



Habitat Drives Body Size Evolution in Mustelidae (Mammalia: Carnivora)

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Abstract

Body size of organisms is often associated with physiological demands and habitat structure. Several theories and models have been proposed to explain body size trends across geographical space and evolutionary time. It is proposed that herbivores are larger due to their more voluminous digestive system, allowing a longer retention time of the digested material. Simultaneously, for carnivores, it is expected that the bigger the prey, the larger the predator. Additionally, some body size trends have been attributed to climatic variation across space and habitat structure. Bergmann's Rule proposes that larger endotherms inhabit colder areas, once a larger body size promotes better heat retention due to reduced surface/volume ratio. Similarly, aquatic endotherms are larger than expected, due to analogous physiological demands to endotherms living in colder environments. Here we tested whether body size of the Mustelidae clade can be explained by diet, habitat structure or environmental temperature. We performed phylogenetic regressions to assess the relationships between body size and the aforementioned predictors in 53 species of Mustelidae. We found that neither diet nor temperature were related to body size evolution. However, habitat was related to body size, with semi aquatic species being larger. Mechanisms involving thermal inertia, predation pressure, better quality resources close to water and bone density are hypotheses that suggest larger body sizes evolution in semi-aquatic vertebrates. We highlight the importance of considering widely accepted ecological traits for large groups, at lower taxonomic levels, in order to expand our understanding of the maintenance of these standards on different scales.

Keywords Bergmann's rule · Habitat structure · Temperature · Trophic niche · Diet · Semi-aquatic

Introduction

Body size is one of the most studied characteristics among organisms at macroecological and macroevolutionary scales (LaBarbera, 1986; Maurer et al., 1992; Cooper & Purvis, 2010; Saareinen et al., 2014; Smith et al., 2016). This attribute has been related to functions of organisms in ecosystems, including resource usage, ecological interactions, population dynamics, community structure and adaptation (Bonner & Peters, 1985; Smith & Lyons, 2013). Historically, researchers have assessed the body size variation along temporal and environmental gradients, which makes this trait an appropriate way to study correlated evolution (Cooper & Purvis, 2010; Saareinen et al., 2014; Smith et al., 2016).

One of the explanations proposed for size evolution is the relationship between diet and body size (Soler et al., 2016). Larger animals require more energy input, feeding on resources on a larger scale and abundance (Price & Hopkins,

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2015). Although plant matter (leaves, fruits, roots and seeds) constitutes most of biomass available as a food resource, organisms that consume this resource have larger digestive system, which increase retention time of the digested material that deal with the difficult digestibility and low caloric value of plant matter (Demment & Soest, 1985; Clauss & Hummel, 2005). Because the gut volume is a constant proportional to body size (Demment & Soest, 1985), herbivores are expected to be larger than omnivores, which are expected to be larger than carnivores (e.g., Pough, 1973; Kramer & Bryant, 1995; Burness et al., 2001; O’Grady et al., 2005). Simultaneously, among carnivores, the relationship between the body size of predators and prey appears to be positive, so large-bodied individuals consume larger preys (Newman, 1999; Aljetlawi et al., 2004; Cooper & Stankowich, 2010; Yvon-Durocher et al., 2011). On the other hand, it may be difficult to predict body size in omnivores when plant diet and prey size is considered, because they present a variation in the quantity of plant matter consumed and prey species of several sizes (e.g., Kollias & Fernandez-Moran, 2015), and are often less studied than other animals (Brooke et al., 2014).

In addition to associations with ecological traits, body size has relationships that depend on physiological mechanisms, such as the body temperature control in endothermic animals (e.g., Schmidt-Nielsen & Knut, 1984). Bergmann (1847) demonstrated that species of endothermic animals inhabiting cold environments are larger than those located in warmer environments, in a trend known as Bergmann’s rule. The proposed mechanism is that larger animals have a smaller surface/volume ratio, which promotes less heat loss to the external environment. However, there are some discussions about how the rule is applied (Blackburn et al., 1999) and its generality inside groups (Freckleton et al., 2003; Meiri & Dayan, 2003; Diniz-Filho et al., 2009; Clauss et al., 2013). Additionally, this relationship and mechanism are similar for mammals that experience or live in aquatic environments, since organisms lose body heat faster inside water than exposed to the air (Ahlborn & Blake, 1999). Although some aquatic mammals also show a Bergmannian trend of body size when correlated to sea surface temperature (Torres-Romero et al., 2016), the interaction of aquatic habitat and environmental temperature remains elusive.

