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# Chimpanzee and felid diet composition is influenced by prey brain size

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**Prey use a wide variety of anti-predator defence strategies, including morphological and chemical defences as well as behavioural traits (risk-modulated habitat use, changes in activity patterns, foraging decisions and group living). The critical test of how effective anti-predator strategies are is to relate them to relative indices of mortality across predators. Here, we compare biases in predator diet composition with prey characteristics and show that chimpanzee (*Pan troglodytes*) and felid show the strongest and the most consistent predator bias towards small-brained prey. We propose that large-brained prey are likely to be more effective at evading predators because they can effectively alter their behavioural responses to specific predator encounters. Thus, we provide evidence for the hypothesis that brain size evolution is potentially driven by selection for more sophisticated and behaviourally flexible anti-predator strategies.**

**Keywords:** prey choice; tropical forests; predation risks; hunting strategies

## 1. INTRODUCTION

Where the risk of predation is high (but mortality not inevitable), incurring the costs of increased defence can, on balance, increase the fitness of individuals relative to less defended individuals. Prey defence strategies include a wide variety of morphological and behavioural traits (reviewed by Caro 2005). Long-lived species are expected to invest in facultative or conditional defences that are appropriate for the varying environmental conditions which they will encounter over their lifetimes; these can include risk-modulated habitat use, activity patterns and foraging decisions, as well as group living (Lima 1998).

Investing an appropriate amount of resources in effective anti-predator strategies should have positive fitness consequences for prey individuals. Efficiently allocating time and resources to anti-predator behaviour will positively impact overall energy budgets for individuals (Lima & Dill 1990). Additionally, a behaviour that is effective at deterring or avoiding one predator species may not be most effective for other predators; prey must decide which behaviour to adopt for specific predator encounters (Cresswell 1993). The complexity and accuracy of decision-making available to a prey individual should be a function of its capacity to integrate information.

Since relative brain size is assumed to be a valid proxy for cognitive capacity and behavioural flexibility (Jerison 1973), we test the hypothesis that predators will show biases against relatively large-brained prey as compared to small-brained prey. We additionally evaluate the importance of several potentially confounding factors. Predation is widely considered to be a major selective force driving the evolution of sociality in vertebrates, and individuals that live in large groups are expected to experience reduced predation risk. We have shown in an earlier study (Shultz *et al.* 2004) that prey group size is negatively correlated with experienced predation rates in Taï National Park, Cote d'Ivoire. In this analysis, we also showed that for some predators, small body size and terrestriality were associated with prey vulnerability (Shultz *et al.* 2004). Thus, we evaluate the association between brain size, body size, group size and strata use and biases in predator diet composition.

## 2. MATERIAL AND METHODS

Data were compiled from predator diets and prey characteristics in five forest communities in two continents: Taï National Park (Côte d'Ivoire, West Africa), Ituri forest (Democratic Republic of Congo), Mahale National Park (Tanzania), Kibale National Park (Uganda) and Manu National Park (Peru). See electronic supplementary material for details and data sources. These communities were chosen because high-quality data were available for both predators' diets and prey community composition. Strata use was defined as a dichotomous variable based on whether species are primarily arboreal or terrestrial. Prey species were limited to those for which data were available for both predation rates and overall population density and those composed of at least 1% of the prey community.

To determine whether predators showed biases towards or against individual prey species, we compared the relative diet composition of each predator with the null hypothesis that prey should appear in the diet in the same proportions as they occur in the habitat. As the ratio of proportion in diet to proportion in the community can vary between zero and infinity, Manly *et al.* (1993) suggested that values should be standardized to fall between 0 and 1; thus, standardized indices of predator bias were calculated using the following formula:

$$\text{standardized forage ratio}: \; B_i = \frac{\hat{w}_i}{\sum_{i=1}^{n} \hat{w}_i}, \quad \text{where } \hat{w}_i = \frac{o_i}{p_i},$$

where $\hat{w}_i$ is the forage ratio of species $i$; $O_i$, the proportion of species $i$ in diet; and $p_i$, the proportion of species $i$ available in the environment. The standardized ratios were then arcsine transformed for all the parametric analyses.

Relative brain sizes were calculated by taking the residuals from a reduced major axis (RMA) regression of log brain size against log body size from a dataset of 206 species of primates, ungulates and carnivores. RMA is the most accurate method of estimating a relationship between two variables that have measurement error, as in this case (Rayner 1985).

