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Population ecology

The bigger they come, the harder they fall: body size and prey abundance influence predator–prey ratios

Chris Carbone[1,*], **Nathalie Pettorelli**[1]
and Philip A. Stephens[2]

[1]*Institute of Zoology, Zoological Society of London, Regent's Park, London NW1 4RY, UK*
[2]*School of Biological and Biomedical Sciences, University of Durham, South Road, Durham DH1 3LE, UK*
**Author for correspondence* (*chris.carbone@ioz.ac.uk*).

Large carnivores are highly threatened, yet the processes underlying their population declines are still poorly understood and widely debated. We explored how body mass and prey abundance influence carnivore density using data on 199 populations obtained across multiple sites for 11 carnivore species. We found that relative decreases in prey abundance resulted in a five- to sixfold greater decrease in the largest carnivores compared with the smallest species. We discuss a number of possible causes for this inherent vulnerability, but also explore a possible mechanistic link between predator size, energetics and population processes. Our results have important implications for carnivore ecology and conservation, demonstrating that larger species are particularly vulnerable to anthropogenic threats to their environment, especially those which have an adverse affect on the abundance of their prey.

Keywords: carnivore ecology; predator–prey relationships; abundance scaling; climate change; metabolism

1. INTRODUCTION

It is well recognized that large carnivores are highly threatened, owing to a combination of environmental change, biological factors and human pressures [1,2]. However, the main processes underlying global declines in large carnivores are still widely debated [3]. Body mass and prey abundance are known to influence average abundance across mammalian carnivores [4]. However, there is also evidence that larger carnivore species are rarer than expected based on typical abundance–mass relationships [5,6]. Carnivores are extremely wide ranging, with day ranges two- to threefold that of herbivores of the same size [7] and, across species, exhibit steeper scaling in day range and home range [8–10]. This increase in ranging behaviour would influence individual energetic rates and is consistent with the finding that energetics may place evolutionary constraints on body size in predators [11,12]. Ultimately, size and energetics may be linked with the intrinsic factors identified in a global analysis of the threat status of mammals [13]. The interplay between the environment, body size and the intrinsic factors driving this vulnerability remains poorly understood. Studies that identify causes of changes in species abundance in relation to size and ecology have the potential to greatly improve our understanding of population processes.

In this study, we present an analysis of predator–prey ratios obtained across multiple sites for 11 species of carnivores. We focus on a key environmental factor, food availability (prey abundance), in order to explore whether large carnivores show a greater population response to changes in the relative abundance of their food resources.

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2. MATERIAL AND METHODS

To compare carnivore abundance across species in relation to variation in prey biomass density (enabling a comparison across different species of carnivores that feed on prey of different sizes [4,14]), we explored how the logarithm (base 10) of carnivore density ($\log N$) relates to log carnivore body mass ($\log M$) and log prey biomass density ($\log P$) for 199 predator–prey population estimates obtained from 11 species of carnivores (all with six or more population estimates; table 1; see also the electronic supplementary material). In our data analysis, we compared the explanatory power of four different linear combinations of these predictors using Akaike Information Criterion (AIC) [15,16]. We excluded data on the population densities of two species, the African wild dog (*Lycaon pictus*) and cheetah (*Acinonyx jubatus*), which are known to be poorly related to prey availability, owing to competition with other carnivores [17–20]. Whether or not wild dogs and cheetahs are included, our conclusions remain unaffected and the fitted models remain significant (electronic supplementary material, table S2); here, however, we focus on the results with wild dogs and cheetahs omitted.

Most of the data used in this study were obtained from studies specifically focused on predator–prey relationships for a single carnivore species. Inevitably, the methods used in these studies somewhat varied. In some instances, data on prey density in one year were compared with predator density estimated in the next; in other instances, these data might be matched within the same year [4]. In addition, given the practical difficulties of getting such information, we found that most data were only available from different locations and periods across the species' ranges. Ideally, longitudinal data (from the same populations across years) should be used; nonetheless, we believe that these data have the potential to provide important insights into predator–prey relationships and a general understanding of consumer–resource relationships [21].

3. RESULTS

The model including all predictors ($\log P$, $\log M$ and the interaction between them) explained 68 per cent of the variability in log carnivore densities, enjoying substantially more support than the next best alternative ($\Delta\text{AIC} = 11.24$ between this and the next best model; table 2). This relationship is best described by a linear model of the form $\log N = 1.06 - 1.29 \log M + 0.33 \log P + 0.21 \log M \times \log P$ (all predictors are significant with $p < 0.001$ and the full model is also significant with $F_{3,195} = 140.9$, $p < 0.001$, $r^2 = 0.68$). The coefficients confirm that carnivore densities are negatively affected by body mass and positively affected by prey availability; crucially, the significant interaction term shows that the densities of the larger species of carnivores are disproportionately lower in areas of low prey density. Intriguingly, the slopes of the predator–prey responses seem to increase linearly with log carnivore body mass (figure 1).

