Biomechanical constraints reverse scaling of the activity budget in carnivores

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Abstract

Current theories predict that the proportion of time that an animal spends actively foraging to balance its energy budget scales negatively (decreases) with body size due to the decrease in mass-specific maintenance costs. Here, we use a mathematical model and extensive data to show that, under field conditions, this scaling can in fact change from negative to positive in predators due to limited detectability and availability of preferred prey sizes. These predictions are supported by a global dataset on 73 terrestrial carnivore species from 8 families (over three orders of magnitude in size). We find that carnivores weighing less than ∼5kg experience strong costs of foraging on relatively small-sized prey, and therefore show a counter-intuitive, positive scaling of activity time. Only a shift to foraging on larger prey above this size yields the previously-hypothesized negative scaling of activity time. We also show how the model can be generalized to other classes of terrestrial and aquatic consumers.

Introduction

The activity budget of an animal, that is, the time that it allocates to different behaviors, strongly affects its fitness by determining interaction rates with resources, predators and competitors. The activity budget can also inform conservation efforts by helping predict the spatial and temporal distribution of resources necessary for an animal population to remain viable (Woodroffe & Ginsberg, 1998; Jetz *et al.*, 2004). For example, accurate models of long-term activity and geographical ranges of mammalian carnivores are necessary for determining the appropriate size of protected areas of endangered mammals (Woodroffe & Ginsberg, 1998; Miller *et al.*, 2014).

However, although empirical patterns of activity budgets in the field are now widely recorded due to recent improvements in tracking technologies, there is currently no theoretical framework for predicting them, or generalizing our knowledge of these patterns across species, habitats, or foraging strategies. Although animals can vary widely in how they manage their time, there is great potential for developing predictive models for activity budgets by including general constraints due to biomechanical (e.g., locomotion and food searching) and energetic (e.g., resting metabolic rate) limitations (Peters, 1983; Schmidt-Nielsen, 1984; Gorman *et al.*, 1998; Savage & West, 2007).

Clearly, activity budgets should be strongly related to the minimum energetic requirements of an animal — more the energy requirement per unit time, more the time spent actively foraging for resources. An animal's energetic requirements are usually estimated from its basal or resting metabolic rate, which scales positively with body mass and, in the case of vertebrates, with a $\frac{3}{4}$-power exponent ($M^{0.75}$; Kleiber, 1932; Schmidt-Nielsen, 1984; McNab, 1989; but see Kolokotrones *et al.*, 2010). Therefore, metabolic rate per unit body mass (mass-specific metabolic rate) scales negatively with body size ($M^{-0.25}$). As a result, individuals from small-sized species have higher maintenance costs per unit body mass and necessarily need to consume energy at a faster rate then those from larger ones. Therefore, a common expectation is that the amount of time in a day an animal spends active in its daily cycle decreases with body mass (Peters, 1983; Savage & West, 2007). However, this prediction hinge on the key assumption that energy intake (consumption) rate scales similarly to the rate of energy use (metabolic) rate.

In reality, consumption rates in the field are typically limited by resource availability (i.e., prey abundance), and ability of the consumer to search, detect, attack and handle prey. This can result in deviations of the scaling of consumption rate (energy intake rate) from that of metabolic rate (McGill & Mittelbach, 2006; Pawar *et al.*, 2012; Giacomini *et al.*, 2013; Pawar *et al.*, 2013). In this scenario, animals of different sizes need to optimize their activity budget by choosing the right resource sizes (e.g., many small vs. few large prey) and foraging strategy (e.g., active-capture vs. sit-and-wait) to meet their energetic needs (Carbone *et al.*, 2007; Pawar *et al.*, 2012; Carbone *et al.*, 2014). These limitations on optimal foraging, and therefore intake rates may thus lead to deviations from the expectation of a universal decrease in activity time with body size.

Here we develop a mathematical model for scaling of the activity budget of consumers under field conditions with respect to their body size, incorporating key metabolic and biomechanical constraints affecting foraging success — prey availability, habitat complexity, and predator-prey size-ratio. We test the model's predictions by compiling a global dataset of high-resolution activity budgets of terrestrial carnivores. We focus on terrestrial carnivores because this group has been the most studied empirically both in terms of energetics and activity budgets in the field. In the *Discussion* we show how our model can be adapted or extended to other classes of consumers.

