



Research Article

The effects of dietary variation and ecology on the relationship between body size and reproductive strategy in extant mammalian carnivores

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Abstract

Diet has a profound impact on the relationship between body mass and reproductive strategy in mammals, and the implications have been of particular interest in recent years. Previous studies have indicated that diet strongly shapes the way that body mass drives reproductive strategy in herbivores and omnivores, but not in carnivores. One suggested explanation for this result is that the differences in resource distribution between invertebrate feeding carnivores (hypocarnivores) and vertebrate feeding carnivores (hypercarnivores) combine to produce a non-significant result when they are analysed as a single unit. In this study, we investigate how dietary and locomotor differences in carnivores influence the relationship between body mass and reproductive strategy within the context of phylogeny, using a reproductive strategy index and performing a phylogenetically informed analysis of covariance (PANCOVA) on 101 evolutionary trees. We examine this question in two distinct ways. First, we separate carnivores by diet (hypocarnivores, mesocarnivores, and hypercarnivores). Second, we separate carnivores based on their mode of locomotion to determine how ecology may affect this relationship irrespective of diet. For all diet categories we find that the effect of diet is significant when taken individually but is not significant when carnivores are investigated as a single unit. When examining locomotion categories individually, we find that statistically significant trends exist for all groups but volant carnivores. When analysed as a single unit the effect is significant. These results suggest future work should investigate ecological differences to understand the variation in reproductive strategies among carnivores. In the end, the aspects of diet investigated here do not influence the relationship between body mass and reproductive strategy in carnivorous mammals, while ecology does. This suggests that evolution in carnivore reproductive strategy is driven by distinctly different factors than those in omnivorous or herbivorous mammals.

Introduction

Diet has had a significant impact on the evolution and radiation of mammals, as indicated by the sheer diversity of mammalian dentitions (Pineda-Munoz et al., 2016; Price et al., 2012; Weller, 1968). Diet also plays a primary role in determining body mass and other physiological characters of mammalian species (Pineda-Munoz et al., 2016; Price and Hopkins, 2015). Additionally, mammalian body size appears to strongly influence reproductive strategy (Famoso et al., 2018; Werner and Griebeler, 2011; Charnov, 1990; Tuomi, 1980). Large mammals tend to be *K*-selected (low numbers of offspring with a greater degree of parental care), while small mammals tend to be *r*-selected (high number of offspring with a lower degree of parental care, or absence of parental care altogether). The relationship between body size and reproductive strategy in mammals is well understood (Famoso et al., 2018; Price and Hopkins, 2015; Wilder et al., 2012; Tuomi, 1980), but the effect that diet has on this relationship is not well known. Diet influences extrinsic ecological factors such as resource distribution, competition, lifestyle, and longevity (Sibly and Brown, 2007). Each of these constraints influences body size and, potentially, reproductive mode in mammals.

Previous studies comparing diet to body mass suggest that herbivorous mammals tend to large size, while omnivores are intermediate, and carnivores tend to be the smallest mammals (Price and Hopkins, 2015). The basal trophic state in mammals is carnivory, specifically insectivory, and the earliest mammals were relatively small (Price et al., 2012; Holliday and Steppan, 2004; Bengston, 2002). Additionally, omnivory likely developed when carnivores diversified their diets, and this generalist diet led to herbivory (Price et al., 2012). Large bodied animals have a variety of benefits, including a relative reduction in metabolic energy requirements. This reduction in metabolic rate creates increased food abundance for large bodied animals, which can consume low quality, hard to digest food items (Hopkins, 2018; Price and Hopkins, 2015). Large size also provides protection from predators (Weterings et al., 2018). While large carnivores are rare compared to large herbivores, their size allows consumption of a wider array of prey species than small carnivores can (Wolf, 2016).

