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addendum

Energetic constraints on the diet of terrestrial carnivores

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Energetic constraints on the diet of terrestrial carnivores

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Species in the mammalian order Carnivora exhibit a huge diversity of life histories with body sizes spanning more than three orders of magnitude. Despite this diversity, most terrestrial carnivores can be classified as either feeding on invertebrates and small vertebrates or on large vertebrates. Small carnivores feed predominantly on invertebrates probably because they are a superabundant resource (sometimes 90% of animal biomass¹⁻³); however, intake rates of invertebrate feeders are low, about one tenth of those of vertebrate feeders^{4,5}. Although small carnivores can subsist on this diet because of low absolute energy requirements, invertebrate feeding appears to be unsustainable for larger carnivores. Here we show, by reviewing the most common live prey in carnivore diets, that there is a striking transition from feeding on small prey (less than half of predator mass) to large prey (near predator mass), occurring at predator masses of 21.5–25 kg. We test the hypothesis that this dichotomy is the consequence of mass-related energetic requirements and we determine the predicted maximum mass that an invertebrate diet can sustain. Using a simple energetic model and known invertebrate intake rates, we predict a maximum sustainable mass of 21.5 kg, which matches the point where predators shift from small to large prey.

After allowing for shared evolutionary history, we found an overall positive correlation between carnivore body mass and the mass of their most common prey (comparative analysis by independent contrasts (CAIC)^{6,7}: prey mass = 1.19 × predator mass; $n = 112$, $r = 0.45$; $P < 0.001$; Fig. 1). There was also a pronounced shift to larger prey items by carnivores at intermediate masses. We defined this shift point statistically as the point where the data can be split into two groups so as to minimize the sum of the mean squares. For this analysis, we excluded the sloth bear (*Ursus ursinus*),

which is clear outlier (see below; Fig. 1a), and found a shift in the data between 21.5 and 25 kg.

We conducted an analysis to predict the maximum body mass that can be sustained on invertebrate prey. Our analysis combined a net-rate model⁸ and estimates for mass-related metabolic rates⁹ and travel speeds¹⁰⁻¹², along with estimates of invertebrate intake rates (Table 1). We selected species that have a range of body sizes, habitats and feeding strategies, including specialist invertebrate feeders (badger¹³, *Meles meles*; bat-eared fox^{12,14}, *Otocyon megalotis*; aardwolf^{11,15} *Proteles cristatus*), a largely invertebrate feeder (banded mongoose¹⁶, *Mungos mungo*) and a generalist (golden jackal¹⁷, *Canis aureus*). We then compared the model's predictions of the maximum body masses that could be sustained on an invertebrate diet with the statistically defined shift point determined above.

The predictions of maximum sustainable mass from the net-rate model varied among species: 5.1 kg for bat-eared fox, 8.5 kg for banded mongoose, 13.0 kg for golden jackal, 20.9 kg for aardwolf, and 21.5 kg for badger (Fig. 2). The differences in species estimates is partly due to differences in feeding ecologies but may also result from practical difficulties in accurately measuring intake rates of very small prey. The highest values estimated from the aardwolf and badger are very similar and correspond closely with the mass at which carnivores shift to feeding on large prey. However, because some species may not be able to achieve such high intake rates, we have included both the minimum and maximum estimate in Fig. 1a–e. Although these extremes cover a range of 16.4 kg, this range is small compared with the total range in carnivore mass, and more than 3/4 of the species in the analysis fall outside of this range.

We summarized the most common prey masses of carnivores in relation to this maximum-mass estimate. Carnivores weighing 21.5 kg or less feed mostly on prey that is 45% or less of their own mass, whereas carnivores above this feed mostly on prey that is greater than 45% of their own mass (the percentage of carnivore mass was chosen to maximize the model fit). This classification holds for 92.1% of 139 species (92.9% of the smaller mass class, 82.6% of the larger mass class). We also summarized diet types of 158 species (including mainly vegetarian species and scavengers) according to this mass estimate. With all of the species combined, only about 1/4 of the species weighing 21.5 kg or less are purely vertebrate feeders, the rest are either omnivores (45%) (often with invertebrate prey included), purely invertebrate feeders (10%) or mixed invertebrate and small vertebrate feeders (19%). Just over half of the carnivores above this weight are purely vertebrate feeders (52%). The rest are omnivores, and bears account for most of these.