The activity budget model

We first derive a simple model for the proportion of time (T_p) that a predator must spend foraging on a daily basis to maintain its individual biomass (Supplementary Information):

$$T_p = \frac{B}{I + B - A} \tag{1}$$

Here, I, B and A are the rates (J · s^{-1}) of energy intake, loss while resting, and loss while moving actively. As such, Eqn. (1) satisfies the condition for maintenance of individual biomass, but does not account for the additional energy needed for allocation to reproduction, somatic growth, or other, non-foraging activities such as searching for mates. Therefore, this model sets a lower bound on the proportion of time spent active by an individual, and when confronting it with empirical data, we expect the right hand side of Eqn. (1) to predict the lower bounds on activity times.

Next, we impose biomechanical and metabolic constraints on each of the components of Eqn. (1) by using size-scaling theory (Supplementary Information, Table S1). For energy loss rate while resting, we use the scaling of resting metabolic rate (Peters, 1983; Brown *et al.*, 2004),

$$B = B_0 m^z \tag{2}$$

where m is the body mass (in kg) of the predator. For energy loss during movement, we use the following equation, which is derived from Taylor *et al.* (1982) (see Supplementary Information for more details):

$$A = A_{0,1} v_0 m^{a_1 + p_v} + A_{0,2} m^{a_2} \tag{3}$$

where v_0, $A_{0,1}$, and $A_{0,2}$ are constants (Table S1). The first term of the sum ($A_{0,1} v_0 m^{a_1 + p_v}$) quantifies increase in energy consumption as a function of body size (exponent a_1) and body velocity (exponent p_v) (incremental cost), while the second term ($A_{0,2} m^{a_2}$) quantifies the energy needed to initiate the movement (zero speed cost). For energy intake rate we use the consumption-rate model derived for individuals foraging in $2D$ (two euclidean dimensions) (Pawar *et al.*, 2012, 2015),

$$I = I_0 m^{p_v + p_d(1 + p_k) + p_k(1 - p_x)} \tag{4}$$

where

$$I_0 = 2 v_0 d_0 x_0 k_0^{1 - p_x + p_d}$$

Here, p_v, p_d and $1 - p_x$ are the scaling exponents of the predator's velocity (same as in eqn. (3)), reaction distance and prey biomass abundance respectively. Reaction distance is the minimum distance at which the consumer can detect the prey and react to it (Pawar *et al.*, 2012). The exponent p_k is for the scaling of prey-predator body size-ratio ($\frac{m_R}{m}$). I_0 is the product of the scaling constants of velocity (v_0), reaction distance (d_0), size-ratio ($k_0^{p_d}$), and prey biomass abundance (x_0). Thus, both the scaling constant and exponent of intake rate depend upon the scaling of size-ratio and reaction distance. Substituting Equations (2) to (4) into eqn. (1) gives the bio-mechanically constrained activity budget model:

$$T_p = \frac{B_0 m^z}{I_0 m^{p_v + p_d(1 + p_k) + p_k(1 - p_x)} + B_0 m^z - (A_{0,1} v_0 m^{a_1 + p_v} + A_{0,2} m^{a_2})} \tag{5}$$

This equation immediately provides a key insight: for a given scaling of energy loss while resting (B; eqn. (2)) and active (A; eqn. (3)), the relationship of T_p with body size depends upon the scaling of intake rate (I; Eqn. (4)). Intake rate in turn depends upon three factors: the scaling of prey biomass abundance (constant x_0, exponent $1 - p_x$), size ratio (constant $k_0^{p_d}$, exponent p_k), and reaction distance (constant $2d_0$, exponent p_d). A weakening of any of these scaling relationships will weaken the scaling of energy intake rate with size, and therefore also

4

¹²⁹ weaken the expected decline of proportion time active, T_p, with predator size (Fig. 1). These
¹³⁰ three scaling factors represent three very general constraints imposed by field conditions on the
¹³¹ energetic costs of foraging: the availability of or preference for resources of different sizes relative
¹³² to predator (prey to predator size-ratio scaling), ability of the predator to detect these resources
¹³³ (reaction distance scaling), and the abundance of resources (scaling of prey abundance).
¹³⁴ We then use (Eqn. (5)) to determine the contribution of each of these constraints alone to
¹³⁵ the size-scaling of intake rate and activity budget (Fig. 1). Values for the scaling constants and
¹³⁶ exponents are given in Supplementary Information (see Table S1). We find that under each of
¹³⁷ these constraints, that is, in the scenario that their scaling becomes weaker, intake rates are
¹³⁸ predicted to scale substantially more slowly with body size than under the idealized scenario
¹³⁹ where prey abundance, prey size, and prey detection distance all scale more proportionally with
¹⁴⁰ predator size (upper panels of Fig. 1). And as a result of this weakening of intake rate scaling,
¹⁴¹ each of these constraints can result in a qualitative (negative to positive) shift in the scaling of
¹⁴² activity budget (lower panels of Fig. 1), with the shift occurring within a size range of about
¹⁴³ 1–10 kg predator body weight.
¹⁴⁴ We now test these predictions using empirical data on intake rates and activity budgets of
¹⁴⁵ terrestrial carnivores in the field.