Carnivory is a unique ecological challenge, as their food supply relies not only on the relative abundance of species, but on the ability of the carnivore to kill and consume another animal (Bengston, 2002). Small to medium sized carnivores invest more time and energy hunting and capturing prey, while large carnivores consume more per feeding while investing less in procurement of food (Rizzuto et al., 2018). This dichotomy is because smaller carnivores only obtain a portion of their daily requirements per feeding, and so are constantly on the hunt; in

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contrast, large carnivores satisfy their daily requirements much more easily (Rizzuto et al., 2018). Because carnivores tend to be the smallest mammals, it is expected that they would be most likely to favour *r*-selection, while herbivores would favour *K*-selection, and omnivores would fall between. Famoso et al. (2018) analysed the effect of diet on the relationship between body mass and reproductive strategy in mammals and showed that diet has a significant impact on this relationship in herbivores and omnivores but not in carnivores. Although the observed relationship was not significant in carnivores, it did indicate the lowest tendency for *K*-selection with increasing size of all the animals studied. Herbivores demonstrated the greatest trend toward *K*-selection with increasing size, and omnivores presented a trend with increasing size which was to be more *r*-selected than herbivores and more *K*-selected than carnivores.

Feeding adaptations in herbivorous mammals are largely restricted to the dentition and musculature of the jaw, while in carnivores these adaptations include the postcranial skeleton and musculature (Davis and Golley, 1963). Locomotion is fundamentally connected to postcranial morphology and is a critical component of ecology (Gutarra et al., 2023; Hildebrand, 1960). Locomotion relates to substrate preference (aquatic, terrestrial, volant, etc.) and, for carnivores, mode of predation (Panciroli et al., 2017). However, morphology restricts the breadth of an animal's movement, as seen in seals: highly mobile swimmers with difficulty moving on land (Panciroli et al., 2017; Taylor, 1989). Locomotion mode may also constrain size, as seen in volant and fossorial mammals, for whom small body size helps meet their physical demands (Van Valkenburgh, 1987). Thus, a carnivore's locomotor mode limits the prey it can feasibly capture (Van Valkenburgh, 1987). Carnivores also show important differences in the proportion of meat, that is, vertebrate flesh, in their diets. Carnivores that eat less than 30% meat, with nonvertebrates constituting most of their diet, are termed hypocarnivores, while mesocarnivores eat between 50–70% meat, and hypercarnivores eat at least 70% meat (Roemer et al., 2009; Holliday and Steppan, 2004; Van Valkenburgh, 1989). Although hypocarnivores eat less than 30% meat, they still require that meat to survive, which sets them apart from herbivores (Van Valkenburgh, 1989). Many omnivorous species may also be described as mesocarnivores or hypocarnivores (Holliday and Steppan, 2004; Van Valkenburgh, 1989). Carnivorous mammals may preferentially consume other vertebrates, invertebrates, or may ingest both indiscriminately. We frame this study on carnivore dietary compositions and differences in ecology as denoted by locomotion, investigating the way these factors affect the reproductive biology of carnivorous mammals.

We seek to understand how diet influences the relationship between body mass and reproductive strategy in carnivorous mammals, in addition to how ecology may affect this relationship. Our hypothesis is that resource distribution and nutritional availability may differ for carnivores based on their diets, producing distinct relationships between mass and reproductive strategy by dietary composition and prey preference. These varying relationships within carnivores would explain why the relationship between body mass and reproductive strategy is not significant for carnivores as a group. If this explanation is the case, then we should find significant relationships between body mass and reproductive strategy in carnivorous mammals when we break out lineages by dietary composition. We consider three specific dietary compositions (hypocarnivore, mesocarnivore, and hypercarnivore). Additionally, if diet does not have a profound influence on the relationship between body mass and reproductive strategy in carnivores, it can be hypothesized that ecology is the primary driving force behind the observed pattern. To this end we consider four categories of locomotion (terrestrial, fossorial, volant, and aquatic). If ecology impacts the relationship between body mass and reproductive strategy, then we should find significant relationships between body mass and reproductive strategy when we break out lineages by locomotion. Our null hypothesis is that there is no distinction in the way that diet or locomotion and body mass drive reproductive strategy in carnivores, so there should be no significant relationships in the regression analyses.