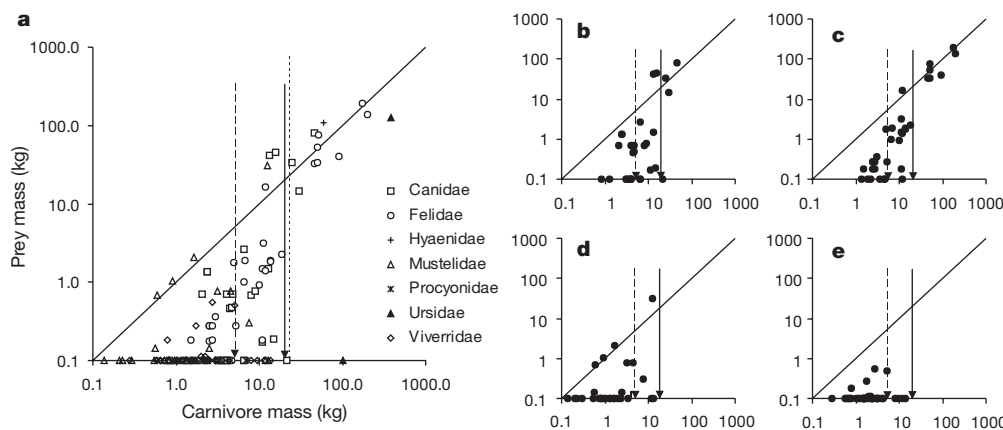


Figure 1 The mass of the most common prey plotted against carnivore mass. **a**, All families combined; **b**, Canidae; **c**, Felidae; **d**, Mustelidae; **e**, Viverridae. Average prey sizes of 0.1 kg or less were grouped into one prey-weight class. The diagonal line represents a slope of 1. The point that separates the prey masses into two groups while minimizing the sum of the mean squares is designated by the dotted line. The upper and

lower estimates of maximum carnivore mass (from Fig. 2) are designated by the vertical arrows. Above the 21.5-kg threshold, all species fit the model (except the sloth bear). Mustelidae and Viverridae do not exceed the threshold mass and almost all these species specialize on very small prey.

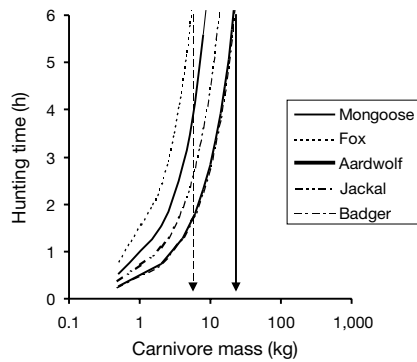


Figure 2 Predicted hunting time required to balance the net energy expenditure against carnivore body mass. As mass increases, the total energy expenditure increases, and so too must hunting time in order to balance the energy budget. Five predictions are presented based on the intake rate and travel speed of the banded mongoose, bat-eared fox, aardwolf, golden jackal and European badger (the aardwolf and badger cases overlap). The high (badger, solid line) and low (fox, dashed line), based on a hunting time of 6 h are designated by the vertical arrows.

Among canids and felids, all species weighing over 21.5 kg are purely vertebrate feeders. Below this weight, 53% of the species are purely vertebrate feeders; the remaining are omnivores (29%), purely invertebrate feeders (2%), and invertebrate and vertebrate feeders (16%).

To see how the variation in model parameters affected our predictions, we calculated the predicted maximum sustainable mass for species in Table 1, over a full range of foraging times (Fig. 3). The overall maximum mass predicted was 52 kg (equivalent to a badger feeding 24 h day⁻¹). This suggests that invertebrates cannot sustain the very largest carnivores even under exceptional prey densities and foraging times. In addition, when estimates of travel speeds vary by ±50%, an average variation occurs in the predicted maximum masses of only -12.3% and +16.8%.

