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Revisiting the cost of carnivory in mammals

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Abstract

Predator–prey relationships play a key role in the evolution and ecology of carnivores. An understanding of predator–prey relationships and how this differs across species and environments provides information on how carnivorous strategies have evolved and how they may change in response to environmental change. We aim to determine how mammals overcame the challenges of living within the marine environment; specifically, how this altered predator–prey body mass relationships relative to terrestrial mammals. Using predator and prey mass data collected from the literature, we applied phylogenetic piecewise regressions to investigate the relationship between predator and prey size across carnivorous mammals (51 terrestrial and 56 marine mammals). We demonstrate that carnivorous mammals have four broad dietary groups: small marine carnivores (< 11 000 kg) and small terrestrial carnivores (< 11 kg) feed on prey less than 5 kg and 2 kg, respectively. On average, large marine carnivores (> 11 000 kg) feed on prey equal to 0.01% of the carnivore's body size, compared to 45% or greater in large terrestrial carnivores (> 11 kg). We propose that differences in prey availability, and the relative ease of processing large prey in the terrestrial environment and small prey in marine environment, have led to the evolution of these novel foraging behaviours. Our results provide important insights into the selection pressures that may have been faced by early marine mammals and ultimately led to the evolution of a range of feeding strategies and predatory behaviours.

Introduction

There is a strong link between physiology and behaviour in carnivorous mammals. For example, much of the variation in ranging behaviour of carnivorous mammals can be attributed to the energetic requirements of being a carnivore and the distribution of preferred prey (Kelt & van Vuren, 2001; Carbone *et al.*, 2005). The population dynamics of predators can also be impacted by prey choice and the population fluctuations of those prey species. This is because a drop in prey density will result in a drop in carnivore density, especially in large predators that require large quantities of prey to survive (Carbone & Gittleman, 2002; Carbone *et al.*, 2011). Carnivorous mammals generally have low population densities and slow growth rates, which make them highly susceptible to population declines whenever changing environmental conditions start to impact the distribution of their prey (Cardillo *et al.*, 2005; Davidson *et al.*, 2009; Carbone *et al.*, 2011; Angerbjörn *et al.*, 2013). The trophic importance and key role of carnivores within their ecosystems (e.g. indirect influence on carbon storage and disease regulation; Ripple *et al.*, 2014) renders them an important group by which to investigate predator–prey interactions on a global scale.

Information on prey choice in mammals and the eco-evolutionary processes that have led to these patterns is important for two reasons. First, building our knowledge of carnivore behaviour is essential for linking patterns and processes of ecosystem structure and function, foraging patterns and predator–prey

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interactions (Carbone *et al.*, 2011; Friedlaender *et al.*, 2015). For example, examining the behaviour of wolves within Yellowstone National Park has illustrated the direct and indirect impacts of their behaviour on this ecosystem, including the population dynamics of plants, herbivorous mammals and scavenger species (Wilmers *et al.*, 2003; Ripple & Beschta, 2012; White *et al.*, 2012). Second, with improved information on carnivore behaviour, we can develop broadscale models of predator–prey relationships that feed back into our understanding of species diversity, in terms of the number of species present in an ecosystem, and the function of carnivore species in an ecosystem (e.g. Yellowstone wolves).

Mammals are an ideal group by which to examine foraging behaviour and predator–prey relationships as it is possible to explore how morphology, physiology and behaviour have been impacted in related species that have evolved within different environments. Tucker & Rogers (2014b) examined the relationship between predator body mass and prey body mass, with a focus on the minimum, maximum and range in body size of prey consumed by terrestrial and marine carnivores. They confirmed the previously documented positive relationship between the mass of predator and prey for terrestrial carnivores (Carbone *et al.*, 1999), but showed that there was no relationship for marine mammals. This was surprising as it suggested that marine mammals no longer face the energetic constraints of terrestrial carnivores, resulting in a reduced effect of allometry on predator–prey relationships. These differences were attributed to differences in phylogenetic relatedness, body mass (and its impact on morphology and energetics) and the characteristics of the environment in which the carnivore has evolved and currently resides. Carbone *et al.* (2014) developed a geometric foraging model to predict the minimum prey size scaling relationship across endothermic and exothermic vertebrate predators in the terrestrial and marine environments. The model reproduced the positive predator–prey relationship documented for terrestrial predators (Carbone *et al.*, 1999; Tucker & Rogers, 2014b), but inferred that similar patterns of wide diet breadth should also exist among marine vertebrate predators (mammals, sharks and rays). Yet for many marine mammals, there is a strong predominance of small prey in their diets (between 35 and 100 g; Carbone *et al.*, 2014; Tucker & Rogers, 2014b).