As opinions currently differ on which methods are most appropriate for model selection in analyses of this kind (Johnson & Omland 2004), we used a twofold approach to identify the characteristics associated with biases in predator diets. Initially, we evaluated whether predator biases towards different prey species were related to prey brain size across all six datasets using Pearson's correlation test and identified minimum adequate models (MAMs) for each site using forward and backward stepwise selection. As our sample sizes, and consequently statistical power, were low, we report all models where parameters reached an alpha level of 0.10. As an alternative, we used an information theoretic approach (BIC, Schwartz's Bayesian information criteria for small sample sizes; Burnham & Anderson 2002) to identify the model that provided the best fit to the data. In order to construct appropriate *a priori* models for BIC analysis, a global model was identified that included site as random factors, and predator type, strata, brain size, group size and body size as fixed factors. The relative weight of evidence for each candidate model was calculated using the following equation: $w_i = \exp(-1/2\Delta_i / \sum \exp(-1/2\Delta_i))$, where $\Delta_i$ is the change in support between the best model (lowest Akaike's

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information criterion) and each alternative model. The relative importance of each factor was calculated by summing the relative weight of all models that included the factor.

## 3. RESULTS

Figure 1 plots prey selection ratios for individual prey species as a function of the species' relative brain volume for two predators from three populations each. Simple bivariate analyses show that predator diet biases were negatively associated with increasing prey brain size across the six sites (Pearson's correlations, felids: Ituri $r=-0.79$ ($p=0.001$, $n=13$), Taï $r=-0.67$ ($p=0.05$, $n=9$), Manu $r=-0.57$ ($p=0.11$, $n=9$); chimpanzees: Mahle $r=-0.88$ ($p=0.02$, $n=6$), Tai $r=-0.94$ ($p=0.001$, $n=7$), Kibale $r=-0.64$ ($p=0.12$, $n=7$)). We then used Fisher's procedure for combining independent tests (Sokal & Rohlf 1995), which indicates that the probability of all tests randomly showing the above trends is very low ($\chi^2=42.87$, d.f.$=2\times6$ tests $=12$, $p<0.001$).

Minimum adequate model analysis consistently identifies brain size and strata use as significant factors influencing predator biases across the sites. Brain size was selected for all populations (table 1), whereas strata use was selected for all populations with the exception of Mahale. By contrast, group size was selected only for Taï chimpanzees (*Pan troglodytes*). Body size was not identified as a significant factor in any of the MAMs. An overall analysis across sites indicated that there was a negative relationship between brain size and predator bias, a weak positive relationship between predator bias and body size and a strong interaction between strata use and predator. This last result stems from the fact that chimpanzees show no bias for prey strata use over all sites (arboreal mean 0.26±s.e. 0.06, $n=13$; terrestrial 0.23±s.e. 0.08, $n=7$; $F_{1,18}=0.07$, $p=0.80$), whereas felids show a strong bias towards terrestrial prey (arboreal mean 0.14±s.e. 0.02, $n=16$; terrestrial 0.37±s.e. 0.03, $n=15$; $F_{1,29}=41.96$, $p<0.001$).

BIC approach allows us to evaluate the relative importance of these factors by comparing Akaike weightings (table 2). Site was incorporated into all models as a random factor, as any difference in mean predator bias may be an artefact of sample size differences (predator biases were standardized between 0 and 1). As there was a significant interaction between predators and strata use, we incorporated these terms *en masse* into the information criteria model selection process (i.e. predator, strata and predator×strata). The support was strongest for all models incorporating brain size (table 2). It was not possible to select between the two best models (brain+strata×predator+body versus brain+strata×predator), as each had a combined weighting of 0.75 and performed much better than any other model (table 2). In descending order, the most important factor was brain size (summed model weights =0.99), then strata×predator (0.77), body size (0.61) and, finally, group size (0.04). Thus, brain size was consistently chosen as a significant predictor using univariate, MAMs and information criterion.

One of the driving factors behind the results was the relatively strong effects of biases against primate species. Across sites, primates were less preferred than non-primates (two-way ANOVA on arcsine predator bias: primate $F_{1,45}=28.01$, $p<0.001$; site $F_{4,45}=4.67$, $p=0.003$). Additionally, among all the prey species considered, primate brain residuals were larger than non-primates (primates 0.014±0.11; non-primates 0.025±0.10). This difference between primates and other prey taxa is not simply a taxonomic effect; if primates are analysed on their own, then the relationship between brain size and predator bias remains significant ($F_{1,30}=8.40$, $p=0.007$).