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Table 1. Summary of carnivore density and prey biomass density used in this study, obtained from Carbone & Gittleman [4] and additional sources (see the electronic supplementary material); see text for details.

				carnivore density, N (km^{-2})				
species	scientific name	ave. weight (kg)	no. populations	range (min–max)	slope	intercept	r^2	prey biomass, P (kg km^{-2}) range (min–max)
least weasel	*Mustela nivalis*	0.14	7	0.52–80.0	0.1615	3.49	0.02	23.9–832.5
arctic fox	*Alopex lagopus*	3.19	14	0.022–0.286	0.2385	0.0268	0.47	1.0–2810.9
Canadian lynx	*Lynx canadensis*	11.2	28	0.02–0.226	0.4954	0.0047	0.65	16.8–1386.0
European badger	*Meles meles*	13.0	9	0.79–8.4	0.3437	12.74	0.73	352.8–71 400.0
coyote	*Canis latrans*	13.0	19	0.023–0.444	0.508	0.0092	0.21	34.5–1485.0
wolf	*Canis lupus*	46.0	20	0.005–0.042	0.6661	0.0003	0.49	89.0–810.5
leopard	*Panthera pardus*	46.5	19	0.005–0.303	0.5079	0.0025	0.51	13.2–4162.9
spotted hyena	*Crocuta crocuta*	58.6	19	0.005–1.842	0.7733	0.0004	0.52	126.0–17 262.6
lion	*Panthera leo*	142.0	40	0.008–0.52	0.5854	0.0011	0.66	35.0–14 198.4
tiger	*Panthera tigris*	181.0	16	0.006–0.168	0.7352	0.0002	0.72	171.0–5828.6
polar bear	*Ursus maritimus*	310.0	8	0.003–0.021	0.8806	00000.9	0.89	41.8–337.0

Table 2. Models fitted to empirical data on carnivore densities.

fitted model[a]	estimated parameters	AIC	ΔAIC	w	r^2
lm($\log N \sim \log M$)	3	−168.22	168.79	0	0.25
lm($\log N \sim \log P$)	3	−156.90	180.10	0	0.20
lm($\log N \sim \log M + \log P$)	4	−325.76	11.24	0	0.66
lm($\log N \sim \log M \times \log P$)	5	−337.00	0.00	1.00	0.68

[a] Model specifications are compatible with R [16] and represent single predictor linear models in the first two cases, a two predictor linear model in the third case and a model containing both predictors and their interaction in the final case.

4. DISCUSSION

Focusing on a common threat, that of declining food resources [22], this study confronts the important question of how mammalian carnivores of different size might respond to differing environmental conditions. Compared with the overall variation across the dataset, the carnivore mass–prey biomass interaction term explains only 2 per cent of the variation; nevertheless, slopes of the relationship between predators and prey vary substantially and carnivore mass explains nearly 80 per cent of the variation in these slopes (figure 1)—a result of great biological significance. A given reduction in prey abundance, leads to a five- to sixfold greater reduction in the larger carnivores when compared with the smallest carnivores.

What mechanisms could drive this apparent vulnerability? One possibility is that, because large carnivores consume large prey [12], which themselves may be vulnerable to threat processes [13], there may be an interaction across populations between predator and prey. However, our analysis of carnivore abundance controls for prey abundance and so does not support this argument unless more subtle processes, unrelated to abundance, are taking place. Alternatively, previous work has shown that energetic costs may limit body size in larger carnivores [11]. It is possible that similar physiological factors influence population processes as well. Physiologists have long been interested in metabolic costs under different levels of exercise [23,24]. Such studies have shown that, at maximum energy expenditure, large animals have relatively high metabolic rates [25–27]. Carnivores have larger home ranges [28–31] and hunt for longer [32,33] in areas of low prey density or productivity. Building on earlier physiological arguments, we might expect that when large carnivores work harder to maintain their energy budgets under conditions of low prey abundance, this in turn may influence their population density. If this is the case, predatory species with extremely high hunting costs will be particularly susceptible to changes in the environment that influence feeding ecology, because any increase in the time spent hunting greatly adds to overall energy expenditure [34]. In energetically stressful situations, both survival and reproduction are subject to reductions; this situation could be exacerbated in large carnivores by life-history attributes that already render them vulnerable to extinction [35]. Future work on this topic, using models of predator–prey dynamics to assess the influence of size and habitat productivity, might be particularly useful in providing specific testable predictions [36,37].

Understanding the links between physiology, behaviour and population phenomena remains one of the great challenges in ecology [38], and the current backdrop of declining environmental conditions, climate change and biodiversity loss makes that challenge particularly important [39]. Carnivores represent ideal

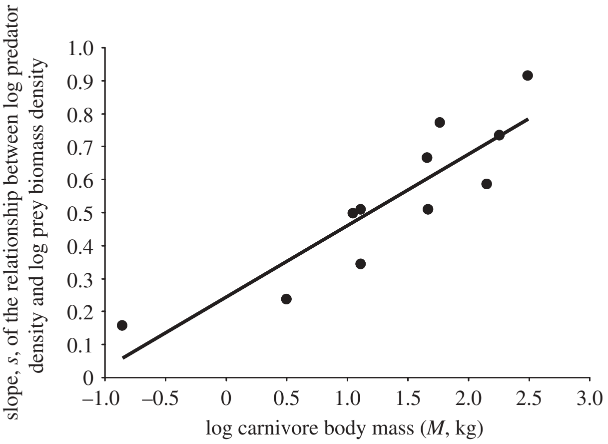

Figure 1. The slope (s) of the predator–prey population responses plotted against log of carnivore mass ($\log M$, in kilograms). Steeper slopes are related to a faster rate of change with changing prey. The best-fit line is $s = 0.217 \times \log M + 0.245$ ($r^2 = 0.79$).

species for exploring such relationships because, not only do we know a great deal about their behaviour and diets [40], but we also have good information on the abundance and distributions of many of their prey [4]. We believe that further research exploring the link between physiology, behaviour and carnivore population dynamics represents a valuable opportunity to establish clear relationships, from individual behaviour to population processes and macroecological patterns. This research also has important implications for the conservation of our largest carnivore species, which seem especially vulnerable to conditions influencing the abundance of their prey.

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