It remains unclear whether allometry broadly is predictive of the prey size used by mammals due to the diversity of foraging behaviours and prey sizes consumed by marine carnivores (Carbone *et al.*, 2014; Tucker & Rogers, 2014b). For terrestrial mammals, Carbone *et al.* (1999) identified two distinct dietary groups: small carnivores below 15–21 kg that generally feed upon small prey (e.g. invertebrates) and large carnivores above 15–21 kg that generally feed upon large prey (e.g. vertebrates). This break point or transition in prey size reflects the different energetic requirements of the different sized predators, where there is a two-fold increase in both energy intake and energy expenditure between 15 and 21 kg (Carbone *et al.*, 2007). Marine mammals with large body size are expected to exhibit higher energetic requirements than smaller marine mammals (Nagy, 2005), similar to terrestrial mammals (Carbone *et al.*, 1999). The precise influence of underlying energetic differences on predator–prey relationships between marine and terrestrial mammalian carnivores has not been examined, but it is likely to be key to understanding the foraging behaviour of marine mammals (*sensu* Carbone *et al.*, 1999).

Our aim was to determine how mammals have overcome the challenges of living within the marine environment and how this has altered the predator–prey body mass relationships found in terrestrial mammals. Specifically, this study aimed to reconcile the previously reported dietary differences between terrestrial and marine mammals (Carbone *et al.*, 2014; Tucker & Rogers, 2014b), and the difficulty in accounting for the diets of many marine mammals using models that assume some type of diet allometry (Carbone *et al.*, 2014). We propose that the marine environment may have (1) enabled marine carnivorous mammals to ‘escape’ or minimize the energetic constraints apparent for carnivores on land and (2) that above a given mass, allometry is no longer the key factor determining what carnivorous marine mammals feed upon, but rather that the distribution and type of prey available and the ability of the carnivorous marine mammals to process this prey has resulted in the evolution of different feeding categories.

First, physiological and behavioural adaptations may offset some of the increased absolute energy requirements of being large. For example, to enhance the digestion and assimilation of food (Slijper, 1976; Stevens & Hume, 1995), marine carnivores have longer small intestines than their terrestrial relatives (Williams *et al.*, 2001) and a diverse gut microbiome more typical of a terrestrial herbivore (Nelson *et al.*, 2013). Marine mammals have achieved impressive sizes because there are fewer mechanical constraints in an aquatic environment and associated advantages of large body size (e.g. reduced thermoregulation costs; Clauset, 2013). Being a large mammal in the marine environment may have reduced the energetic constraints seen for mammals on land.

Second, there are differences in the primary productivity and food web structures of the marine and terrestrial environments (Shurin *et al.*, 2006; Brose, 2010; Tucker & Rogers, 2014a), which have driven the abundance of small species that form dense aggregations (e.g. invertebrates and vertebrates). The abundance of small prey and the three-dimensional nature of the ocean have resulted in an increase in the encounter rates between marine carnivores and small prey species, as well as providing a resource with sufficient energy to support populations of marine carnivores (Scharf *et al.*, 2000; Goldbogen *et al.*, 2011; Pawar *et al.*, 2012; Tucker & Rogers, 2014b). This has enabled both smaller carnivores (e.g. crabeater seals) and large carnivores (e.g. blue whales) to consume small prey species (< 50 g) (Dalla Rosa *et al.*, 2008; Brierley & Cox, 2010; Hückstädt *et al.*, 2012). This in turn means that the quantity of prey consumed by marine carnivores becomes more important than the size of the prey to meet the increase in the energy required by larger marine carnivores. We expect that any shift in foraging strategy with body size will occur at larger sizes than those typically seen on land. This is because feeding upon large, often highly agile marine prey is a limiting factor for large marine carnivores with reduced mobility (Goldbogen *et al.*, 2010). Indeed, this reduction in mobility has been cited as the main reason that large marine carnivores (> ~1000 kg) tend to feed on swarms of small prey species (Goldbogen *et al.*, 2010; Carbone *et al.*, 2014; Tucker & Rogers, 2014b).

Third, the ability to process large prey has probably been severely constrained in many marine mammals. The model by Carbone *et al.* (2014) shows that a broad range of prey sizes should be available to marine predators. However, those marine predators that do actually exploit large prey also tend to have highly specialized prey-processing capabilities that allow them to do so. For example, there are a high number of large prey-feeding elasmobranchs (e.g. sharks) that target large fish, turtles, seabirds, seals and small cetaceans. Elasmobranchs have hundreds of replaceable teeth, pointed lower jaw teeth for gripping and triangular upper jaw teeth with serrated edges for cutting that enable them to tear flesh from large, floating prey. To some extent, adequate positioning and handling of prey can circumvent the need for such specialized teeth morphologies and arrangements. For example, terrestrial mammals process a large carcass by holding prey against the ground and positioning the body between the post-canine (cheek) teeth (carnassial teeth, e.g. in cats) for tearing and chewing, but this type of prey handling is rarely possible for marine mammals (Taylor, 1987).