Materials and methods

We define carnivores as an ecological grouping rather than a phylogenetic one, and in this regard we can analyse predatory taxa that do not fall within the carnivora, such as whales and bats. We build upon the data set and R code from Famoso et al. (2018), which related diet and body mass to reproductive strategy. Original life history data for Famoso et al. (2018) was downloaded from the PanTHERIA database (Jones et al., 2009). Famoso et al. (2018) defined Reproductive Strategy Index (RSI) as principal component one extracted from a principal components analysis (PCA) run on three variables: offspring per year, percentage of the year dedicated to parental care, and sexual lifespan. RSI explains 64.13 percent of the variance in the reproductive data, making it a robust measure of reproductive strategy. Famoso et al. (2018) presented information on body size and life histories of female animals belonging to 561 species of mammal. We removed Herbivores and Omnivores from the data set to focus on primarily carnivorous mammals, and we added information for each species about its carnivorous diet using data from Price et al. (2012). A total of 206 carnivorous species were then separated into three subcategories based on specific diet: hypocarnivore (carnivores with meat composing less than 30% of their diets), mesocarnivore (carnivores with meat composing 50–70% of their diets, and hypercarnivore (carnivores with meat composing over 70% of their diets). The number of species examined varied by category, with 155 species being hypocarnivorous, 25 hypercarnivorous species, and 28 mesocarnivorous species. To account for any effects of phylogenetic relatedness on the relationship between diet and body size for each diet category, we performed a phylogenetically informed analysis of covariance (PANCOVA) on these data using the caper package version 1.0.1 (Orme et al., 2018) in R version 4.1.2 (R Core Team, 2021). Following Famoso et al. (2018), we used 101 mammalian phylogenetic trees created by Fritz, Bininda-Emonds, and Purvis (2009). Our code was prepared with the intent of comparing both phylogenetically informed least squares (PGLS) regressions within each specific diet grouping, plotting the body mass and reproductive strategy index on continuous evolutionary contour maps in phytools version 1.0-1 (Revell, 2012), and checking for statistical significance in PANCOVAs between the diet categories over 101 iterations, each of which considered the evolutionary signal for a different phylogenetic tree. We modified code from Famoso et al. (2018) (Supplementary Material). To determine the effect that aquatic and volant mammals had on the significance in the results of the PANCOVA due to their unique evolutionary histories, bats and whales were removed entirely from an iteration of the complete analysis. A second complete analysis, built on a modification of the first, compared carnivores based on their mode of locomotion. For this comparison, the species were categorized in terms of locomotion mode for which sufficient samples were available (terrestrial, fossorial, aquatic, and volant) and the analysis was conducted on these categories according to the procedures described above. Again, the number of species considered in the analysis varied by category: 108 terrestrial species, 18 aquatic species, 10 fossorial species, and 67 volant species. Given the nature of the analysis based on locomotion, only one was performed with aquatic and volant animals included as excluding these would eliminate two locomotion categories of interest. Arboreal animals were included in the data set, and are shown in the figure, but were excluded from analysis due to poor sample size. Locomotion was considered independently of diet to determine how ecological differences may affect the relationship between body mass and reproductive strategies in carnivorous mammals.

Values for slope, intercept, *p*-values, and standard errors for each stat were obtained from the outcomes of the 101 iterations in each analysis. Results obtained through testing PGLS regression intercepts against each other, and the general carnivore trend were denoted PANCOVA result 1, while PANCOVA result 2 was obtained by testing both PGLS slopes and intercepts against each other and the general carnivore trend. The median *p*-values for slope and intercept across all analyses were then taken from the lists of results and reported in Tab. 1-3. Median slope and intercept values from repeated PGLS were then used to plot regression lines (Fig. 1-3) which are more repres-

entative of the data than single standard PGLS regression lines alone. Median values for PANCOVA results were considered in the final interpretations.