All these ecotrophic and environmental factors that can contribute to body size evolution have been usually studied separately, so Mustelids are an interesting group to test predictions involving the effects of all these factors simultaneously. Mustelidae is the most diverse family within the order Carnivora, comprising 58 species (Law et al., 2018). These organisms collectively exhibit important modifications in relation to body patterns, such as the elongated body, reduction in size, and contraction of the limbs (Law et al., 2019). They also have terrestrial and semi-aquatic lineages, with

various diets, from plant matter to invertebrates and vertebrates (Kollias & Fernandez-Moran, 2015). Despite exhibiting a wide geographic distribution (Koepfli et al., 2008), previous studies found no evidence for the Bergmann’s rule, but testing only for environmental temperature or latitude without considering other ecological factors (Ashton et al., 2000; Meiri & Dayan, 2003; Clauss et al., 2013). These demonstrate the need for a more comprehensive study that considers more ecological parameters to provide additional robust evidence for the evolution of Mustelidae body size.

In this context, we investigated here how environmental factors drive the evolution of body size in Mustelidae. We used a comprehensive trait database and the most complete phylogenetic hypothesis for Mustelidae. Adopting a phylogenetic comparative approach, we expect that: (I) body size has a positive relationship with the more a species feeds on plant matter; (II) larger species feed more frequently on larger prey; (III) species that live at lower temperatures and (IV) have semi-aquatic habits have larger body sizes.

Material and Methods

Data Collect

First, we constructed the Mustelidae tree using the phylogenetic hypothesis proposed by Law et al. (2018), which has 53 of the 58 species inserted (Fig. 1), and the package “phySketch” (Revell, 2017) to draw and extract the phylogenetic structure values. We obtained body size, habitat structure, and diet data from the Phylacine 1.2 (Faurby et al., 2018), a platform containing information on 5,831 mammal species.

We define body size as the natural logarithm of the mass (in g) of each species. For diet information, we used percentage values of food items consumed by species. More specifically, as vegetable matter ingested (I), we directly considered the percentage of vegetable diet for each species. For the larger prey predation (II), we considered vertebrates as indicative of larger prey, as they are predominantly larger than invertebrates. Then, we calculated the proportion of vertebrates ingested dividing the proportion of vertebrates by the sum of proportion of vertebrates and invertebrates. As information on habitat (III), we used habitat structure data (terrestrial, marine or freshwater) for each species and categorically considered semi-aquatic those living in a marine and freshwater environment. As temperature information (VI), we used the mean annual temperature (BIO1) values for the centroid of the species geographic distribution, obtained from the CHELSA database (Karger et al., 2020). Centroids were defined by recording latitude and longitude data from polygons based on species’ geographic range (IUCN Red List database; www.iucnredlist.org, access: July 2021). We performed the polygons’ manipulation and the