Our objective was to examine the underlying energetic requirements of marine mammals as it relates to body size for the first time, with explicit comparison to those of terrestrial mammals, and to recharacterize carnivore dietary groups by identifying the specific feeding behaviour used to meet these energetic requirements, given the type of resources available in terrestrial and marine environments. In doing so, our broad goal was to realign the types of foraging strategies exhibited by mammalian carnivores to their underlying allometric and ecological requirements.

Materials and methods

Data

We compiled data from the literature on the prey mass and predator mass of 107 carnivorous mammal species across the marine and terrestrial environments. Carnivores were defined as those species with diets compromising of at least 90% meat. This classification included insectivores as carnivores (Kelt & van Vuren, 2001). Insectivores were also included as they represent carnivorous behaviour for species below ~10 kg and contribute towards the break point in terrestrial predators (Carbone *et al.*, 2007). Mean prey mass data were obtained in two ways: (1) from published prey mass values ($n = 53$) and (2) using data from the literature to calculate mean prey mass values based on the proportion of prey species consumed by that carnivore ($n = 54$). When prey preference information was not available, we calculated the mean prey mass from the listed prey species ($n = 2$). Mean prey mass values were calculated using information on both sexes and dietary information across populations.

We also collected published information on adult daily energy expenditure (DEE) in kJ day^{-1} for species where these data were available. In this study, the main purpose of the energetic data is to examine whether patterns in mean prey mass are similar to those of DEE, not whether there is a relationship between DEE and body mass. We are aware that there are different methodologies utilized to directly measure energetics in mammals, including accelerometry, doubly labelled water and calorimeter/respirometry chambers, and that there is variability across these methodologies (e.g. Dalton *et al.*, 2014). If there are strong effects of these different methodologies, we would expect to see distinct differences between marine and terrestrial mammals, such as all marine species sitting on one side of the break point and all terrestrial species on the other side. However, at the scale of this study and with all of the data undergoing a log10 transformation prior to analysis, these effects are likely to have little effect on our results.

Phylogeny construction

Phylogenetic information was based on a pruned version of the mammalian supertree of Faurby & Svenning (2015), in which branch lengths were proportional to time since divergence (Figs S3 and S4). Divergence times were calculated using a heuristic–hierarchical Bayesian approach based on genetic and morphological information. Due to topological uncertainties, the phylogenetic information from Faurby & Svenning (2015) consisted of 1000 random trees, and these trees provided the basis for all of the phylogenetic comparative analyses. All analyses were run across the 1000 phylogenetic trees, resulting in 1000 result sets for each analysis. We then calculated the mean of the parameter estimates (e.g. the slope, intercept and AIC) and the mean of the standard error of those estimates across the 1000 results. We performed all tree manipulations using R version 3.0.2 (R Core Development Team, 2013).

Analysis

A model selection approach was applied to test the level of support for alternative models of predator–prey body mass break points in carnivorous mammals. The best model was selected using second-order Akaike's information criterion with a correction for sample size (AICc; Field, 2005; Johnson & Omland, 2004). The model with the lowest AICc value reflects the model with the highest support, although any other model within two units of this lowest model is also essentially considered to be an equally credible candidates (i.e. ΔAIC < 2.0; Burnham & Anderson, 2002). To compute AICc values, we applied each model as a phylogenetic generalized least squares (PGLS) regression using COMPARE version 4.6b (Martins, 2004). Computed log-likelihood estimates from these analyses were converted into AICc values using equations presented in Burnham & Anderson (2002). PGLS regression also computes a parameter, α, using maximum likelihood, that estimates the extent to which phenotypic variation among species (here, mean predator mass and associated prey mass) is correlated to phylogeny. When α is close to 0, phenotypic differentiation among present day taxa reflects the phylogenetic relationships among those species and is the product of Brownian motion. When α is large (e.g. 15.50), phenotypic differentiation is unrelated to phylogeny and might be the outcome of adaptive evolution (Martins & Hansen, 1997; but also see Revell *et al.*, 2008).

We investigated the relationship between predator body mass and prey body mass for marine and terrestrial mammals separately. We did this so that we could specifically look for any change in intercept to identify whether there has been a major shift in dietary strategy within marine mammals. We used piecewise regression to examine this relationship, which tests whether the x variable (i.e. prey mass) is partitioned into groups (often 2) and a regression model was fitted to each group (McGee & Carleton, 1970). The value where one group transitions to the next group is the break point (BP). Piecewise regression can be described by:

$$\ln(y) = \begin{cases} b_1 \ln(x) + c, \ln(x) \leq \text{BP} \\ b_2 \ln(x) + d, \ln(x) > \text{BP} \end{cases} \tag{1}$$

where, b_1 is the slope when x is equal to or below BP, b_2 is the slope when x sits above BP, c is the intercept when x is equal to or below BP and d is the intercept when x sits above the BP. The break point analyses for predator mass and prey mass were performed using $\beta_{\text{intercept}} + \beta_{\text{mass}} + \beta_{\text{break\_}x} + \beta_{\text{mass}} \times \beta_{\text{breakpt\_}x}$, a model to examine the average prey size consumed by predators, including predator mass (β_{mass}) and the potential break point ($\beta_{\text{breakpt\_}x}$), where 'x' represented a percentile value between 0 and 0.95 titrated at 0.05 increments. An interaction term was included ($\beta_{\text{mass}} \times \beta_{\text{breakpt\_}x}$) to test whether the slope of the relationship (i.e. predator mass vs. predator body mass) differs above the break point. The upper and lower credible support limits associated with the best-supported break point were determined by the minimum and maximum break point values within two AICc units of the best-supported model. The same piecewise regression models were run to examine the relationship between DEE and body mass (also see Appendix S1).