Empirical Results

¹⁴⁷ We compiled data on activity budgets from databases and the published literature on 38 species
¹⁴⁸ of terrestrial carnivores spanning the entire body size range of the Order (details of methods
¹⁴⁹ in Supplementary Information). From these activity budget data, we calculated the proportion
¹⁵⁰ of time spent active (T_p) on a daily time scale. We restricted the data compilation to radio
¹⁵¹ telemetry and GPS tracking studies because other methods such as camera-trapping and direct
¹⁵² observation are likely to undersample the proportion of time active in smaller animals due do
¹⁵³ their poorer temporal and spatial resolution. We also compiled an independent dataset on intake
¹⁵⁴ rates for terrestrial carnivores to test the mechanistic link between the scaling intake rates and
¹⁵⁵ activity budget predicted by our theory (Fig. 1). We used phylogenetic independent contrasts
¹⁵⁶ (Felsenstein, 1985) to check for phylogenetic signal among our data but found no evidence of
¹⁵⁷ it. As such, there was no need to account for phylogenetic relatedness.
¹⁵⁸ The results show that there is overall a tent-shaped relationship between T_p and consumer
¹⁵⁹ body size across the entire size range (Fig. 2), with larger carnivore species generally become
¹⁶⁰ less active (T_p decreases) as body size increases while smaller carnivores become more active
¹⁶¹ (T_p increases) as body size increases. The overall pattern is best explained by a piecewise
¹⁶² regression (Supplementary Information, Table S2; $R^2 = 0.43$, $p = 0.0038$, AICc = -37.167).
¹⁶³ When we re-analysed the data separately for only the three most data-rich Families, the same
¹⁶⁴ pattern emerged (Felidae, Canidae, and Mustelidae; $R^2 = 0.44$, $p = 0.0092$, AICc = -27.92).
¹⁶⁵ Specifically, across these three families, we find that Mustelids show a positive scaling of T_p,
¹⁶⁶ whereas Felids and Canids both independently show a negative scaling. This suggests that there
¹⁶⁷ is a phylogenetic component to this reversal of scaling of the activity budget.
¹⁶⁸ Remarkably, the breakpoint — the body weight where the scaling relationship reverses
¹⁶⁹ — was estimated by the piecewise regression to be 3.42 kg (95% confidence intervals (CIs)
¹⁷⁰ of 1.79 and 6.52), lying within the 1–10 kg range predicted by our model (cf. Fig. 1 & 2).
¹⁷¹ This breakpoint is around the average weight of a Gray Fox (*Urocyon cinereoargenteus*). When
¹⁷² considering just Mustelids, Canids and Felids, the breakpoint shifted to 5.66 kg (95% CIs of 2.69,
¹⁷³ 11.94), around the average weight of a Crab-eating Fox (*C. thous*). The slopes of the piecewise
¹⁷⁴ model's two segments, to the left and to the right of the breakpoint, were also significantly
¹⁷⁵ different in both versions of the analyses (all data: below breakpoint slope = 0.34 ± 0.11,
¹⁷⁶ above breakpoint slope = -0.2 ± 0.18, $p < 0.0001$; just three families: below breakpoint slope
¹⁷⁷ = 0.25 ± 0.09, above breakpoint slope = -0.25 ± 0.07, $p = 0.0015$).