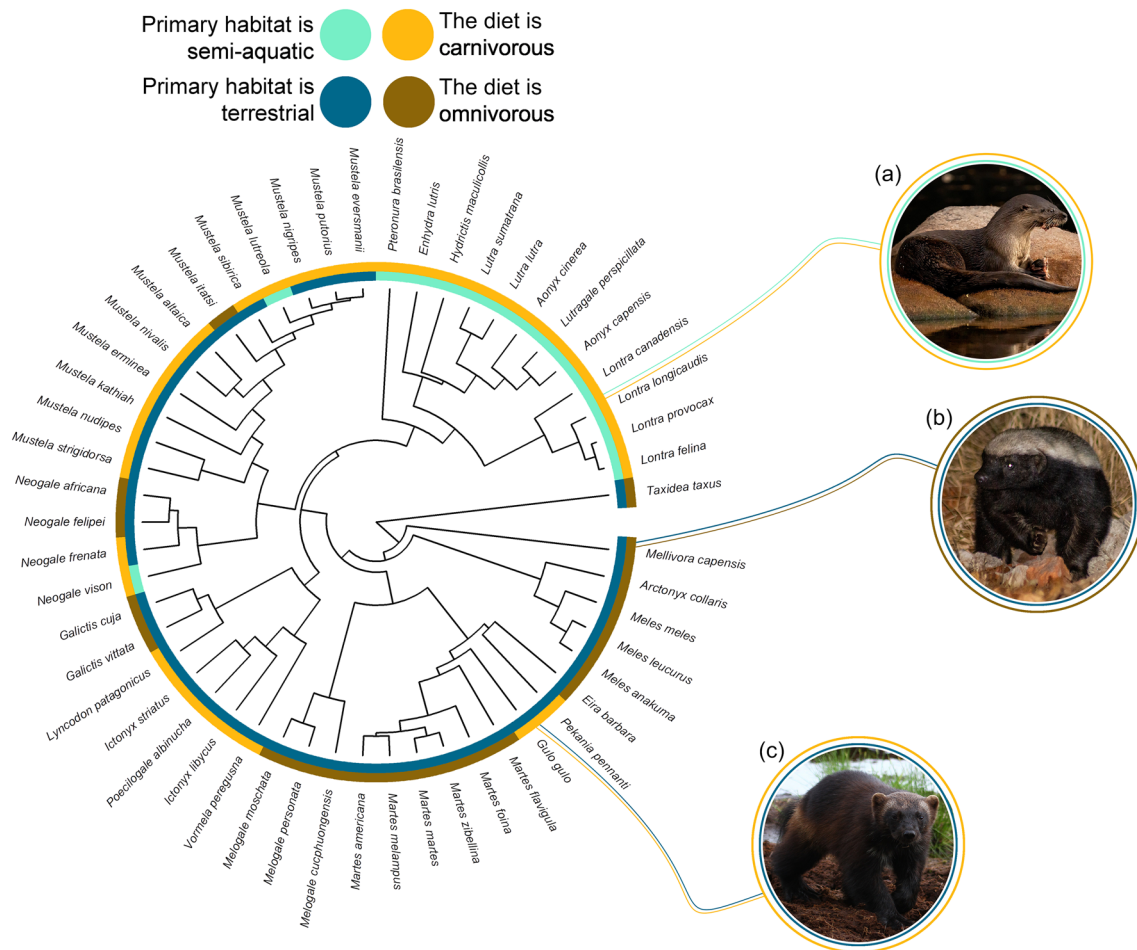


Fig. 1 Phylogenetic distribution of habitat structure and diet. Examples of species in each category: **a** the Neotropical Otter (*Lontra longicaudis*; photograph by Jéssica dos Anjos) is carnivorous and semi-aquatic, **b** the Honey Badger (*Mellivora capensis*; photograph

by Callum Evans) is omnivorous and terrestrial and **c** the Wolverine (*Gulo gulo*; photograph by Manuel Ruedi) is carnivorous and terrestrial

extraction of centroids using “rgdal” (Bivand et al., 2021) and “letsR” (Vilela & Villalobos, 2015) packages. Finally, we extracted the temperature values from the centroid of the distribution of each species using the “raster” package (Hijmans, 2020).

Statistical Analysis

Initially, to minimise multicollinearity between our predictors, we evaluated Spearman’s correlation coefficients. We evaluated the effect size of predictors according to Cohen (1988) and removed variables highly correlated ($r_s > 0.5$ or $r_s < -0.5$; Supplementary Table 1). Then, we sought to determine whether our predictors had phylogenetic non-independence (see Revell, 2010). We built a multiple regression model among the mass and predictors. Subsequently, we extracted the residuals from this model and analysed the presence of autocorrelation through Moran’s I coefficients.

Because we identified a positive autocorrelation in model residuals (see Results), we considered the phylogenetic structure in all subsequent analyses.

To establish the phylogenetic dependence, we calculated the Pagel’s lambda phylogenetic signal (λ ; Pagel, 1999) of the response variable, \ln of mass, using “phyloSignal” (Keck et al., 2016) and “phylobase” (Bolker et al., 2011) packages. Additionally, we evaluated the evolution of attributes through the phylogenetic signal representation curve (PSR; Diniz-Filho et al., 2012). The PSR models an attribute along the phylogenetic tree based on the relation of the phylogenetic signal of that attribute (the R^2 of a multiple regression of trait against eigenvectors produced from the phylogenetic distance matrix) and the accumulated phylogenetic representation (respective eigenvalues). We calculated the PSR curve using the “PVR” package (Santos et al., 2018) and we estimated the lambda statistic using the “phylosignal” package (Keck et al., 2016).

