey use to mitigate predation risk include increasing vigilance, refuge use, altering activity patterns, and trade-offs in resource patch decisions (reviewed in Lima 1998). Aggregation also reduces predation risk, either to the benefit of dilution, confusion, early warning, and coordinated defense (Pulliam 1973). A vast literature has documented grouping responses to predation risk (Lima 1998). Individuals in smaller groups increase investment in antipredator behavior, and group size has been shown to change in response to high predation risk (e.g., Whitfield 1988).

A more general facultative trait that could allow prey to reduce predator capture success is behavioral flexibility. In the wider literature, brain size has often been used as a proxy for cognitive capacity (and hence of behavioral flexibility). Behavioral flexibility and innovativeness are usually presented in ecological terms: larger brained individuals/species will be better able to employ novel resources (e.g., Lefebvre et al. 1997) and respond to ecological change (Shultz et al. 2005; Sol et al. 2005) and lower mortality rates (Sol et al. 2007). However, behavioral flexibility may also provide prey species with adaptive and unpredictable anti-predator responses. In fact, Jerison (1973) originally proposed the evolutionary trend toward larger relative brain size across ungulates and carnivores to be the result of a predator–prey coevolutionary arms race. An inverse correlation between relative prey brain size and predator diet composition has been demonstrated in a limited selection of Afrotropical vertebrate predator communities (Shultz and Dunbar 2006).

Predators, however, are not passive participants in their relationship with prey and should show biases for profitable and vulnerable prey. These choices can either be active, where predators preferentially search for specific prey items, or passive, where biases result from predators being unable to locate, capture, or process certain types of prey items (Sih and Christensen 2001). In either case, the result of biases in predator foraging will result in differential predation pressure on prey individuals. In addition to the prey strategies summarized earlier, vulnerability can be affected by condition, spatial positioning, and variation in morphology/behavior across age/stage classes (Lima 1998; Quinn and Cresswell 2004). An example of spatial positioning is habitat use by both predators and prey. A terrestrial predator will encounter more terrestrial prey than arboreal species, resulting in a passive bias due to encounter frequency. A few studies have demonstrated an association between prey vulnerability and individual predation risk (e.g., Cresswell 1994, see also Lima 1998; Quinn and Cresswell 2004). In addition to vulnerability, optimal diet
theory (ODT) also predicts that predators should select prey based on their profitability because predators have to expend energy capturing prey; they should prefer those that offer the highest net returns (Emlen 1966; Krebs et al. 1977).

Despite the wide-ranging literature that documents prey behavior and decision making under predation risk, the evidence that evaluates predator foraging decisions in relation to prey characteristics is more limited (Lima 2002). A few studies have documented predator attack rates on prey groups of different sizes in experimental systems, but the connection between attack and capture rates does not appear to be straightforward (Turchin and Karieva 1989; Krause and Godin 1995). Although captive studies are informative about predator foraging decisions, they are unable to accurately reflect the choices and conditions predators face in wild populations (Lima 1998). The data relating predator foraging to prey behavior from wild populations are more limited (e.g., Lindstrom 1989; Cresswell 1994; Hebbelwhite and Pletscher 2002). However, most of these studies focus on single communities or predator species. Some studies have evaluated predator foraging decisions using preferences derived from the ratio of species in the diet to that in the environment. Götmark and Post (1996) used spearthrow ratios to demonstrate a link between prey exposure and habitat use and predation risk in passerines. Götmark and Andersson (2005) later demonstrated that predation rates are inversely related to breeding aggregation size in great tits. Shultz et al. (2004) used a community-level approach to evaluate relative predation risk over a suite of predator and prey species and showed that high predation risk is associated with terrestriality and small group size.

Apart from differences in prey defense and vulnerability, a wide literature suggests that foraging predators select prey based on their encounter frequency or relative abundance (Pulliam 1974; Van Orsdel 1984). Searching predators are expected to show apostatic predation or biases toward the most abundant prey types (Murdoch 1969). Apostatic predation has been proposed as a primary mechanism for promoting the maintenance of polymorphisms and species richness in a prey community (e.g., Sherratt and Harvey 1993). Although there still is not widespread evidence for apostatic predation in natural populations, positive frequency-dependent selection has been demonstrated in a number of experimental and natural systems (Allen and Greenwood 1988; Bond and Kamil 1998; Bond 2007). In contrast, in antipostatic predation, predators preferentially prey on rare or distinctive prey types (Pielowski 1961; Bond 1983). Much of the evidence supporting frequency-dependent selection by predators comes from foraging experiments using passive or immobile prey; however, predator choice has been shown to be very different when predators are utilizing mobile prey (Sih and Christensen 2001).