Next, using an independent dataset (Supplementary Information), we tested our prediction that this qualitative change in the activity budget scaling is because of a weakening of the intake rate scaling in smaller carnivores (Fig. 1). Figure 2 shows that this is indeed the case, with a qualitative change in the scaling relationship at about 3.74 kg (95% CIs of 0.86, 8.34), — statistically indistinguishable from the breakpoint for the scaling of the activity budget (Fig. 2), as predicted by the model (Fig. 1). Furthermore, the slope above the threshold point confirms predictions by Pawar *et al.*, 2012. The even shallower value on the left of the threshold points provides a good example of how strong an effect size ratio can exert on the energetics of these species. This provides strong support for the mechanistic link between intake rate and activity budget predicted by our theory. Here again, we repeated the analysis for just the three most data-rich Families (Mustelids, Canids and Felids) and found similar results. And here again, Mustelids contributed to most of the data points below the breakpoint, indicating a phylogenetic component to the overall pattern. The slopes of the piecewise model's two segments, to the left and to the right of the breakpoint, were significantly different for both versions of the analyses (all data: below breakpoint slope $= 0.51 \pm 0.29$, above breakpoint slope $= 1 \pm 0.15$, $p = 0.01363$; the three families: below breakpoint slope $= 0.51 \pm 1.30$, above breakpoint slope $= 1.1 \pm 0.17$, $p = 0.003345$).

Thus overall, our results indicate the existence of strong constraints on intake (foraging) rates, and therefore activity budgets in small terrestrial carnivores (below a body size of $\sim$5kg). Our theory predicts that these constraints arise in small carnivores because some or all of the following: prey biomass abundance increases too weakly with increasing predator body mass, prey body sizes increase too weakly (that is, larger species among small carnivores feed on prey that are sub-optimally small), or reaction distance does not increase or increases too weakly (Fig. 1).

To determine what combination of these constraints could explain the observed patterns in activity budget scaling, we compiled a third dataset — on prey-predator body sizes relationships for terrestrial carnivores (Supplementary Information). We then tested whether smaller carnivores fed on qualitatively different relative prey sizes than larger carnivores. The results (Fig. 3) show that there is indeed a significant shift in the relative size of preferred prey between small and large carnivores — prey sizes scale strongly and positively with body size in large carnivores, but not in small carnivores. Here again, breakpoint regression indicates that the shift lies within the 1–10 kg size range, at about 4.8 kg (95% CIs of 2.34, 7.25). This value is somewhat larger but statistically indistinguishable from the breakpoints for the activity budget and intake rate scaling relationships (Fig. 2).

Thus, the fact that smaller terrestrial carnivores tend to feed on prey items of somewhat constant size that are much smaller then themselves (Fig. 3) at least partly explains the reversal of scaling of the activity budget. In addition, differences in the scaling of prey abundance and reaction distance in small carnivores may contribute to this reversal, but data are currently not available on these constraints.

Discussion

We have developed a new mechanistic model to predict the body size-scaling of the time terrestrial predators need to be active (i.e., foraging) for maintaining energetic balance, and tested it with a large global dataset on carnivores. We find that in contrast to current thinking, small and large terrestrial carnivores have an opposite scaling of the proportion of time spent active (T_p) in a day. Specifically, small carnivores below a 1–10kg size range show an increase in daily activity time with body size, with only larger carnivores showing the decrease in activity time with size expected from their lower mass-specific energy needs (Peters, 1983). This reversal of scaling occurs because small carnivores face additional biomechanical constraints while foraging, which limits their intake rate and negates the advantage of decreasing mass-specific metabolic

rates with increasing size. Our results reveal ecological challenges faced by smaller predators, and shed new light on the behavioral adaptations involved in offsetting the higher energetic requirements of increasing size.

The three constraints — prey-predator size ratio, reaction distance, and resource abundance — are general in that all of them are likely to be experienced by predators under field conditions. Of the three, size-ratio and reaction distance are tightly interlinked, because smaller size-ratios (prey much smaller than predator) also decreases reaction distance (Pawar *et al.*, 2012; McGill & Mittelbach, 2006). Although data are currently lacking on the scaling of reaction distance across terrestrial carnivores, the fact that both intake rates and prey sizes scale weakly with size in small carnivores indicates that species in this size class (up to about 10kg) face somewhat insurmountable challenges in the way of feeding on optimally-sized prey. That is, unlike in larger carnivores, where bigger species feed on proportionally bigger prey (Carbone *et al.*, 1999; DeLong & Vasseur, 2012) (Fig. 3), in small carnivores preferred prey size changes little as body size increases. Thus, in small carnivores, though foraging on small prey is initially relatively easy due to low hunting costs, as predator size increases, prey become increasingly difficult to detect, attack and handle. Because carnivore species above the 1–10kg size range have escaped this constraint by feeding on relatively larger prey, this results in a switch to a steeper scaling of intake rate and correspondingly, a negative scaling of activity time (Fig. 2).