To test the effect of temperature, habitat, plant diet, and vertebrate diet on body size, we fitted phylogenetic generalised least squares models (PGLS; Freckleton et al., 2002) and compared our models through the Akaike Information Criterion corrected (AIC_C). We calculated the AIC_C difference (Δ_i) and Akaike weights (w_i) to interpret the relative likelihood of a model given the data (Burnham & Anderson, 2002). We selected the models with Δ_i less than 2.0 and calculated the weighted estimates and standard errors for the variables that appeared in the selected models using w_i as the weight. We used the “nlme” (Pinheiro et al., 2017) and “phylobase” (Bolker et al., 2011) packages for the analyses.

Results

Exploratory Analysis

Despite the relative low values, there is a significant positive phylogenetic autocorrelation (Moran's I) in the residuals from the mass regression model with temperature, habitat structure, and plant and vertebrate diets (Observed Moran's I = 0.071; SD = 0.031; Expected Moran's I = 0.019; $p = 0.003$). Therefore, we consider the phylogenetic structure in the subsequent models to test the correlation of mass with other traits.

Two exploratory analyses of the phylogenetic signal presented consistent results with each other. First, the λ for the mass of Mustelidae species returned a value of 0.543 ($p = 0.002$). Similarly, the PSR curve converged to a pattern coherent with intermediate values of λ (Fig. 2), indicating a phylogenetic signal that departs from Brownian motion.

Model Selection and Traits Correlation

From the comparison of the AIC_C values of the PGLS models, using $\lambda = 0.543$, we selected four models with $\Delta_i \leq 2.0$ (Table 1; see Supplementary Table S2 for detail on the statistical models). Only habitat types appeared in all four models (Table 1). We found that semi-aquatic species were more than three times larger (weighted estimates in ln: $x = 9.215$, SE = 0.639; Fig. 3a) than the terrestrial species (weighted estimates in ln: $x = 7.976$; se = 0.539; Fig. 3a). Additionally, terrestrial species presented a greater body size variation than semi-aquatic species, however, both showed similar maximum values (terrestrial: 9.742 and semi-aquatic: 10.086, Fig. 3). In contrast, semi-aquatic species showed a greater minimum body size than terrestrial species (terrestrial: 4.783 and semi-aquatic: 6.087, Fig. 3). The other variables, such as temperature (estimates in ln: $m = 0.009$; SE = 0.014; Fig. 3b), vertebrate diet (estimates in ln: $m = -0.009$; SE = 0.006; Fig. 3c) and plant diet (estimates in ln: $m = 0.010$; SE = 0.014; Fig. 3d) showed small

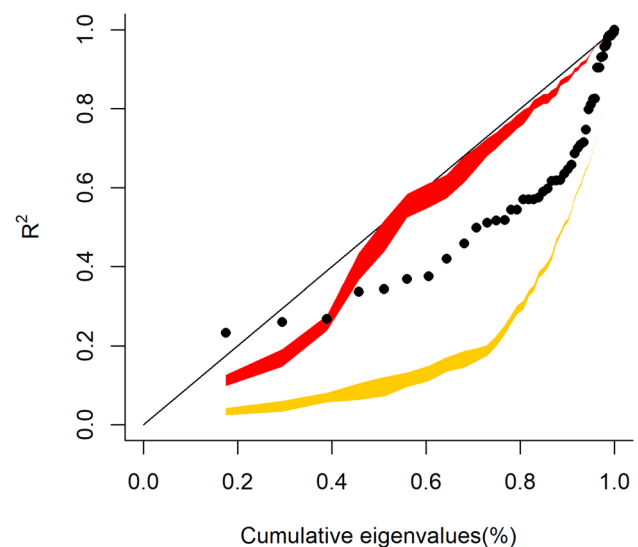


Fig. 2 PSR curve representing the body size of Mustelidae, including the Brownian evolution model curves (red) and the null model (yellow) (Color figure online)

and possibly no effects in body size and each appeared only once in the four models (Table 1).