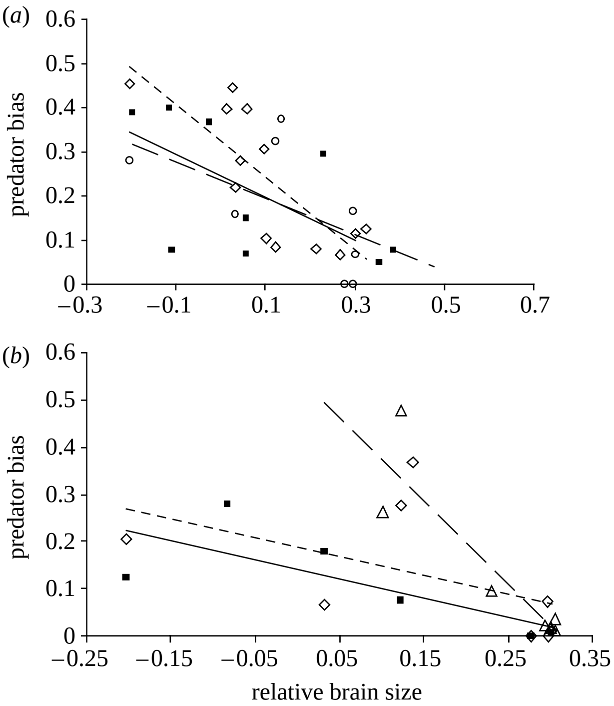

Figure 1. The relationship between prey brain size and biases in predator diets for (*a*) felids (diamonds, Ituri; squares, Manu; circles, Taï) and (*b*) chimpanzees (diamonds, Kibale; squares, Mahale; triangles, Taï). The prey selection ratios are shown that represent a normalized ratio of the proportion of each species in a predator's diet over their proportion in the prey community.

## 4. DISCUSSION

Relative brain size was selected as the most important predictor of biases in predator diets in all three statistical approaches. The data that we present thus provide direct evidence for a link between brain size and predation by mammalian predators in tropical forests. Body size, prey strata use and group size also appear to predict biases in predator diet composition, albeit less significantly and consistently than the relative brain size.

Although the measure of vulnerability in this study (cognitive capacity) is very different from previous studies, these results mirror previous findings that predators are influenced by prey vulnerability (Krause & Godin 1995; Quinn & Cresswell 2004). However, it is important to appreciate that this analysis approaches the problem from the perspective of the contents of predators' diets. Foraging predators have a choice of items to incorporate into their diet. The inclusion of any particular prey item may be through a process of

Table 1. Results for predator bias models across all sites. (MAMs identified by forward and backward selection. Near significant results presented for two sites. If non-significant factors are excluded, then no significant model is identified for Kibale, and the MAM for Taï felids retains only strata use.)

| predator | site | parameter | $\beta$ | $F$ (d.f.) | $p$ | power | model adj $r^2$ |
|---|---|---|---|---|---|---|---|
| chimpanzees | Taï | brain size | −1.77 | 32.90 (1,4) | 0.005 | 0.99 | 0.89 |
| | | group size | 0.14 | 25.61 (1,4) | 0.007 | 0.96 | |
| | | strata | | 23.24 (1,4) | 0.009 | 0.94 | |
| | Kibale | brain size | −0.82 | 11.49 (1,5) | 0.02 | 0.77 | 0.58 |
| | | strata | | 5.79 (1,5) | 0.06 | 0.49 | |
| | Mahale | brain size | −0.94 | 14.02 (1,3) | 0.02 | 0.49 | 0.72 |
| felids | Taï | strata | | 15.91 (1,7) | 0.005 | 0.93 | 0.77 |
| | | brain size | −0.50 | 4.60 (1,6) | 0.08 | 0.44 | |
| | Ituri | brain size | −0.52 | 9.74 (1,10) | 0.01 | 0.80 | 0.78 |
| | | strata | −0.12 | 6.40 (1,10) | 0.01 | 0.86 | |
| | Manu National Park | brain size | −0.17 | 11.23 (1,8) | 0.01 | 0.83 | 0.95 |
| | | strata | | 100.05 (1,8) | $<0.001$ | 0.99 | |
| all | | brain size | −0.59 | 26.33 (1,41) | $<0.001$ | 0.99 | 0.64 |
| | | body size | 0.10 | 4.41 (1,41) | 0.04 | 0.54 | |
| | | site | | 6.03 (3,41) | 0.001 | 0.98 | |
| | | predator | | 0.64 (1,41) | 0.43 | 0.12 | |
| | | strata | | 0.01 (1,41) | 0.92 | 0.05 | |
| | | strata × predator | | 15.83 | $<0.001$ | 0.97 | |