Current models and data suggest that reaction distances scale positively with body size when considering visual constraints, so that larger species have bigger reaction "bubbles" (Kiltie, 2000; McGill & Mittelbach, 2006; Pawar *et al.*, 2012). However, field conditions impose multiple constraints on how far an animal can see, including vantage point, line of sight, prey conspicuousness and maneuverability, all of which likely raise additional challenges for small predators hunting for prey much smaller than themselves. Indeed, it has been suggested that natural habitats show fractal (i.e., "self-similar") visual structure (Field, 1987), which implies that compared to large-prey eaters, small-prey eaters hunt for better-hidden prey in effectively more complex landscapes. Thus when target prey remain about the same size despite increasing predator size, a weaker scaling of effective reaction distance with size would be expected under field conditions. Handling time, which includes the time spent in pursuing and capturing prey (Pawar *et al.*, 2015) following prey detection (and subsequent reaction), would be subject to similar constraints. Handling rates are unimodal with respect to prey-predator size ratios, that is, they decline at both extremes of prey-predator body size ratios (Carbone *et al.*, 2007; Vucic-pestic *et al.*, 2010; DeLong & Vasseur, 2012). Therefore, the main advantage of feeding on small prey — a relatively short handling time(Carbone *et al.*, 2007; DeLong & Vasseur, 2012) — is increasingly negated for larger small-prey eaters as their prey become sub-optimally smaller relative to themselves. This would compound the constraints of reaction distance. Future work should aim to directly test this hypothesized weaker scaling of reaction distance among small carnivores, as well as the variation in handling time scaling across different size-classes of carnivores.

A weak scaling of prey abundance can further accentuate the constraints faced by small carnivores (Fig. 1). Resource biomass abundance, which scales positively with resource body mass and therefore also predator body mass, (the exponent $1 - p_x$; Eqn. (4), Supplementary Information, Eqn. S13), can partly offset the higher cost of foraging for small prey in small carnivores. If the numerical abundance of the prey (exponent p_x) of small-prey eaters itself scaled more strongly, such that larger prey items were rarer, small-prey eating would become more costly with increasing predator size, leading to an even stronger positive scaling of the proportion of time active with size. Whether, in general, this is true within the size range of prey species relevant to small carnivores is currently unknown. Therefore, future work should also aim to quantify the scaling of abundance of target prey for different size-classes of carnivores.

The end result of these constraints on foraging is that in order to maintain energetic balance, small-prey eaters have to start taking preferentially larger prey beyond a certain body size range (Carbone *et al.*, 2007), or evolve morphological and behavioral specializations to feed on small

prey (e.g., the Aardwolf; *Proteles cristata*, De Vries *et al.*, 2011). In this regard, it is notable that we do find an abrupt diversification of prey sizes taken (including the Aardwolf example) within the 1–10kg size range (the shaded area in Fig. 3, consisting mostly of "transitional" species). This may explain why small carnivores (Viverrids, as well as many Canids and Felids) in the 1–10 kg body weight range increase the diversity of size range of their prey — becoming more generalized to offset the increased costs of foraging. This pressure on diversifying one's diet could be the basis for the great diversity of extant intermediate-sized carnivore species.

Our results also provide the first ever test and confirmation of the long-assumed decreasing trend of activity time among large carnivores. We find a scaling exponent for activity among large carnivores (-0.2 ± 0.18) which is statistically indistinguishable from that of mass specific metabolic rate (-0.25). Because the same biomechanical constraints highlighted here for small-prey eaters could apply to large-prey eating terrestrial carnivores if sufficiently large prey are unavailable (or go extinct), our model may also provide a mechanistic explanation for body size limits to large carnivores, and why gigantic forms in many extant carnivore families have appeared and become extinct time and again in the paleontological record Carbone *et al.* 2007; Peters 1983.

Our results have a number of implications for both applied and theoretical research. On the applied side, our results suggest that small carnivores may be particularly susceptible to habitat degradation, if this leads to an increase in foraging activity and therefore adds to an already sub-optimal activity budget. As human-induced environmental changes become ever more common and severe, these species may be among the first and more seriously affected — calling for further studies to inform adequate conservation polices.