Discussion

We sought to know if the body size evolution in mustelids was related to diet, environmental temperature, and habitat structure. We speculated that all these attributes could partly explain the body size evolution in Mustelidae. More specifically, we expected that (I) species that ate more plant matter, (II) hunted larger prey, (III) lived in colder environments and (IV) had a semi-aquatic habit would have larger sizes. Our study only showed that Mustelidae from semi-aquatic habitats were larger than terrestrial ones. Dietary habits and environmental temperature did not show biological implication to the evolution of body size.

Relationships between larger sizes and semi-aquatic species were also shown in families of small rodents (Wolff & Guthrie, 1985). This demonstrates that this pattern, often found within large taxonomic groups, such as birds (Gaston & Blackburn, 1995) and mammals (Smith & Lyons, 2011; Tucker & Rogers, 2014), can also be maintained at lower taxonomic levels, such as families. Different mechanisms can explain the observed trend: (I) thermodynamic models, (II) ecological interactions, and (III) limb bone density. Regarding thermodynamics (I), due to surface/volume ratio, homeotherms have minimal size restrictions due to constant heat loss caused by water submersion (Downhomer & Blumer, 1988). Considering that thermal energy loss is dependent on the surface area

Table 1 Set of four PGLS models for Mustelidae body size, ordered by the least Δ_i

| Habitat difference | DietVert | DietPlant | Temperature | df | AIC _c | Δ_i | w_i |
|--------------------|----------|-----------|-------------|----|------------------|------------|-------|
| 1.274 | – | – | – | 3 | 158.5 | 0 | 0.383 |
| 1.117 | –0.009 | – | – | 4 | 158.9 | 0.40 | 0.314 |
| 1.348 | – | 0.010 | – | 4 | 160.3 | 1.77 | 0.158 |
| 1.289 | – | – | 0.009 | 4 | 160.4 | 1.93 | 0.146 |

Habitat difference values represent the arithmetic difference between body size for Semi-Aquatic and Terrestrial species, in that order. DietVert and DietPlant values represent, respectively, the decrease of body size as the proportion of vertebrate ingested increases and the increase of body size as plant consumption increases. Temperature represents the increase in body size as temperature increases

df degrees of freedom, AIC_c Akaike criterion's information corrected, AIC_c differences, w_i Akaike weights