Table 2. Model BIC values are used to identify the model with the best fit to the data and to calculate the relative importance of each factor. (Site was included in all models as a random factor. Δ represents the difference between each model and the 'best model'. The calculation of model weights is discussed in the text.)

| model | factors | BIC | Δ | weight |
|---|---|---|---|---|
| 1 | brain, body, strata × predator | −54.27 | 0 | 0.44 |
| 2 | brain, strata × predator | −53.53 | 0.74 | 0.31 |
| 3 | brain, body | −51.93 | 2.34 | 0.14 |
| 4 | brain | −50.06 | 4.21 | 0.05 |
| 5 | brain, strata × predator, group | −48.47 | 5.8 | 0.02 |
| 6 | brain, body, group, strata × predator | −48.46 | 5.81 | 0.02 |
| 7 | brain, group, body | −46.31 | 7.96 | 0.01 |
| 8 | brain, group | −44.35 | 9.92 | $3.11\times10^{-3}$ |
| 9 | body, strata × predator | −35.63 | 18.64 | $3.97\times10^{-5}$ |
| 10 | body | −33.02 | 21.25 | $1.08\times10^{-5}$ |
| 11 | body, group | −32.84 | 21.43 | $9.83\times10^{-6}$ |
| 12 | body, group, strata × predator | −32.09 | 22.18 | $6.76\times10^{-6}$ |
| 13 | strata × predator | −31.59 | 22.68 | $5.26\times10^{-6}$ |
| 14 | strata × predator, group | −26.46 | 27.81 | $4.05\times10^{-7}$ |
| 15 | group | −21.29 | 32.98 | $3.05\times10^{-8}$ |

active choice or may be the result of a successful attack. Conversely, the exclusion, or low frequency of occurrence, of an item in a predator's diet may simply be the result of unsuccessful attacks rather than a proactive decision to avoid a particular prey type.

These results support Charnov's (1993) proposal that predation-driven mortality is an important variable driving life-history evolution. Individuals must either mature early and reproduce before becoming a victim of a predation event or opt for long-term survival, which demands investment in either physical (large body size, or chemical or morphological) or behavioural defence strategies. As behaviour is a particularly labile phenotypic trait (West-Eberhard 1989), we would expect the long-lived individuals to invest in behavioural flexibility. Species (and especially primates) with disproportionately large brains (and high potential flexibility) can learn effective anti-predator strategies during a prolonged dependence period.

From the prey's point of view, the situation may be very different from that of a predator's. Prey species generally live in a multi-predator environment, and the predation rate experienced by them as a population is cumulative over all predator species. Although chimpanzees are important predators of primates, for example, they inflict lower overall predation rates than the other predators of primates in Taï (Shultz *et al.* 2004). The present analyses identify the factors that affect predator diet composition; these may or may not be the factors that are most critical for an individual prey species. To understand how overall mortality owing to predation is related to behavioural characteristics, it is necessary to evaluate the predation rate incurred by all predators in a community. This global picture may be very different from the one that emerges from a predator by predator analysis (Shultz *et al.* 2004).

Across vertebrate taxa, relationships have been demonstrated between relative brain size and sociality (Barton 1996; Dunbar 1998; Shultz & Dunbar 2006) and feeding innovations (Lefebvre *et al.* 1997; Reader & Laland 2002). However, finding a consistent and strong relationship between predator diet composition and prey brain size raises the question of what causal factors are driving increases in brain size. Reduced predation risk, resulting from more complex behavioural decision-making, may provide a functional benefit for large-brained individuals. We might envisage a sequence in which predators selecting for small-brained prey impose a modest selection pressure favouring the evolution of larger brains. As brain size increases, the greater cognitive capacities that result permit more complex socially defined anti-predator strategies (e.g. living in larger and/or more cohesive groups), and this acts as a positive feedback mechanism to drive very rapid coevolution of brain size and group size.

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