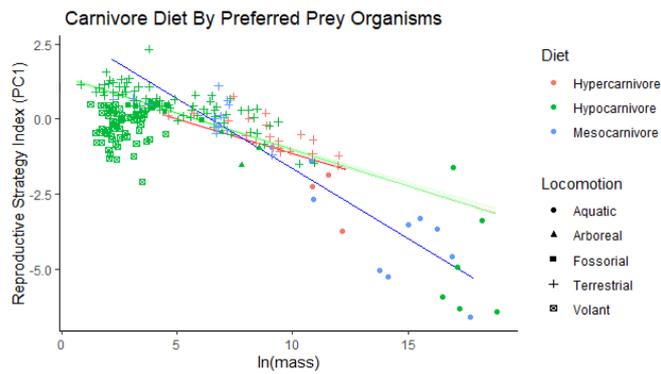


Figure 1 – Regression lines relating the natural log of body mass to the reproductive strategy index of carnivorous mammals based on dietary composition, after phylogenetic correction. Colours denote diet with the green line representing hypocarnivores, blue representing mesocarnivores, and the red representing hypercarnivores. While a general trend exists for lower reproductive rates in larger animals, the degree to which this occurs varies based on diet. The image shows solid lines based on the median coefficients and faded lines represent where 101 iterations were plotted.

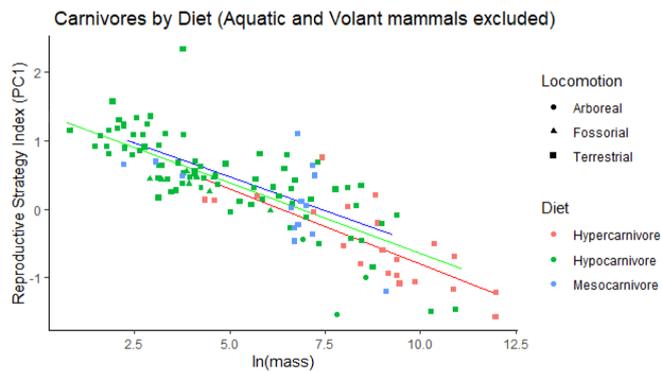


Figure 2 – A modification of Fig. 1, excluding whales and bats. The image shows regressions plotted based on median slopes and intercepts, generated through analysis of 101 phylogenetic trees. Faded lines represent the 101 individual iterations while solid lines represent the median coefficients.

Results and Discussion

While we found a difference in the relationship between body mass and reproductive strategy in three subcategories of carnivore when separated based on diet (hypocarnivore, mesocarnivore, or hypercarnivore), the overall model is not statistically significant when slopes and intercepts of subcategory PGLS regressions are tested against each other and the general carnivore trend which disregards diet information ($p=0.8044$). When bats and whales are removed from the analysis, so only terrestrial carnivores are considered, there is a striking decrease in the p -value of the effect of diet on the relationship between body mass and reproductive strategy ($p=0.0745$), though focusing on terrestrial carnivores does not yield a statistically significant result for the model as shown in (Tab. 2). While unique trends appear to exist, the median results of PANCOVA analyses run on 101 phylogenetic trees indicate that differences according to diet are not enough to exclude this observation from being an artifact of random chance (Fig. 1). The PANCOVA results and other statistics obtained from the analysis are shown in Tab. 1-2. Running the analysis on carnivorous mammals predicated on locomotion returned a significant result for the overall model ($p=0.008$), as detailed in Tab. 3. Significant results were observed for terrestrial, fossorial, and swimming animals but not for volant animals (bats). The results for terrestrial mammals were noteworthy as p -values

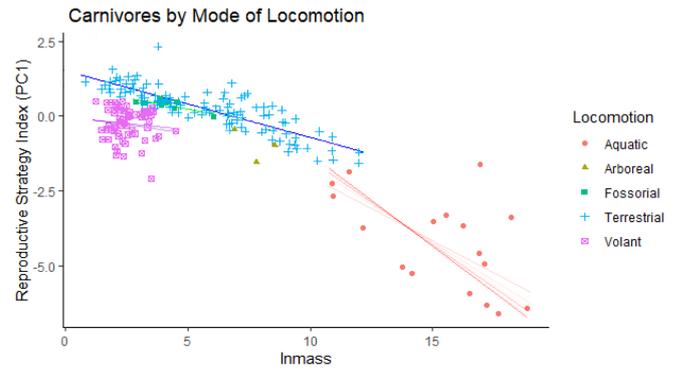


Figure 3 – The relationships between diet and body mass based on carnivore locomotor guilds irrespective of diet. The green line represents the regression for aquatic animals, the yellow line represents the regression for fossorial animals, the blue line represents the regression for terrestrial animals, and the purple line represents the regression for volant animals. Arboreal animals are represented by red circles but were not considered in this study. Lines were plotted based on median slope and intercept values generated through the analysis of 101 phylogenetic trees. Solid lines represent the median coefficients for slope and intercept while the faded lines represent each of the 101 iterations.