From a theoretical perspective, our model framework could be adapted and extended to explore the role of biomechanical constraints in the field on activity budgets for a wide range of organisms, thus opening up new and exciting research avenues for understanding links between behavioral and population processes. Although we have restricted our focus to terrestrial verte-brate carnivores, the model framework can be generalized to other types of consumer-resource interactions. With appropriate scaling models for reaction distance and resource abundance, the model can be extended to herbivores, invertebrate predators, or consumers that forage in three spatial dimensions ($3D$; such as in pelagic environments (Pawar *et al.*, 2012; Carbone *et al.*, 2014)). Extending the model to ectothermic consumers (e.g., all invertebrate predators) would require appropriate models for temperature dependence of metabolic rates, body velocity (Dell *et al.*, 2014; Pawar *et al.*, 2015). For example, to generate predictions for aquatic predators, the equations and parameter values for the energy costs of inertial aquatic locomotion (Eqn. 3) and basal metabolic rate (Eqn. 2) for aquatic organisms could be used, coupled with a change from a $2D$ to $3D$ intake rate model (Pawar *et al.*, 2012). Although herbivores may be less constrained by reaction distance, they may still be subject to size-ratio or resource abundance scaling constraints on intake rate (Shipley *et al.*, 1994). Indeed, a recent camera-trapping study of terrestrial mammals that combines carnivore, herbivore, and omnivore species in the Western Ghats of India(Ramesh *et al.*, 2015) also indicates a dual scaling of the activity budget, sug-gesting that the difference in small vs. large carnivore scaling of activity proportions we have found here may be seen across other classes of terrestrial mammals as well.

Finally, the mechanistic insights that our model framework also has implications for our understanding of the evolution of sleep in animals. Assuming that a constant proportion of resting time in a daily cycle ($= 1 - T_p$) is dedicated to sleep, our results suggest that sleep time may not increase montonically with body size as current theory suggests (Savage & West, 2007). This is not surprising, given that sleep time has evolved under the constraints on the activity budget imposed by field conditions. However, the majority of research on evolution of sleep is conducted on a few model organisms under idealized laboratory conditions. Future theoretical and empirical research on the evolution of sleep needs to incorporate more realistic, mechanistic models for energy supply (that is, intake, forging, or consumption rate) relevant to

³²⁹ field conditions, as we have done here.

Conclusions

³³¹ In summary, contrary to the common expectation of a single negative scaling across all animals
³³² due to the decrease in mass-specific metabolic rate, the proportion of time that animals need to
³³³ dedicate to foraging depends upon the biomechanical constraints they face in the field. We have
³³⁴ shown that small terrestrial carnivores do face such constraints, likely arising from a combination
³³⁵ of sub-optimal prey-predator size ratios, weak scaling of reaction (effective detection) distance
³³⁶ and possibly, prey abundance. These constraints change the energetic advantage of increasing
³³⁷ body size to a disadvantage, and the scaling of proportion of activity time reverses in small
³³⁸ vs. large carnivores. By quantifying the mechanistic links between field conditions and activity
³³⁹ budgets, our model offers new insights into the constraints on animal fitness in the field, and
³⁴⁰ what foraging strategies may be preferred in different biotic and abiotic contexts. Further
³⁴¹ work along these lines would provide field scientists, conservationists, and theoreticians with a
³⁴² powerful tool with which to explore how species adjust to both environmental and physiological
³⁴³ changes, expanding on our knowledge of the ecology, evolution, and conservation of as of yet
³⁴⁴ poorly understood consumer species and consumer-resource interactions.