Terrestrial mammalian predators offer an ideal system to examine commonalities across population in how prey characteristics relate to predator foraging biases. Within populations, considerable work has been done on foraging behavior. For example, wild dogs (Lycaon pictus) show seasonal biases toward temporally abundant prey and large-bodied prey (Kruger et al. 1999; Pole et al. 2004), lions show preferences toward small groups and profitable prey (Scheel 1993), and tigers selectivity choose large-bodied prey (Karanth and Sunquist 1995). Such studies do much to illuminate our understanding of the short-term interactions between predators and prey. However, there has to date, been no systematic evaluation of cross-community patterns of predator foraging choices.

Here, we utilize a range of studies that have been completed on vertebrate predators to extend the approach used in Shultz and Dunbar (2006). We provide the first broad evaluation of the relationship between prey behavioral and ecological characteristics and predator diet composition at the population level. We compiled diet and community composition data from terrestrial communities. We predicted the following:

1. According to ODT, predators should prefer larger prey across their suite of prey species.
2. Prey in smaller groups should be preferred to those in larger groups.
3. Predators should show apostatic selection and show biases toward abundant prey.
4. Terrestrial predator diets will be biased toward terrestrial prey.
5. If brain size is a proxy for behavioral flexibility, relatively large-brained prey should be less preferred than small-brained prey.
6. If life history is a derivative of mortality rates, predator biases should be associated with faster life-history strategies (i.e., earlier age at first reproduction).

MATERIALS AND METHODS

The predator diet composition data were collected from reliable sources providing concurrent diet and community composition estimates (see Table 1 for data and sources). Although there are many more studies than we have included on mammalian predator foraging behavior, we were only able to include those studies that had a contemporary estimate of prey density. The communities included savannah, temperate rainforest, and alpine habitats, encompassing data from 3 canids (dhole [Cuon alpinus]; wild dog [L. pictus], and wolf [Canis lupus]), 6 felids (leopard [Panthero pardus], golden cat [Felis aurata], tiger [P. tigris tigris], jaguar [P. onca], puma [F. concolor], and ocelot [F. pardalis]), and chimpanzees (Pan troglodytes). As we were unable to collate information on population density for all possible prey species, the data set contains a subsample of total available prey species. Likewise, it is not possible to determine which species that do not occur in the diet are potential prey and which are not. We assume that the omitted species do not share characteristics that would bias the analyses. For analyses, we aggregated predators into type: chimpanzee, canid, feline felids, and tigers. In total, we compiled data from 16 terrestrial communities, incorporating 9 species of predators, 47 species of prey, resulting in a total of 131 data points.

The prey characteristics we evaluated were body size, brain size, group size, population density, habitat use, and strata use (see Supplementary Materials for data and sources). We also evaluated the relationship between predator biases and prey life history using age at first reproduction. All data were checked for normality and transformed where necessary: In the analyses, we used log10 (body size), log10 (brain size), ln (geometric mean of reported group size range), and log10 (population density).

To evaluate the relationship between predator biases and prey brain size, we have used a different approach to that in Shultz and Dunbar (2006). Rather than calculating a relative brain size via regression residuals, we have incorporated both brain and body size in models to evaluate whether there is an independent effect of each variable on predator foraging biases. The rationale behind this is that the calculation of residuals is fraught with criticism, as a least squares regression underestimates slopes and the complement of species used in the regression biases the resulting residuals (also potentially introducing phylogenetic confounds) (Freckleton 2002). Additionally, calculating brain size residuals over a wide group of distantly related taxa will inevitably introduce scaling and ontogenetic confounds (Deacon 1990). However, for comparison, we also used residual brain size calculated from a major axis regression and reran the analyses (see Supplementary Materials).
Table 1
SOURCES STUDIES AND SPECIES