for the slopes and intercepts of this group returned apparent zeroes, indicating a high degree of confidence in the generated regression. The slope for volant carnivores was found to be not statistically different from zero, which may relate to a narrow range of body size likely related to adaptations for flight (Fig. 3). Confounding factors related to the unusual modes of parental care, locomotion, and ecosystem energetics found in flying or aquatic carnivores are likely responsible for the observed discrepancies and limiting the diet analysis to terrestrial carnivores eliminates these variables (Fig. 2). Diet does not appear to have a significant impact on the relationship between body mass and reproductive strategy in carnivorous mammals. However, ecology as denoted by locomotion seems to significantly impact the relationship between body mass and reproductive strategy in carnivores. Inferences were made based on median P -values returned when PANCOVA analysis was performed on 101 mammalian family trees for the variables in question. Similar methodology was used in (Bolt et al., 2022). We emphasize that the uncertainty produced from each individual iteration was not considered when making these inferences, so any interpretations in this regard should be made with a degree of caution.

When the relationships between body mass and reproductive strategy are compared on the basis of diet between herbivores, carnivores, and omnivores a significant result is observed for herbivores and omnivores, but not for carnivores though the overall model is significant (Famoso et al., 2018). It was presumed that the reason for the deviation seen in carnivores was a difference in resource distribution and availability between carnivores that preferentially feed on other vertebrates and those that feed primarily on invertebrates (Famoso et al., 2018; Carbone et al., 1999). We have found that diet does not impose a significant influence on the way that body mass drives reproductive strategy in carnivores, but that ecological differences observed among carnivores do impose a significant influence on this relationship. One reasonable explanation for our results is that carnivores represent a more basal dietary state, subsisting on easily digested and highly nutritive animal protein that is homogeneous in nutritional value across prey species. It could be that dietary nutrition varies more based on the relative amounts of meat consumed, and that these differences could be offset by factors such as frequency of feeding or the nutritional value of invertebrate or plant materials that supplement the diet. Locomotion introduces another variable as the kinds of foods that animals can obtain is contingent upon their mode of locomotion. For example, a bat has access to a selection of prey species that is distinctly different than those available to a marine mammal. It appears that the effect diet has on the relationship between body mass and reproductive strategy in carnivores is subtle, with differences in ecology shaping this relationship.

Table 1 – Statistical results for the three carnivore diet categories and accompanying PANCOVA results. Values ≤ 0.05 are taken to be statistically significant. Slopes, intercepts, *t*-values and *p*-values are medians from 101 random replicates. The Standard Errors of the Slopes and Intercepts reflect variation in values among the 101 random replicates.

	Value	Standard Error	<i>t</i> -value	<i>p</i> -value
Slope (Overall Model)	-0.1960	0.005967863	-6.039	<0.0001
Intercept (Overall Model)	1.1876	0.03347238	1.512	0.1320
Hypocarnivore Slope	-0.2427	0.00049481	-6.921	<0.0001
Mesocarnivore Slope	-0.4662	$1.025 \cdot 10^{-10}$	-12.476	<0.0001
Hypercarnivore Slope	-0.2274	0.00031171	-3.693	0.001201
Hypocarnivore Intercept	1.4329	0.00253749	2.684	0.008086
Mesocarnivore Intercept	3.0333	$6.253 \cdot 10^{-10}$	8.114	<0.0001
Hypercarnivore Intercept	1.1432	0.00296614	1.456	0.158819
PANCOVA result 1	NA	NA	NA	0.8613521
PANCOVA result 2	NA	NA	NA	0.8043951

Table 2 – Statistical results for the three specific diet subcategories of carnivores when bats and whales are removed from the data set. Values ≤ 0.05 are taken to be statistically significant. Slopes, intercepts, *t*-values and *p*-values are medians from 101 random replicates. The Standard Errors of the Slopes and Intercepts reflect variation in values among the 101 random replicates.