We propose that the maximum size that can be sustained on an invertebrate diet is roughly 21.5 kg, and that this results from the simple energetic constraint of relying on a small particle-sized food source. This can explain the general absence of medium to large carnivores (more than 21.5 kg) feeding on very small prey (Fig. 1a). Although there are conditions under which higher maximum body mass might be predicted, these rely on exceptionally high intake rates that are patchily or temporally limited and not relevant to long-term energetic constraints. For example, badger intake rates may greatly exceed the long-term average used in our analysis¹³, but this only occurs seasonally and in areas with intensive farming^{13,18}. There are also exceptions to the overall pattern that we describe

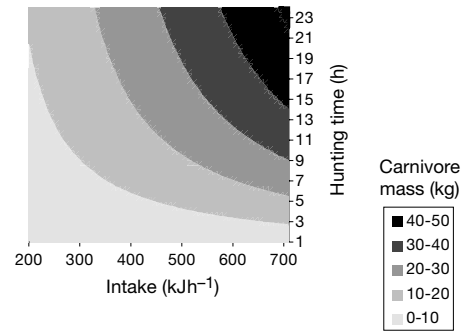


Figure 3 A contour plot of the maximum carnivore body mass predicted from the net-rate model for a range of invertebrate intake rates and hunting times. The range of intake rates used is based on the examples in Table 1.

here. Aquatic carnivores were excluded because of different thermoregulatory constraints and lower transport costs due to buoyancy¹⁹. Bears are also generally an exception; only the polar bear (*Ursus maritimus*) and the sloth bear feed predominantly on live animal foods. The polar bear is consistent with our model predictions, being large and feeding on large prey. The sloth bear probably maintains its large size both through its unusual ability to suck termites from the core of excavated colonies and by feeding heavily on fruits when available²⁰. In conclusion, our results provide a powerful framework for interpreting general trends in diet choice and evolution of body size in this diverse group. Our results also support the idea that large carnivores are a distinct group, both ecologically and physiologically, rather than simply a scaled-up version of a small carnivore, and that energetic constraints may be important for understanding their vulnerability²¹. □

Methods

Carnivore diet

To examine dietary preferences, we collated data on the diets and body sizes of 158 species of terrestrial carnivores from the literature (the main sources were refs 22–27). We excluded aquatic carnivores, including pinnipeds and other species that are largely dependent on aquatic habitat and prey (for example, otters, mink, and three species of viverrids, see ref. 19). We recorded the body mass (mean mass, or midpoint of stated range) of each species and that of its common prey. We conducted a separate analysis on 139 species excluding those which feed primarily on carrion or vegetable foods. Where there was no information on prey preference, mean prey size was calculated from the prey species listed. For small prey, where species weights were not given, masses were estimated from average weights for the genus, or were estimated at 0.001 kg for insects, 0.005 kg for aquatic invertebrates, 0.1 kg small rodents and birds and 0.5 kg for small mammals.

Invertebrate intake rates

Estimates of energetic intake rates on a diet of invertebrates were based on studies of the banded mongoose¹⁶, the bat-eared fox^{13,15}, the aardwolf^{11,15} the golden jackal¹⁷ and the

Table 1 Values used in the estimates of energy expenditure while hunting (E_h) and intake rates (I) for five species of carnivores

Species	Species mass (kg)	Speed* (m s ⁻¹)	Prey mass (g)	Estimated intake rate† (I) (kJ h ⁻¹)	Notes
Banded mongoose	1.5	0.276	529 Insects spp (0.0085) 102 Diplopoda (0.75) 5 Archnida (1.0) 1 Mollusca (3.25)	347.0	Invertebrates captured over 590 min
Bat-eared fox	4.1	0.348	Termites 82% (0.0075) Beetles 12.3% (0.17)	234.0	% stomach volume Capture rate of 12 min
Aardwolf	10.0	0.434	Termites (<i>Trinervitermes</i> and <i>Hodotermes</i> spp.)	693.4	Average of winter and summer rates
Golden jackal	11.0	0.454	Beetles (0.17)	480.0	1.23 min
European badger	13.0	0.463	Worms (10,460 J each)	709.2	1.13 min (long-term average)

All travel speed were calculated from the equation of travel speed in relation to body mass (see Methods).
* These values are close to observed speeds (for example, mongoose (D. De Luca, unpublished data), bat-eared fox^{12,14} and aardwolf^{11,19}).
† Energetic values for the invertebrates were estimated at 38,258 J g⁻¹ (ref. 4), except for earthworms, for which a per-teritem energetic value is given¹⁸ and termites (ref. 15). Invertebrate weights were obtained from published references; and D. De Luca and P. Pearce-Kelly, personal communication.