<table>
<thead>
<tr>
<th>Predator</th>
<th>Site</th>
<th>Source</th>
<th>(\chi^2)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chimpanzee</td>
<td>Mahale</td>
<td>Nishida et al. (1992) **</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Kibale</td>
<td>Mitani and Watts (1999) **</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Tai</td>
<td>Boesch and Boesch-Achermann (2000) **</td>
<td></td>
</tr>
<tr>
<td>Forest felids</td>
<td>Jaguar, puma, ocelot</td>
<td>Leo</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Leopard</td>
<td>Emmons (1987) **</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Nagarhole</td>
<td>Karanth and Sunquist (1995) **</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Bandipur</td>
<td>Johnsingh (1983, 1992) NS</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Serengti</td>
<td>Schaller (1972) **</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Tai</td>
<td>Zuberbühler and Jenny (2002) **</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Leopard, golden cat</td>
<td>Ituri</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Hart et al. (1996) **</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tiger</td>
<td>Bandipur</td>
<td>Johnsingh (1983) **</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Nagarhole</td>
<td>Karanth and Sunquist (1995) **</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Pench</td>
<td>Bissas and Sankar (2002) **</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Ranthambore</td>
<td>Bagchi et al. (2003) **</td>
<td></td>
</tr>
</tbody>
</table>

Canids

<table>
<thead>
<tr>
<th>Predator</th>
<th>Site</th>
<th>Source</th>
<th>(\chi^2)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dhole</td>
<td>Bandipur</td>
<td>Johnsingh (1983) **</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Nagarhole</td>
<td>Karanth and Sunquist (1995) **</td>
<td></td>
</tr>
<tr>
<td>Wolf</td>
<td>Poland BN</td>
<td>Jedrzejewski et al. (1992)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Banff</td>
<td>Huggard (1993) *</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Alps</td>
<td>Gazzola et al. (2005) *</td>
<td></td>
</tr>
<tr>
<td>Wild dog</td>
<td>Selous</td>
<td>Creel and Creel (2002) NS</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Serengeti</td>
<td>Schaller (1972) **</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Savé</td>
<td>Pole et al. (2004) **</td>
<td></td>
</tr>
</tbody>
</table>

NS, not significant. \(\chi^2\) term indicates whether prey selection differed significantly from random.

\(\ast P < 0.05, \ast\ast P < 0.01\)

If a predator is truly opportunistic, the most abundant prey will also be the most abundant item in the diet. Thus, to determine whether predators are utilizing prey disproportionately to their abundance, we calculated a standardized forage ratio. Prey occurrence in the diet and abundance in the environment were used to calculate selectivity (bias) for each prey species, then standardized to allow for value distribution between 0 and 1 using the following calculation (from Manly et al. 1993):

\[
\text{Standard forage ratio } : B_i = \frac{\hat{w}_i}{\sum_{i=1}^{n} \hat{w}_i},
\]

where \(\hat{w}_i = \frac{p_i}{n}\) and \(\hat{w}_i = \text{forage ratio for species } i\)

\(\alpha_i = \text{Proportion of species } i \text{ in diet}\)

\(p_i = \text{proportion of species } i \text{ available in the environment}\)

An equal proportion of prey in the diet and the community indicates no bias toward or against a species. To normalize the standardized ratios, they were arcsin and square root transformed for all analyses. Where we refer to preferences, we do not infer active choice by the predators; we simply indicate a positive bias.

To determine whether predators’ diets were more selective than random, we used equation of Manly et al. (1993):

\[
x^2 = 2 \sum_{i=1}^{n} u_i \ln \left( \frac{\hat{w}_i}{U_i} \right),
\]

where \(n\) 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.

To evaluate the association between selectivity and prey characteristics, we then used a 2-pronged analytical approach. First, we correlated prey characteristics with selectivity across each predator type. Second, we used stepwise information criteria (Akaike’s Information Criterion [AIC]) to select the best-performing model relating to predator diet composition (step.aic command in R package MASS). We ran the model selection procedure twice, once with and once without interactions.

Although it is possible that related predators show similar preferences for prey characteristics, the nature of the data (with nested prey within predator types) is not amenable to conventional phylogenetic analyses. Additionally, we assume that predator diet choices are determined by prey characteristics, not by the degree of relatedness between prey species, effectively rendering prey-independent data points.

RESULTS

We first correlated predator selectivity with prey characteristics (Table 2). Residual brain size was negatively correlated across all predator types except for tigers. Likewise, there was a negative correlation between selectivity and age at first reproduction for all predators except tigers. Body size was positively correlated with selectivity for forest felids and tigers. Both of these predator types also showed a bias toward rare prey species. All predators except for chimpanzees were biased toward terrestrial prey. Canids and tigers both showed a bias toward prey in smaller groups.