	Value	Standard Error	<i>t</i> -value	<i>p</i> -value
Slope (Overall Model)	-0.1318	0.005967863	-4.521	<0.0001
Intercept (Overall Model)	1.0235	0.03347238	1.756	0.0816
Hypocarnivore Slope	-0.2053	0.000113197	-7.890	<0.0001
Mesocarnivore Slope	-0.1976	$9.5000 \cdot 10^{-12}$	-3.130	0.0064
Hypercarnivore Slope	-0.2188	$6.1944 \cdot 10^{-11}$	-5.305	<0.0001
Hypocarnivore Intercept	1.4144	0.000485875	6.939	<0.0001
Mesocarnivore Intercept	1.4673	$7.7605 \cdot 10^{-12}$	3.566	0.0025
Hypercarnivore Intercept	1.3976	$6.1663 \cdot 10^{-10}$	3.799	0.0011
PANCOVA result 1	NA	NA	NA	0.1485993
PANCOVA result 2	NA	NA	NA	0.0541655

Differences in reproductive biology observed in various locomotor groups can likely be attributed to a combination of morphological deviation from a generalized terrestrial body plan, biological constraints such as body size, and the unique ecosystem energetics experienced by some groups. For example, in insectivorous bats there seems to be no correlation between reproductive strategy and body mass, which suggests that the evolution of reproductive biology in bats is driven by factors unrelated to body mass. However, terrestrial mammals demonstrate a very strong correlation between body mass and reproductive strategy suggesting that these are fundamentally connected in terrestrial carnivores. It may be that diet began affecting this relationship in a significant way when carnivores diversified their diets to include larger amounts of plant material, and certainly a transition to herbivory led to a change in focus from food collection to food processing. Because the relationship between body mass and reproductive strategy appears to operate independently of diet in carnivores, we can infer that the evolutionary biology of carnivores is driven by different factors than those seen in omnivores or herbivores. These ideas are reinforced by the restriction of morphological adaptations to diet in herbivores to the teeth and jaws, while in carnivores they include the postcranial musculoskeletal system (Davis and Golley, 1963). Additionally, in carnivores it appears that dental morphology reflects diet, but may be shaped more by competition for food among sympatric carnivores, which results in resource partitioning (Van Valkenburgh, 1989). For example, polar bear teeth are not significantly different in form than those of a grizzly bear, despite polar bears being much more carnivorous, suggesting that in the absence of competition, the ancestral tooth form was retained in polar bears despite dietary changes (Van Valkenburgh, 1989). It is worth noting that behavioural adaptations like pack hunting can increase the efficacy of a predator beyond its physical means and can serve to expand or improve diet (Taylor, 1989). Behavioural adaptations in carnivores can also allow a carnivore to rear more offspring per litter than would otherwise be possible (Oftedal and Gittleman, 1989).

Terrestrial carnivores returned *p*-values so small they were represented as “0” for both slope and intercept which suggests a high degree of confidence. The strong connection between body mass and reproductive strategy in terrestrial carnivores is likely reflective of physical demands of supporting extra weight during pregnancy in addition to energetic demands faced by these animals. Energy requirements increase significantly during pregnancy which is due to a combination of increased metabolic rate and increased activity levels (Oftedal and Gittleman, 1989). Litter size has a strong positive correlation to body mass in mammals which speaks to the importance of litter size when it comes to maternal expense, and the ability of larger mammals with lower metabolic rates to care for greater numbers of offspring. The energetic requirements for producing a litter drastically exceed the energy deposited in foetal tissues and involves the production of mammary, uterine, and placental tissues. Carnivores are generally altricial and require extensive parental care to survive which is related to the energy deposited in foetal tissues by the mother during gestation (Oftedal and Gittleman, 1989). Precocial ungulate neonates contain 20–40 percent more energy than what has been observed in the tissues of neonate domestic carnivores. Additionally, carnivore milk tends to be more nutritively rich than ungulate milk (Oftedal and Gittleman, 1989). A domestic cat that has a litter of 5 kittens will spend about twice the energy of a cat with 2 kittens during intense lactation (Oftedal and Gittleman, 1989). These limitations can be buffered by behavioural adaptations as in some species conspecific individuals may cooperate in the feeding, defence, and transport of young.