Results

Energetics

The DEE model applied to data for all carnivorous mammals that had the lowest AIC value inferred that there was a single break point at 14.5 kg (the 40th percentile, with a two-unit credible range of 25th to 60th percentile or 3.67 to 41.42 kg; Figs 1 and S1a), and an increase in energy expenditure above the break point of approximately 120% (Table 1; NB: we did not observe any effect that might be consistent with differences in the way DEE was measured between different types of taxa (see methods); i.e., there were similar DEE patterns between marine and terrestrial mammals, with marine mammals included among the terrestrial mammals above the break point; see Fig. 1).

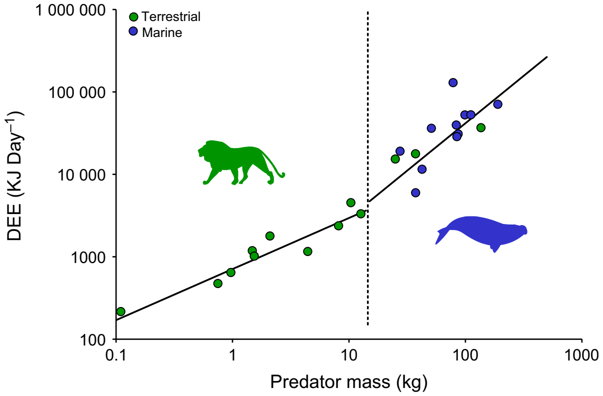

Fig. 1 Estimates of daily energy expenditure (DEE) against carnivore body mass (n = 24) in marine and terrestrial mammals combined. The solid lines represent the break point regression fit, and the dotted lines represent the DEE break point at 14.5 kg. Eubalaena silhouette by Chris Huh and Panthera silhouette (uncredited) were downloaded from http://phylopic.org.

Table 1 Level of support for explanatory models of DEE, with models including a term that allows the intercept to vary (but not the slope), or terms that allow both the intercept and slope to vary around the break point. Models with the strongest support have small AIC values. Results are from phylogenetic generalized least squares (PGLS) regression computed for 1000 alternative resolutions of the mammalian phylogeny.

	Model*	Rank	ΔAIC	α
Linear	$\beta_{\text{intercept}} + \beta_{\text{mass}} + \beta_{\text{environment}} + \beta_{\text{mass}} \times \beta_{\text{environment}}$	4	4.46	15.28
	$\beta_{\text{intercept}} + \beta_{\text{mass}} + \beta_{\text{environment}}$	3	3.58	15.48
Null	$\beta_{\text{intercept}}$	5	146.38	15.48
Piecewise (2 groups)	$\beta_{\text{intercept}} + \beta_{\text{mass}} + \beta_{\text{large}}$	**2**	**1.42**	**15.50**
	$\beta_{\text{intercept}} + \beta_{\text{mass}} + \beta_{\text{large}} + \beta_{\text{mass}} \times \beta_{\text{large}}$	**1**	**0**	**15.46**

*Large = species above the 14.5 kg break point.

Prey size

For terrestrial mammals, the PGLS model with the lowest AIC value included a break point at ~11 kg (70th percentile, with a two-unit credible range of 65th to 75th percentile or 9.7 to 11.5 kg; Table 2 and Fig. S3a) that was associated with a shift to feeding on prey which were 49 times larger (from 0.1 kg to 4.9 kg). However, for marine mammals, there was a unique break point at ~11 000 kg (80th percentile, with a two-unit credible range of 60th to 85th percentile or 5875 to 27 047 kg; Table 2 and Fig. S2b) that was associated with a dramatic drop in prey size (~971 times smaller, from 0.24 kg to 0.0002 kg). The phylogenetic effect sizes (*r*) of the piecewise models were 0.48 and 0.46 for terrestrial and marine mammals, respectively. These results show that contrasting feeding behaviours are associated with differing predator mass thresholds between terrestrial and marine mammals (Fig. 2). Although large terrestrial mammals greater than 11 kg make an abrupt transition to feeding on large prey (see also Carbone *et al.*, 1999), marine mammals greater than 11 kg continue to feed predominantly on small prey less than 2 kg, up to a point, after which the largest marine mammals make a major shift to feeding on very small prey (< 0.0001 kg). The distribution of data in Fig. 2 indicates that smaller marine species exploit similar sized prey to the smaller class of terrestrial species (0.01–1 kg).