We then used AIC stepwise model selection to identify the best-performing model (Table 3). For the main effects model, body size, brain size, group size, and strata use were retained in the best-performing model. Predator selectivity was positively associated with body size and negatively associated with brain size and group size. Predators showed an overall bias toward terrestrial prey. For the model selection including interactions, the best-performing model retained all the main effects of the first model but additionally included interaction terms between predator type and each prey characteristic (Tables 4 and 5). The interaction between predator type and brain size and group size are shown in Figure 1. Chimpanzees are strongly biased toward small brain prey, whereas tigers are less influenced by prey brain size. Chimpanzees showed the least effect of group size on selectivity (the overall effect across predators was negative, the apparently positive effect in Figure 1a is relative to the canid baseline).

We reran the model selection procedure with relative brain size and obtained very similar results (see Supplementary Materials). We also include correlations and minimum adequate models for individual predators in the Supplementary Materials.

Prey behavior

In order to understand the variation in biases across predators, we evaluated the influence of habitat type on the relationship between prey characteristics and predator biases (Table 6). For open habitat species, group size and population density were negatively correlated with predator bias. In closed habitats, predator bias was positively associated with body size and negatively associated with brain size. For mixed habitats, predator bias also was positively associated with body size and negatively associated with brain size and group size. Prey behavior varied across habitats. In open habitats, large-bodied animals gathered in larger groups than small-bodied prey in the same.
environment (Pearson’s $r = 0.51, n = 15, P = 0.03$). In contrast, in closed habitats, small-bodied species were in larger groups ($r = -0.24, n = 79, P = 0.03$). Overall group size was highest in open habitats, intermediate in mixed habitats, and lowest in closed habitats ($F_{2,127} = 17.24, P < 0.001$; Figure 2).

We compared predator biases with female age at first reproduction to see whether those species that are being particularly heavily hit by predation tend to have “faster” life-history strategies. There was a significant negative correlation between age at maturity and predator bias (Table 2) such that “preferred” prey reach sexual maturity earlier than nonpreferred prey.

### DISCUSSION

Our results suggest that some prey characteristics are consistently associated with predator biases, including relatively larger body size, small brain size, terrestriality, and small group size. The prey characteristics associated with biases in diets varied across predators, leading to an interaction between prey traits and predation risk across predator species. Thus, to fully understand the predation pressure exerted on a prey species, it is necessary to consider the impact of multiple predators (Sih et al. 1998; Shultz et al. 2004) as the cumulative predation rate from all predators will determine the overall mortality rate experienced by a prey species.

A few caveats need to be made with the analyses presented. First, the data that we have compiled are by their very nature noisy as there is measurement error in both diet composition and population density data. We would, however, expect that the noise introduced by such measurement error would obscure relationships between prey characteristics and predator foraging biases rather than creating them. Second, we have used a small subset of prey characteristics. We do not doubt that there are additional characteristics such as flight speed, morphological traits such as defenses, or coloration that impact on predator choices. However, the traits we have used here explain considerable variation in predator diet composition.

Third, we acknowledge that there is variation within populations, both between individual predators and across time. However, as this study is the first attempt to construct a cross-population evaluation of the relationship between prey characteristics and predator diet composition, we believe that it provides valuable insight into evolutionary trends in predator–prey systems.

Most predators were biased toward larger bodied prey within their suite of prey species. This does not necessarily lead to the largest prey suffering the highest predation rates, as each predator exploited a different suite of prey body sizes. This bias toward large-bodied prey is consistent with ODT as the profitability of a prey individual increases with body size (Emlen 1966). That our data support ODT is interesting as across studies, support for ODT where prey are mobile has been equivocal (Sih and Christensen 2001). Our data also suggest that group-hunting predators (wolves and wild dogs) were able to exploit the largest and most profitable prey classes, which suggests that cooperative hunting may allow (or force) predators to utilize more profitable prey. However, these cooperative hunting species did not show biases toward the largest prey items within their range of utilized prey species.

The consistent negative association between group size and selectivity indicates that group living provides antipredator benefits at the population level. Prey have limited ability of a prey individual increases with body size (Emlen 1966). That our data support ODT is interesting as across studies, support for ODT where prey are mobile has been equivocal (Sih and Christensen 2001). Our data also suggest that group-hunting predators (wolves and wild dogs) were able to exploit the largest and most profitable prey classes, which suggests that cooperative hunting may allow (or force) predators to utilize more profitable prey. However, these cooperative hunting species did not show biases toward the largest prey items within their range of utilized prey species.
different group size within species. This has been shown in a few experimental systems (Krause and Godin 1995) and wild populations (Lindstrom 1989; Cresswell 1994). Given the cross-population nature of these analyses, it was not possible to evaluate the impact of prey group size within populations. Charnov (1993) proposed that life-history strategies, and reproductive rates in particular, are driven by mortality rates. Under high mortality, individuals should mature faster and reproduce earlier than where mortality rates are low. Our results are consistent with this proposal as predator biases were associated with early age at maturity. It is likely that predators are differentially preying on juveniles as they are more vulnerable. Thus, species may mature early to minimize the time spent in vulnerable age classes. However, we do not have information on age/stage biases in these predators.