Adaptations to flight place restrictions on body size, and this may explain why the observed slope for volant carnivores was not statistically different from zero (Fig. 3), as a narrow range of body mass is demonstrated by insectivorous bats. A variety of reproductive strategies are present in insectivorous bats: delayed ovulation, delayed implantation, sperm storage, and reproductive synchrony with the environment (Altringham, 2001). In each case the reproductive strategy seems to circumvent pregnancy during hibernation and facilitate birth during the

Table 3 – Statistical values obtained for mammalian carnivores when categorized on the basis of locomotion. Values ≤ 0.05 are taken to be statistically significant. Slopes, intercepts, *t*-values and *p*-values are medians from 101 random replicates. The Standard Errors of the Slopes and Intercepts reflect variation in values among the 101 random replicates.

	Value	Standard Error	<i>t</i> -value	<i>p</i> -value
Slope (Overall Model)	-0.1966	0.0063871	-6.0366	<0.0001
Intercept (Overall Model)	1.1914	0.0366161	1.5147	0.1314
Terrestrial Slope	-0.2231	2.76986*10 ⁻⁵	-13.7031	0
Fossorial Slope	-0.1508	5.0773*10 ⁻¹²	-3.4793	0.0083
Aquatic Slope	-0.5450	0.0038437	-2.9889	0.0087
Volant Slope	-0.1072	0.0018691	-1.0171	0.3129
Terrestrial Intercept	1.5380	9.4086*10 ⁻⁵	13.4174	0
Fossorial Intercept	0.9933	2.6150*10 ⁻¹¹	5.3845	0.0006
Aquatic Intercept	3.9187	0.0534845	1.4290	0.1722
Volant Intercept	-0.0191	0.0034335	-0.0584	0.9117
PANCOVA result 1	NA	NA	NA	0.001463948
PANCOVA result 2	NA	NA	NA	0.008043177

most productive time of the year when food is most abundant. This maximizes survivability for both mother and offspring as reproduction is energetically expensive. Energy transfer from mother to offspring through milk production and feeding is costly for bats as well. Bats tend to “burn hot” even for small mammals, which is part of the reason why they are such effective vectors for disease as they are perpetually running a fever, but this elevated body temperature combined with small size may necessitate the need to prevent gestational overlap with hibernation or periods of prey scarcity to avoid starvation. It is worth noting that the group of herbivorous bats classically referred to as the Megachiroptera are much larger than their insectivorous counterparts, the Microchiroptera which likely reflects energetic differences between herbivorous and carnivorous lifestyles. The size discrepancy between megachiropterans and microchiropterans is likely also related to the necessity for maneuverability in predatory bats rather than strictly size limitation related to flight. It turns out that bats are generally K strategists, which likely reflects the burden that carrying and rearing altricial young exacts on these creatures. Bats tend to fly with their young clinging to them which for a small flying carnivore is physically laborious (Altringham, 2001).

Marine environments represent a unique set of conditions both physically and energetically. In marine ecosystems, the largest animals are carnivores with whales representing some of the largest animals to ever exist (Bianucci et al., 2019). The incredible size of marine carnivores can be attributed to a combination of low energy feeding mechanisms, an abundant and stable food supply of high-quality animal protein, and the unique physical conditions of occupying an aquatic habitat (Goldbogen et al., 2019). In general, mammals that are adapted to an aquatic lifestyle are larger than their terrestrial relatives. Mustelids are one group in which aquatic species are significantly larger than terrestrial species, an adaptation believed to reduce heat loss in the aquatic environment (Estes, 1989).

Future research should consider behavioural adaptations or adaptations to various environmental conditions with respect to the relationship between body mass and reproductive strategy in carnivores. A statistically significant result might be found in carnivores when the effects of ecological characteristics such as feeding strategy or degree of social behaviour on the relationship between body mass and reproductive strategy are tested. We find that diet does not significantly influence the way in which body mass drives reproductive strategy in carnivores, however ecology seems to strongly influence this relationship.

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