To determine whether small terrestrial mammals and small marine mammals select similar sized prey, we formulated a series of models to detect similarities and differences in slope and intercept of the relationship between predator mass and prey mass among four subgroups: small terrestrial mammals (< 11 kg), large terrestrial mammals (> 11 kg), small marine mammals (10 kg to 10 999 kg) and large marine mammals (> 11 000 kg). The results confirmed the best-supported models were those that assumed some combination of difference in intercept and slope among the four subgroups (Table 2). The patterns seen in Fig. 2 imply that there are similarities in prey preference between small terrestrial mammals and small marine mammals (small prey < 1 kg). However, the models that tested this were not strongly supported (Table 1). This result suggests that terrestrial mammals (< 11 kg) and marine mammals (< 10 999 kg) do not sit within the same dietary group. Additionally, the models testing whether the break points were specifically associated with the transition to the marine environment and not body mass *per se* also received little support (Table 2), suggesting that both body mass and environment have shaped the transitions in prey size selection.

Discussion

We have shown that four broad dietary groups have evolved in carnivorous mammals as opposed to two, as previously thought (Carbone *et al.*, 1999): small terrestrial carnivores (less than 11 kg) feed on small terrestrial prey less than 2 kg, large terrestrial carnivores (above 11 kg) feed on large terrestrial prey above 3 kg, small marine mammals (below 11 000 kg) feed on small marine prey less than 5 kg and larger marine carnivores (above 11 000 kg) feed on very small marine prey less than 0.0005 kg (or 0.5 g). Mammals in the marine environment below 11 000 kg generally seem to behave in a manner broadly similar to terrestrial carnivores below 11 kg, as they feed predominantly on small prey (for marine species, this includes squid and fish, but may also include zooplankton and some large vertebrates such as seals). However, once marine carnivores reach 11 000 kg, there is a major shift in feeding ecology to feeding upon massive quantities of very small prey (~0.01% of the predator's body mass; this study) to meet their large energetic requirements (Fig. 1). For example, minke whales (*Balaenoptera bonaerensis*) consume up to 300 kg of prey per day, which is equal to enormous quantities of individual krill (i.e. thousands of individuals; Reilly *et al.*, 2004).

Table 2 Level of support for explanatory models of predator–prey body mass relationship, with models including a term that allows the intercept to vary (but not the slope), or terms that allow both the intercept and slope to vary around the break point. Models with the strongest support have small AIC values. Results are from phylogenetic generalized least squares (PGLS) regression computed for 1000 alternative resolutions of the mammalian phylogeny.

	Model*	**Rank**	**ΔAIC**	**α**
Linear	$\beta_{\text{intercept}} + \beta_{\text{mass}} + \beta_{\text{environment}} + \beta_{\text{mass}} \times \beta_{\text{environment}}$	13	28.58	15.18
Null	$\beta_{\text{intercept}}$	14	50.44	8.11
Piecewise (4 groups)	$\beta_{\text{intercept}} + \beta_{\text{mass}} + \beta_{\text{terrestrial\_large}} + \beta_{\text{terrestrial\_large}} \times \beta_{\text{mass}} + \beta_{\text{marine\_small}} + \beta_{\text{marine\_large}}$	**1**	**0**	**15.5**
	$\beta_{\text{intercept}} + \beta_{\text{mass}} + \beta_{\text{terrestrial\_large}} + \beta_{\text{terrestrial\_large}} \times \beta_{\text{mass}} + \beta_{\text{marine\_small}} + \beta_{\text{marine\_small}} \times \beta_{\text{mass}} + \beta_{\text{marine\_large}}$	**2**	**0.97**	**15.5**
	$\beta_{\text{intercept}} + \beta_{\text{mass}} + \beta_{\text{terrestrial\_large}} + \beta_{\text{terrestrial\_large}} \times \beta_{\text{mass}} + \beta_{\text{marine\_small}} + \beta_{\text{marine\_large}} + \beta_{\text{marine\_large}} \times \beta_{\text{mass}}$	**3**	**1.57**	**15.5**
	$\beta_{\text{intercept}} + \beta_{\text{mass}} + \beta_{\text{terrestrial\_large}} + \beta_{\text{terrestrial\_large}} \times \beta_{\text{mass}} + \beta_{\text{marine\_small}} + \beta_{\text{marine\_small}} \times \beta_{\text{mass}} + \beta_{\text{marine\_large}} + \beta_{\text{marine\_large}} \times \beta_{\text{mass}}$	**4**	**2.48**	**15.5**
	$\beta_{\text{intercept}} + \beta_{\text{mass}} + \beta_{\text{terrestrial\_large}} + \beta_{\text{terrestrial\_large}} \times \beta_{\text{mass}} + \beta_{\text{marine\_small}} + \beta_{\text{marine\_large}} + \beta_{\text{marine\_large}} \times \beta_{\text{mass}}$	**5**	**2.78**	**15.5**
	$\beta_{\text{intercept}} + \beta_{\text{mass}} + \beta_{\text{terrestrial\_large}} + \beta_{\text{marine\_small}} + \beta_{\text{marine\_large}}$	**6**	**8.28**	**15.5**
	$\beta_{\text{intercept}} + \beta_{\text{mass}} + \beta_{\text{terrestrial\_large}} + \beta_{\text{marine\_small}} + \beta_{\text{marine\_large}} + \beta_{\text{marine\_large}} \times \beta_{\text{mass}}$	**7**	**8.47**	**15.5**
	$\beta_{\text{intercept}} + \beta_{\text{mass}} + \beta_{\text{terrestrial\_large}} + \beta_{\text{marine\_small}} + \beta_{\text{marine\_small}} \times \beta_{\text{mass}} + \beta_{\text{marine\_large}}$	**8**	**9.94**	**15.5**
Piecewise (3 groups)	$\beta_{\text{intercept}} + \beta_{\text{mass}} + \beta_{\text{terrestrial\_large}} + \beta_{\text{terrestrial\_large}} \times \beta_{\text{mass}} + \beta_{\text{marine\_large}}$	9	20.81	14.75
	$\beta_{\text{intercept}} + \beta_{\text{mass}} + \beta_{\text{terrestrial\_large}} + \beta_{\text{marine\_large}}$	10	20.82	14.08
	$\beta_{\text{intercept}} + \beta_{\text{mass}} + \beta_{\text{terrestrial\_large}} + \beta_{\text{terrestrial\_large}} \times \beta_{\text{mass}} + \beta_{\text{marine\_large}} + \beta_{\text{marine\_large}} \times \beta_{\text{mass}}$	11	22.45	14.76
	$\beta_{\text{intercept}} + \beta_{\text{mass}} + \beta_{\text{terrestrial\_large}} + \beta_{\text{marine\_large}} + \beta_{\text{marine\_large}} \times \beta_{\text{mass}}$	12	22.63	14.07