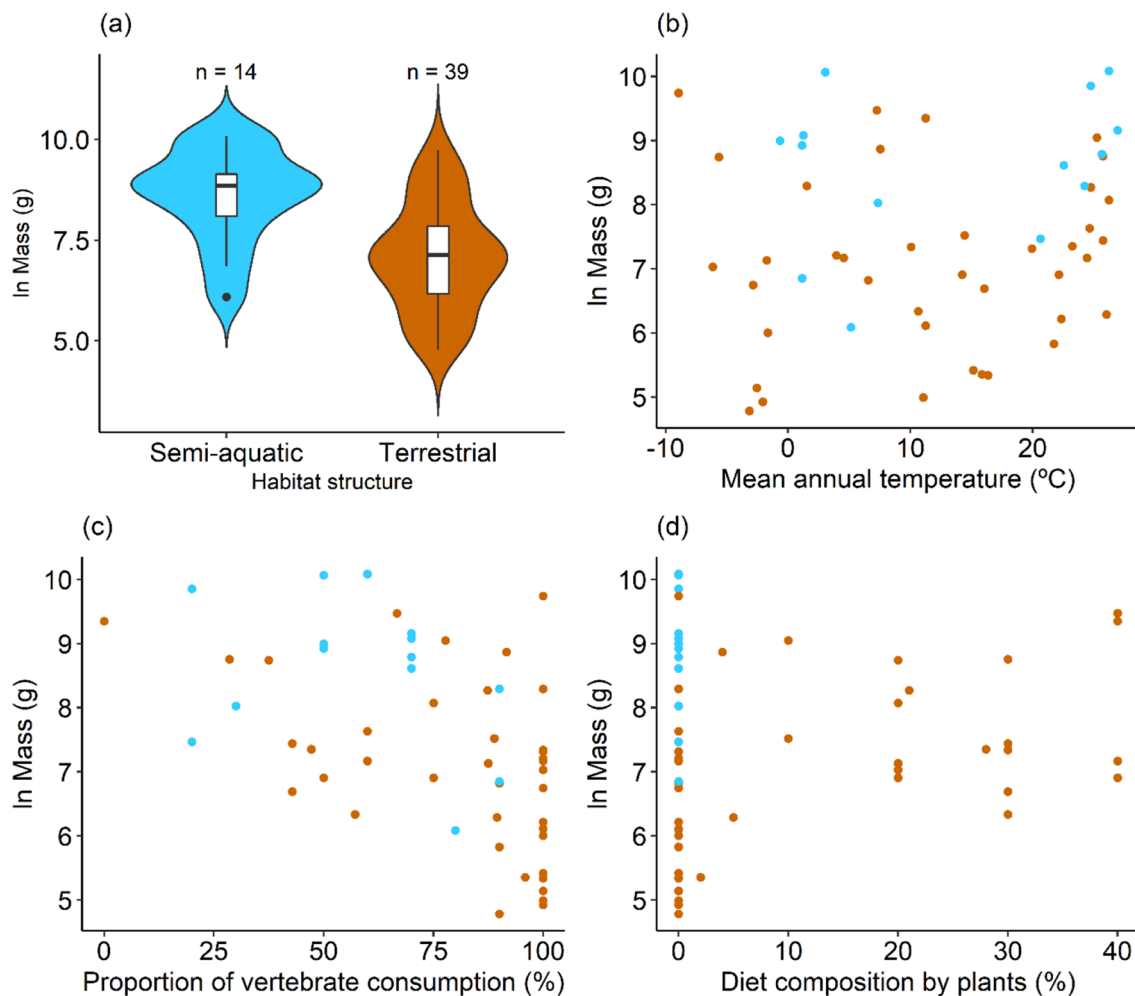


Fig. 3 Relationships among body size and habitat structure (a), mean annual temperature (b), proportion of vertebrate consumption (c) and diet composition by plants (d). Points in brown indicate terrestrial

mustelids, while points in blue indicate semi-aquatic mustelids (Color figure online)

of a body, an aquatic environment is unfavorable for small mammals, once they have to deal with a faster energy loss than large mammals (Gaston & Blackburn, 1995; Ahlborn & Blake, 1999; Gearty et al., 2018). Concerning ecological

interactions (II), larger sizes in aquatic species could result from predation pressure by fishes on small prey, while on land larger individuals would be less cryptic and more vulnerable, evolving smaller sizes (Wolff & Guthrie,

1985). Additionally, water habitats have increased protein availability in food webs (Gaston & Blackburn, 1995; Tucker & Rogers, 2014), as well as the quality of available resources, since high-quality patches of vegetation are located close to water bodies (Wolff & Guthrie, 1985). The increased interspecific competition favours larger individuals which have priority access to resources (Wolff & Guthrie, 1985). Finally, larger sizes might be related to greater limb bone density (III), which is observed to be higher in semi-aquatic and lower in terrestrial mustelids (Fish & Stein, 1991). Hence, denser bones would be a by-product or a consequence of larger bodies and would work to counteract buoyancy and allow deep dives for foraging (Fish & Stein, 1991). The bone density mechanism apparently is correlated to habitat in Mustelidae, reinforcing this hypothesis (Kilbourne & Hutchinson, 2019).

The larger sizes of semi-aquatic species evidenced by our results can be explained by both thermodynamic and bone density-related mechanisms, but partially by ecological interactions mechanisms. We observed that semi-aquatic species did not exhibit sizes smaller than a certain threshold, which they could not retain heat efficiently, whereas larger species living in water could better cope with the increase in bone density. Simultaneously, pressures exerted by predation or nutritional needs in an aquatic environment explain larger mustelids, while conspicuity in a terrestrial environment apparently does not, as we observed a wide range of sizes, including large animals. Given the strength of habitat effects on body size, we can assume selection pressures being exerted by one of these mechanisms, or an interaction of two or more of them. The strength of these pressures is even more evident in the fact that the trait is evidently expressed in semi-aquatic species, which leads us to believe that even partially living in an aquatic environment is sufficient to select large sizes.

We found no biological implication for neither diet nor temperature on body size evolution. Regarding the plant matter consumption, we assume that the selection for larger body sizes for plant consumers is not as strong as the pressure exerted by the aquatic environment to be larger. Therefore, we observed larger individuals in the water that most likely overcame the physiological restrictions imposed by this habitat, in spite of their exclusively carnivorous habit (Fig. 3d). Despite body size of predators and prey being positively correlated in some groups (Shine, 1991; Portalier et al., 2018), a previous study revealed that abiotic constraints were crucial on evolutionary shifts in mustelids body plan (Law, 2019), that allowed them to explore new environments for resources (see below; King & Powell, 2006). One of these modifications was the broader cranial shape and large jaw muscles, which compensate for their small bodies allowing them to consume prey up to 10 times larger than their own body mass (Law, 2019). As a consequence, these

morphological innovations may have hampered body size evolution driven by item consumption from specific trophic guilds, although aspects of the diet may have contributed to the evolution of body shape rather than size.