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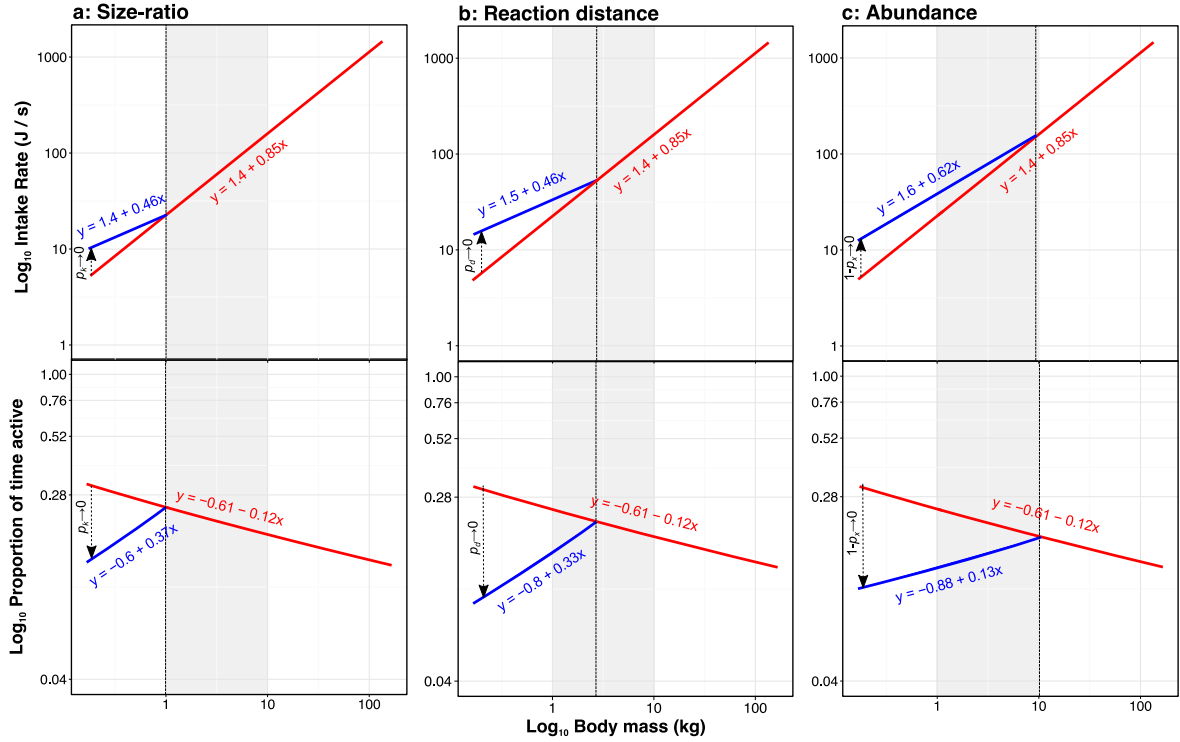
Figures