*Terrestrial/marine_large = species above 11 kg/11 000 kg break points, terrestrial/marine_small = species below the 11 kg/11 000 kg break points.

Based on our data, we did not find a second DEE break point for marine carnivores, suggesting that there is no shift in energetics for large carnivores in aquatic environments. Currently, too few marine and terrestrial species have been examined to make it possible to independently examine the energetic thresholds by environment. Improving tagging technologies will allow more energetic information to become available in the near future and will improve our ability to examine the energetic thresholds across marine and terrestrial carnivores.

Nevertheless, our results provide reasonable evidence that terrestrial and marine carnivorous mammals have broadly similar energetic requirements and that they manage the increase in energy demand associated with increased body size via opposing strategies. Terrestrial mammals make an abrupt transition to consuming much larger prey, whereas this transition to consuming larger prey does not occur often in marine mammals. Therefore, there are only a few examples of marine mammals exploiting large prey (*Zalophus californianus, Hydrurga leptonyx and Orcinus orca*; Fig. 2).

We propose that there are three main reasons for these different prey size use strategies. First, there is a wide variety of usable protein resources in the ocean. The presence of phytoplankton and zooplankton communities supports enormous densities of predatory marine invertebrates (e.g. krill, copepods and amphipods). For example, in the Southern Ocean, the density of krill has been measured up to 2559 individuals m^{-3}, with swarms measuring up to 18 km long and spanning an area of 132 798 m^{-2} (Tarling & Thorpe, 2014). The combination of high-density prey species and the three-dimensional nature of the marine environment has resulted in the increased encounter and ingestions rates of small schooling prey by marine species (Pawar *et al.*, 2012), providing a means by which both small and large carnivorous marine mammals can meet their energetic requirements which is not exploited by many of their terrestrial counterparts. In addition, abundant swarming prey have shaped the evolution of marine carnivore morphology, such as feeding structures (e.g. baleen and expanding buccal cavity; Goldbogen *et al.*, 2013; Pyenson *et al.*, 2012) and diving abilities (Boyd, 1997).

In the terrestrial system, it is not as common for mammals to utilize invertebrate prey despite the presence of grouping (e.g. eusocial invertebrate) species. A range of mammal species, including the aardwolf, anteater and pangolin, utilize aggregations of terrestrial invertebrates in mounds (e.g. termites, densities of 2139 individuals m^2; Bodine & Ueckert, 1975), and small bats exploit transitory aggregations of insects in the air (e.g. microbats). However, in general, this strategy can only support small terrestrial carnivores (this study; Carbone *et al.*, 1999). There are several reasons for this, the most important being the associated increase in energy expenditure (i.e. cost) associated with capturing these small prey items and the decrease in energy assimilated with increasing body mass, which makes this resource inefficient for large terrestrial carnivores (Carbone *et al.*, 2007). This is also the reason why carnivores above 11 kg feed upon prey greater than 1 kg, due to the increased energetic requirements for capturing the larger prey, and the relative inefficiency of feeding upon small prey species (Carbone *et al.*, 2007). Also, these invertebrate aggregations are not as abundant as concentrations in the ocean and are often buried underground or flying above the ground, thus requiring specific and often energetically expensive adaptations (e.g. flight) to use these resources.