Large relative brain size was consistently associated with negative biases by predators. Thus, these results support Jerison’s (1973) conjecture that the evolutionary trend toward larger brains in prey species may be the result of a co-evolutionary drive between predators and prey. Given that brain and body size appear to be strongly associated with predator diet choices, why do not all prey have relatively small body size and large brain size? The variation in body size biases shown by different predators indicates that there is unlikely to be an optimal body size that minimizes overall predation rates (except when body size is large enough to fall outside all/most predator body size ranges). Growing a large brain is a trickier proposition. Not only is it metabolically costly to invest in cognitive architecture but large brain size is also associated with a slowing down of maturation and first reproduction (Western 1979; Eisenberg and Wilson 1981; Isler and van Schaik 2009). Thus, life-history trade-offs, phylogenetic constraint, and multiple adaptive peaks result in some species opting out of a costly strategy and instead adopting alternative “fast” life-history strategies. In other words, species that have “cheap” behavioral characteristics are better off investing in maturing quickly and maximizing reproductive rates rather than maturing late and emphasizing survival. That small-brained species are associated with positive predator bias, which should consequently result in higher predation/mortality rates, is consistent with Sol et al. (2007), who demonstrated that large-brained bird species suffer lower mortality rates than smaller brained species. Thus, predation, in addition to other environmental factors, could be a mechanism for the differential mortality they reported.

Although there were relationships between prey characteristics and selectivity, the strength of the relationships varied across predators. For example, although tigers showed significant biases toward terrestrial, large-bodied, and low-density prey, they did not appear to show any bias toward small-brained prey. The positive correlation between total brain size and selectivity is an artifact of body size effects as there was no relationship between residual brain size and selectivity. Conversely, canids, chimpanzees, and felids all showed biases toward small-brained prey. Canids also appear to be biased by prey group size and strata use and felids by population density and strata, whereas chimpanzees appear to be less influenced by other characteristics. Chimpanzees are very different from the other predators in that they are not obligate carnivores; vertebrate prey compose a seasonally variable (and minor) component of their overall diet. Thus, they may make decisions about prey choice using different criteria than the other predators. What these results do tell us is that predators key into prey characteristics differently, and any given antipredator strategy may not be effective against all predators.

**Table 5**

Coefficients and effects on model performance for main factors in best performing model with interactions

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Coefficient</th>
<th>Standard error</th>
<th>T</th>
<th>P</th>
<th>ΔAIC</th>
</tr>
</thead>
<tbody>
<tr>
<td>Brain size</td>
<td>-0.40</td>
<td>0.25</td>
<td>-1.73</td>
<td>0.09</td>
<td>20.4</td>
</tr>
<tr>
<td>Body size</td>
<td>0.17</td>
<td>0.15</td>
<td>1.14</td>
<td>0.26</td>
<td>12.44</td>
</tr>
<tr>
<td>Predator</td>
<td>-0.35</td>
<td>0.15</td>
<td>-2.35</td>
<td>0.02</td>
<td>9.98</td>
</tr>
<tr>
<td>Predator × brain size</td>
<td>-0.35</td>
<td>0.15</td>
<td>-2.35</td>
<td>0.02</td>
<td>9.98</td>
</tr>
<tr>
<td>Predator × body size</td>
<td>0.40</td>
<td>0.23</td>
<td>1.73</td>
<td>0.09</td>
<td>17.48</td>
</tr>
<tr>
<td>Predator × group size</td>
<td>0.40</td>
<td>0.23</td>
<td>1.73</td>
<td>0.09</td>
<td>17.48</td>
</tr>
<tr>
<td>Group size</td>
<td>-0.07</td>
<td>0.02</td>
<td>-2.75</td>
<td>0.01</td>
<td>4.08</td>
</tr>
<tr>
<td>Strata × predator</td>
<td>2.12</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Change in AIC calculated by sequentially dropping each main factor and associated interaction terms from model.

**Figure 1**

The relationship between (a) brain size and (b) group size across predator types and selectivity. Overall species, there are negative associations between both group size and brain size and selectivity, but the strength of the effect varies across predators. Canids are the baseline for both analyses (tigers: dark solid line, chimpanzees: light solid line, canids: large dashes, and felids: small dashes).