Finally, while Bergmann's rule is valid (Torres-Romero et al., 2016) or not applicable (Rule et al., 2022) to diverse marine mammals, we confirmed that the body size in mustelids does not follow any temperature trend using a comprehensive dataset. Despite previous studies revealed positive results when investigating mammals in a general way (Freckleton et al., 2003; Blackburn & Hawkins, 2004; Rodríguez et al., 2006, 2008; Clauss et al., 2013), as Blackburn et al. (1999), we believe that some caution is necessary when using data from several species and very different taxa within groups, and consider that the observed trend also applies to all of them when treated as orders or families. For instance, Ashton et al. (2000) and Meiri and Dayan (2003) observed that mammals follow Bergmann's rule, but they also noticed specific groups that do not follow this trend, such as Mustelidae and families within Rodentia. Later, Meiri et al. (2004) and Diniz-Filho et al. (2009), studying the Carnivora order, did not obtain positive evidence of the rule's validity. Already Medina et al. (2007) detected a reverse pattern to the rule when studying rodents from genus *Ctenomys*. All these evidences reinforce the caution in interpreting very broad higher taxa and the relevance of focus on monophyletic clades if we are pursuing interspecific differences.

But why does Mustelidae not follow any temperature influence in the development of different sizes? The body shape in some mustelids, as weasels, represents a huge loss of energy efficiency, as they are elongated and thin, which increases the surface area and consequent heat loss (Brown & Lasiewski, 1972). Even so, this format remains in many terrestrial species in the group. Why? This heat loss can be offset by the extreme efficiency of these predators in hunting prey, which allows them to enter burrows and crevices, precisely because of their body shape (Brown & Lasiewski, 1972) and changes associated with the skull, which increased their efficiency as predators (Law, 2019). These evolutive modifications as response to open habitat expansions and prey diversification (Law, 2019) provided the energy input necessary to supply the high losses and were triggered by very strong selection pressures towards this specific shape. However, becoming too elongated can decrease swimming efficiency, and that's why we see larger and robust sizes in the water, as otters (Law, 2021), given that the habitat constrains the body shape in the semi-aquatic species, as discussed. Additionally, there is evidence that the tendency to Bergmann's rule be weaker in smaller mammalian species (up to 500 g; Meiri & Dayan, 2003; see also Freckleton et al., 2003), which constitutes about 23% of mustelid species. Although this statement is accompanied

by indication that small mammals present a restricted range, this is not the case with mustelids. The species live in areas with temperatures ranging from -10 to 30 °C (Fig. 3b), and some species exhibit large distribution along several biomes and latitudes, with very diverse characteristics of temperature, humidity and vegetation (Rheingantz et al., 2014; Do Linh San et al., 2016; Helgen & Reid, 2016). Hereupon, this great diversity of environments would allow the display of temperature effects, if any, were it not for the strong pressures exerted by the aquatic environment.

Despite body size can be predicted by trophic niche or environmental temperature in several animal groups, we found no evidence that size evolution in Mustelidae can be explained by these factors. On the other hand, habitat structure was a good predictor of body size evolution, with larger species being semi-aquatic while smaller ones being terrestrial. We proposed thermodynamic and bone density mechanisms being the main selective pressures to evolve larger sizes in semi aquatic mustelids. We also highlight the selective strength of habitat, because even Mustelidae being an assorted group in terms of diet diversity and distribution across the globe, habitat was a predominant factor in determining body size. Perhaps other variables could emerge in the evolution of body size in other animal groups in absence of environmental pressures as strong as those exerted by water. Finally, we reinforce the importance of investigating widely accepted ecological standards for large groups, at lower taxonomic levels, in order to expand our understanding of the maintenance and robustness of these standards on a smaller phylogenetic scale.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s11692-023-09597-1>.

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Data Availability Data is provided in supplementary tables.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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