Another potential reason why terrestrial carnivores do not utilize invertebrate prey is related to the heterogeneity of terrestrial landscapes, which provide adequate refuges for invertebrates. By comparison, large regions of the ocean are open environments, providing fewer refugia for small invertebrate prey species. The interaction between marine predators and their schooling prey may have played an important role in marine mammals attaining large sizes. Swarming is a predator avoidance behaviour adopted by small pelagic marine prey (e.g. fish, euphausiids). By swarming, many small prey become (energetically) one single prey item, which can be exploited by a predator that can harvest multiple individuals with one mouthful. The avoidance behaviour of the prey may have provided their predators with the capacity to develop larger size, and so greater harvesting capacity.

A second factor behind the range of marine carnivore foraging behaviours is related to the differences in energy allocation across species in the marine and terrestrial environments. Marine carnivores have a higher hunting efficiency than terrestrial carnivores, where the amount of energy ingested is greater than the energy expended (Williams & Yeates, 2004). In addition, some of the largest marine carnivores have evolved strategies to cope with their high absolute energetic requirements and the elevated costs associated with prey capture (Potvin *et al.*, 2012). For example, baleen whales have high costs associated with lunge feeding including bursts of high-energy muscle activity and the associated elevated metabolic demands (Potvin *et al.*, 2012). The costs of lunge feeding are mitigated by decreasing the number of lunges per dive and passive feeding (e.g. cooperative feeding at the surface) and increasing post-diving recovery periods (Potvin *et al.*, 2012).

Third, the modification of forelimbs for swimming has limited the ability of marine mammals to position a prey carcass between the post-canines for processing (see Introduction). This has restricted marine mammal predators to the use of small prey, where prey can be swallowed whole without requiring mastication. There are few marine mammals that exploit large marine prey species (e.g. fish, seabirds, seals, small cetaceans). The polar bear (*Ursus maritimus*) feeds on large prey (e.g. seals; Derocher *et al.*, 2002); however, they process the prey carcases on the ice and they do not have fully aquatic-adapted forelimbs, or the simplified dentition typical of other marine mammals. Polar bears use their clawed forelimbs to hold and position the carcass between crushing post-canines. The polar bear is a comparably recent convert to a marine lifestyle (~1.1 Myr; Nyakatura & Bininda-Emonds, 2012), so it is perhaps not surprising that they retain a terrestrial-like feeding ecology. Some marine mammals have overcome the difficulties of processing large prey in the water using specialist techniques. For example, the killer whale (*Orcinus orca*) feeds on large prey (including other whales and seals), the leopard seal (*Hydrurga leptonyx*) feeds on a mixture of vertebrates, fish and zooplankton, but predominantly large vertebrate prey (Hall-Aspland & Rogers, 2004), and the Californian sea lion (*Zalophus californianus*) feeds on fish and squid (Pauly *et al.*, 1998). Furthermore, all rely on shake feeding (Taylor, 1987) for prey processing (Rogers, 2009; Block *et al.*, 2011; Pitman & Durban, 2012).

Some interesting patterns have arisen in regard to the variation in the size of prey consumed by carnivorous mammals. Terrestrial carnivores below 11 kg have the greatest variation in prey size (Fig. 2). Within this group, there is a mixture of feeding ecologies from invertebrate specialists (e.g. anteaters) to small vertebrate specialists (e.g. martens), whereas the majority of terrestrial carnivores above 11 kg feed upon medium-to-large vertebrates (e.g. lions) (this study; Carbone *et al.*, 2007). For terrestrial carnivores over 11 kg, the combination of high energetic requirements, increased energy expenditure associated with prey capture and a decrease in the assimilation of energy (this study; Carbone *et al.*, 2007), has resulted in the need to consume single large prey within a certain range of body sizes (~10 kg to 180 kg). In contrast, terrestrial mammals below 11 kg have reduced energetic constraints (this study; Carbone *et al.*, 2007) and this enables energy efficient foraging and consumption of a wide range of prey sizes (~0.01 g to 5 kg; Tucker & Rogers, 2014b). In the marine environment, carnivorous mammals also display a range of foraging strategies, from