European badger¹³ (Table 1). The estimates of intake rates and travel speeds used in the calculations are presented in Table 1.

Net-rate model

We used the net-rate model assuming a balanced energy expenditure and solving for time hunting, T_h (in h) (see ref. 8), $T_h = 24E_r/(I + E_r - E_h)$, where E_h and E_r are the energetic expenditure rates (in kJ h^{-1}) while hunting and resting and I is the intake rate while hunting (in kJ h^{-1}). The resting and hunting rates of energy expenditure (in Watts) for a carnivore of a given mass (M_b) (in kg) was calculated from the equations, $E_r = 3.34 M_b^{0.73}$; and $E_h = 10.7 M_b^{0.684} \nu + 6.03 M_b^{0.697}$ where ν is the average speed (in m s^{-1}) during hunting⁹. We estimate ν using the equation $V = 0.25 M_b^{0.24}$ (ref. 10). The constant, representing m s^{-1} (for a 1 kg animal), is based on travels speeds in the aardwolf¹¹, but this equation produces travel speeds within observed limits for other carnivore species listed in Table 1 (refs 11, 12; D. De Luca, unpublished data). Our calculations are based on a foraging time of 6 h which represents typical foraging times for a number of invertebrate feeding carnivores (for example, see refs 4, 11, 28, 29). Additional estimates of maximum body mass were made for varying intake rates and a full range of hunting times (Fig. 3).

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Total lipid energy as a proxy for total egg production by fish stocks

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The indeterminate relationship between the total biomass of mature fish (spawner biomass) and the number of offspring produced (recruitment) has puzzled population dynamicists¹ and impeded fisheries management². The relationship assumes that spawner biomass (in tonnes) is proportional to the total number of eggs produced (TEP) by the stock³, an assumption under increasing challenge^{4–8}. Most stocks require proxies for TEP because contemporary and/or historical fecundity data are lacking. Here we show a positive association between recruitment and the liver weights of spawners in the Barents Sea cod stock which suggests that recruitment is constrained by the amount of lipid energy stored in the liver. This stimulated our interest in estimating total lipid energy (TLE; in kilojoules) for mature females in the stock. We examined the suitability of TLE as a proxy through correlation and simulation analyses. The results indicate that TLE is proportional to TEP and exhibits a similar response to varying food abundance. Replacing spawner biomass with more accurate measures of reproductive potential is essential to developing a rational basis for stock conservation⁹. Correctly specifying the first-order maternal effect on TEP is a prerequisite to detecting environmental and ecological effects on recruitment¹⁰.

The protein and lipid reserves used for metabolism, gonad development and spawning behaviour of fish co-vary in response to the abundance of food¹¹. In gadoid species, such as Atlantic cod, lipids are stored primarily in the liver¹² making liver weight a rapid and inexpensive measure of spawner quality. Russia began recording liver weights of Barents Sea cod in 1927. Since 1967, liver weights have been recorded monthly for fish in 10-cm length classes¹³. These data are archived as the liver condition index (LCI) which expresses

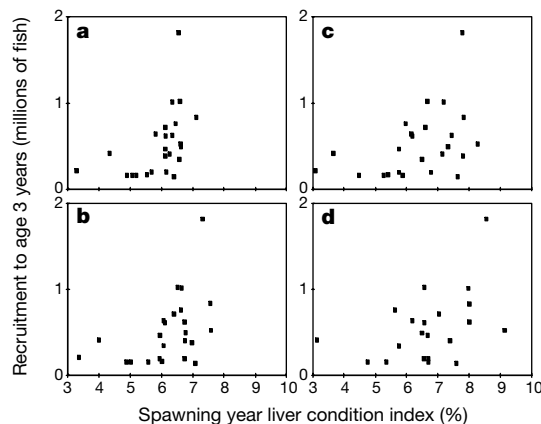


Figure 1 Empirical relationship between recruitment to age three years¹⁸ and the mean liver condition index estimated for a single spawning year (defined as the mean of monthly values recorded for July the preceding year through to June of the spawning year). The spawning years 1968–1994 are represented. Length classes of fish: **a**, 51–60 cm; **b**, 61–70 cm; **c**, 71–80 cm; **d**, 81–90 cm.