**Table 6**

Minimum adequate models for predator biases across the 3 habitat types

<table>
<thead>
<tr>
<th>Habitat</th>
<th>Factor</th>
<th>Degrees of freedom</th>
<th>B</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Open</td>
<td>Site</td>
<td>3, 8</td>
<td>0.40</td>
<td>0.76</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Predator</td>
<td>1, 8</td>
<td>0.45</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Group size</td>
<td>1, 8</td>
<td>-0.20</td>
<td>14.75</td>
<td>0.005</td>
</tr>
<tr>
<td></td>
<td>Population density</td>
<td>1, 8</td>
<td>-0.19</td>
<td>7.01</td>
<td>0.03</td>
</tr>
<tr>
<td>Mixed</td>
<td>Site</td>
<td>11, 19</td>
<td>1.96</td>
<td>0.10</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Predator</td>
<td>2, 19</td>
<td>0.43</td>
<td>0.66</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Body size</td>
<td>1, 19</td>
<td>0.46</td>
<td>12.29</td>
<td>0.002</td>
</tr>
<tr>
<td></td>
<td>Brain size</td>
<td>1, 19</td>
<td>-0.51</td>
<td>7.66</td>
<td>0.012</td>
</tr>
<tr>
<td></td>
<td>Group size</td>
<td>1, 19</td>
<td>-0.05</td>
<td>5.55</td>
<td>0.03</td>
</tr>
<tr>
<td>Closed</td>
<td>Predator</td>
<td>3, 61</td>
<td>0.17</td>
<td>0.92</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Body size</td>
<td>1, 61</td>
<td>0.52</td>
<td>25.56</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>Brain size</td>
<td>1, 61</td>
<td>-0.67</td>
<td>13.01</td>
<td>0.001</td>
</tr>
</tbody>
</table>
Brain size was negatively associated with predator biases in mixed and closed habitats, whereas group size was negatively associated with predator biases in open habitats. In complex mosaic habitats, a variety of potential escape strategies (e.g., refuge use, flight, crypsis) is likely to be of more benefit than in open habitats where the options would be limited to fleeing or safety in numbers. In open habitats, small-bodied species tended to gather in smaller groups than larger bodied species, even though group size was negatively associated with predator biases. There are several potential explanations for this behavior. The first is that the smaller bodied gazelles use mixed-species associations to augment group size (Fitzgibbon 1990b); thus, the average number of conspecific individuals within a group may not accurately reflect total group size. The second is that smaller bodied species are cryptic or restrict their habitat use to areas closer to cover, especially around calving where their young use “prone” responses by hiding in vegetation (Fitzgibbon 1990a). In contrast, larger bodied species are more likely to use open spaces and adopt communal defense against predators (especially in terms of protecting young) (Jarman 1974; Caro et al. 2004). For overall models, terrestrial strata use was associated with higher predator foraging biases than arboreal strata use. However, changing strata use to avoid the risks of terrestrial predators is an option for few of the prey species in our database (mainly primates).

Given the vast literature on predator-switching behavior, we predicted that predators might show biases toward the most common prey species as they would have the highest encounter rates. Although the most common prey species are the most abundant in the predator diets, we calculated selection based on relative abundance in the diet. Using this metric, our results did not demonstrate a consistent bias toward or against prey species relative to their abundance. In open habitats, predators appeared to show antiapostatic biases toward rarer species.

This is the first study to tackle cross-population patterns of mammalian predator selectivity. We provide evidence that a number of factors assumed to be related to predation avoidance (large group size, habitat use, and body size) are related to predator foraging behavior. However, we also demonstrate that predators vary in the characteristics that are associated with prey choice, meaning that to understand prey investment in antipredator behavior, it is necessary to consider the entire predator community; a strategy that works against one predator may not be effective against all. Large brain size is associated with negative predator biases, and this may be especially so for cooperatively hunting predators. Finally, we suggest that trade-offs between longevity and reproductive rates may be partially driven by brain size, whereby cognitive capacity may help prey evade predators, but it comes at a cost of low reproductive rates. We also suggest that population or community perspectives are key to understanding the impact of predation on evolutionary and ecological trends.

SUPPLEMENTARY MATERIAL
Supplementary material can be found at http://www.beheco.oxfordjournals.org/.

REFERENCES


Cresswell W. 1994. Flocking is an effective anti-predation strategy in redshanks, Tringa totanus. Anim Behav. 47:433–442.