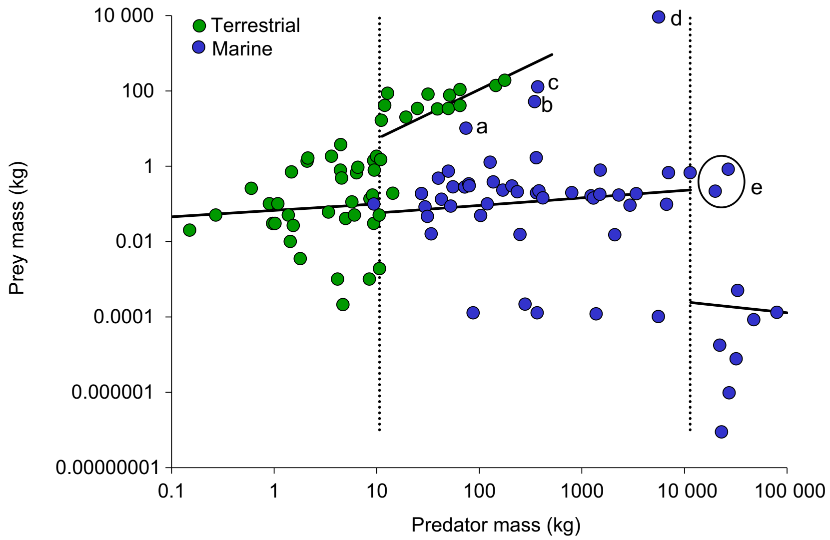

Fig. 2 Mean prey body mass as a function of carnivore body mass for 107 species of marine and terrestrial carnivores. The solid lines are the break point regression fit for marine and terrestrial species. The dotted vertical lines represents the 10.7 kg threshold where terrestrial carnivores shift from feeding on small prey to large prey, and the 11 380 kg threshold where marine carnivores shift from feeding large prey to feeding on smaller prey. Letters a-d represent the few marine species that utilize large-bodied prey; (a) California sea lion (*Zalophus californianus*), (b) leopard seal (*Hydrurga leptonyx*), (c) *polar bear (Ursus maritimus)*, (d) killer whale (*Orcinus orca*), whereas the letter (e) represents the few large-bodied species that use medium-sized prey (odontocete whales including *Physeter macrocephalus and Balaenoptera edeni*).

large vertebrate specialists (e.g. Orca whales) to invertebrate specialists (e.g. baleen whales). Specializing on invertebrates has evolved across a range of marine carnivores of varying sizes due to the abundance of dense aggregations of invertebrates (Fig. 2; Tarling & Thorpe, 2014). However, for carnivores above ~30 tonne, it appears that the switch to invertebrate prey is necessary (Fig. 2). These large marine carnivores have very large energetic requirements, and the utilization of the large aggregations of small invertebrate prey provides a food resource that maintains the balance between the energy expended although foraging with the energy intake from the prey consumed (Goldbogen *et al.*, 2010; Carbone *et al.*, 2014; Tucker & Rogers, 2014b). Overall, prey size variation has most likely arisen as a result of the different abundances of available prey sizes and the evolution of different carnivore feeding strategies across different body sizes and environments.

Our study provides an explanation as to how mammals have overcome the challenges of living within the marine environment, resulting in drastic changes in the predator–prey body mass relationships between marine and terrestrial mammals. We have shown that carnivorous marine mammal predator–prey relationships are driven by different allometric constraints to those in terrestrial carnivores. The mammalian colonization of the marine environment has had a profound effect on carnivore diets, resulting in the evolution of feeding and behavioural strategies that differ to those found in terrestrial carnivores. Understanding mammalian diets is important for three reasons. First, it provides a clearer understanding of the selective forces that have shaped predator–prey relationships and the associated behavioural and foraging strategies adopted by extant carnivorous mammals. Second, it provides critical information on how species interact (i.e. consumers and their resources), how energy is transferred through an ecosystem (i.e. from small species to large species) and how trophic structures are shaped across different environments (i.e. food chain length). Third, information on the prey consumed by carnivores and the physiological underpinnings of carnivore behavioural strategies that we have identified have potentially important conservation implications, such as the identification of scenarios where conflict may arise between human activities and mammals. For large marine carnivores, the combination of the elevated energetic requirements of being large (and often dramatically so, compared to their relatives on land), the reliance upon dense aggregations of small prey species and the fact that these same prey species are also being commercially harvested highlights one of the many threatening anthropogenic processes currently faced by marine mammals (Forcada *et al.*, 2012). More generally, given that both marine and terrestrial carnivorous mammals are under threat from climate change and increasing human activities at a global scale (Ripple *et al.*, 2014), understanding the dynamics behind carnivore diets could provide the information needed to help minimize some of these negative impacts faced by carnivorous mammals.

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Supporting information

Additional Supporting Information may be found online in the supporting information tab for this article:

Appendix S1 Additional analyses.

Figures S1–S2 AIC plots and associated piecewise regression figures for DEE and prey mass, illustrating support for break point selection.

Figure S3–S4 Examples of the phylogenetic trees used in the predator–prey and DEE analyses.

Data deposited at Dryad: doi: 10.5061/dryad.9p311.

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