Figure 1: **Predicted size-scaling of energy intake rate and activity budget in terrestrial carnivores**. The three panels show effect of a decrease in the strength of scaling of three factors on scaling of the activity time (lower figures), through a weakening of intake rate scaling (upper figures). **a**: Scaling of prey-predator size-ratio, which captures the constraint of availability of suitable (relative) prey size with increasing predator size; **b**: Scaling of reaction distance, which captures the constraint on ability of predators to detect prey of a certain size relative to themselves; **c**: Scaling of prey biomass abundance, which captures the constraint of availability of sufficient prey individuals with increasing predator size. In all plots, blue lines represent the deviation of scaling of intake rate or activity budget from the "normal" scaling (red lines) — when none of these constraints exist. Note that all the intersection points of pairs of scaling (red and blue) lines lie between 1–10 kg predator weight range (range highlighted).
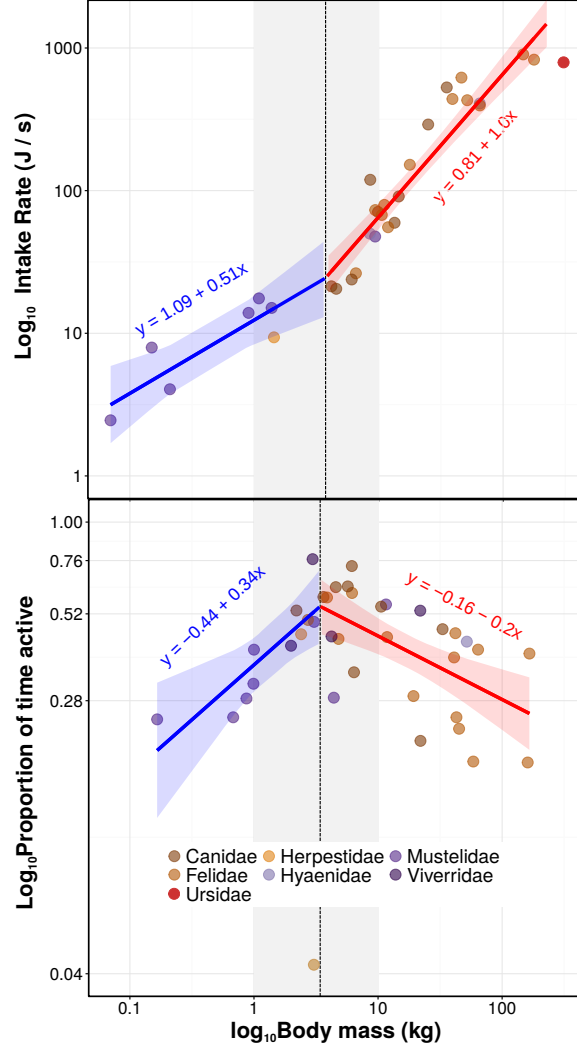
Figure 2: **Observed size-scaling of Energy Intake Rate and Activity Proportions among Carnivores**. In both panels, the blue and red lines represent the two segments of the breakpoint regression (with 95% prediction bounds), the vertical line is their intersection (the breakpoint), and the vertical shaded area the 1–10 kg interval predicted by the theory (Fig. 1). **a**: The scaling of energy intake rate ($n = 32$ species). Breakpoint is at 3.74 kg, and the two scaling exponents (i.e., the slopes) are significantly different (Davies' test, $p = 0.014$). **b**: Activity budget scaling ($n = 38$ species). Breakpoint is at 3.42 kg, and the two scaling exponents are significantly different (Davies' test, $p = 0.0006$). The outlier represents activity data of one Egyptian mongoose, *Herpestes ichneumon*, collected over the course of 1 month in Doñana National Park, Spain (Delibes & Beltran, 1985).
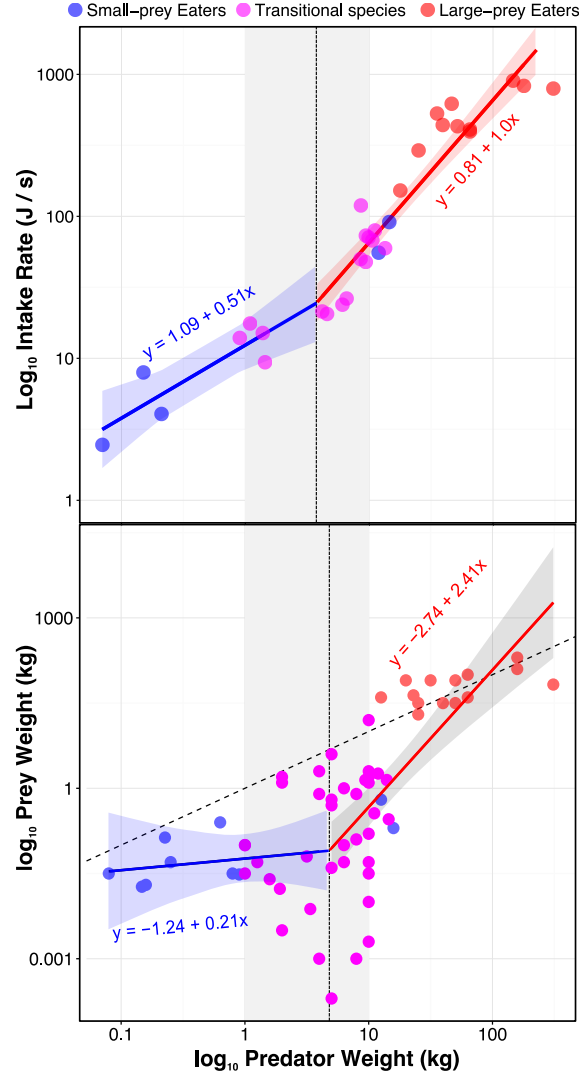
Figure 3: **Scaling of intake rate and prey vs. predator size (size-ratio) among carnivores.** In both panels, the blue and red lines represent the two segments of the breakpoint regression (with 95% prediction bounds), the vertical line is their intersection (the breakpoint), and the vertical shaded area the 1–10kg interval predicted by the theory (Fig. 1). **a**: Same as Fig. 2a, but with the data classified by relative prey-size based feeding strategies instead of taxonomy. **b**: scaling of prey with predator size ($n = 63$ species). The breakpoint estimated here is 4.8 kg: above this, size of preferred prey scales positively with predator size, whereas below this, prey size remains roughly constant even though consumer body mass increases. The two slopes are significantly different (Davies' test, $p = 0.0025$). The diagonal dashed line represents the predator-prey sizes where the size-ratio equals 1; values below it indicate prey are smaller than the predator. The classes of prey-size based feeding strategies shown were defined on the basis of the range of prey types taken, as explained in Supplementary Information Section 2.4. Note that in both plots, the transitional species lie largely within the 1–10kg (shaded) range.