RESEARCH PAPER

Evolutionary predictors of mammalian home range size: body mass, diet and the environment

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ABSTRACT

Aim Mammalian home range patterns provide information on spatial behaviour and ecological patterns, such as resource use, that is often used by conservation managers in a variety of contexts. However, there has been little research on home range patterns outside of the terrestrial environment, potentially limiting the relevance of current home range models for marine mammals, a group of particular conservation concern. To address this gap, we investigated how variation in mammalian home range size among marine and terrestrial species was related to diet, environment and body mass.

Location Global.

Methods We compiled data on home range size, environment (marine and terrestrial), diet and body mass from the literature and empirical studies to obtain a dataset covering 462 mammalian species. We then used phylogenetic regression analyses (to address non-independence between species) to examine the relative contribution of these factors to variation of home range size among species.

Results Body size explained the majority of the difference in home range size among species (53–85%), with larger species occupying larger home ranges. The type of food exploited by species was also an important predictor of home range size (an additional 15% of variation), as was the environment, but to a much lesser degree (1.7%).

Main conclusions The factors contributing to the evolution of home ranges are more complex than has been assumed. We demonstrate that diet and body size both influence home range patterns but differ in their relative contribution, and show that colonization of the marine environment has resulted in the expansion of home range size. Broad-scale models are often used to inform conservation strategies. We propose that future integrative models should incorporate the possibility of phylogenetic effects and a range of ecological variables, and that they should include species representative of the diversity within a group.

Keywords
evolutionary allometry, marine, phylogenetic comparative analysis, spatial behaviour, terrestrial.

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INTRODUCTION

In animals, a broad range of physiological, ecological and behavioural factors scale with body size (Peters, 1983). Body mass, a measure of body size, accounts for a large proportion of the variation in home range size among terrestrial mammals (Kelt & van Vuren, 2001; Jetz *et al.*, 2004). Among the various potential

consequences of allometry, the size of an animal's home range provides valuable information on a variety of ecological variables, including resource use, social behaviour and other activities (Knight *et al.*, 2009). The strong positive relationship between home range size and body mass reflects the balance between the cost of locomotion and metabolic requirements with increasing body mass (McNab, 1963). Larger individuals

can travel further than smaller individuals, but larger individuals have higher absolute energetic demands and need to travel further to gain the resources to meet those demands (McNab, 1963).

In addition to an animal's size, diet is another important factor that is believed to dictate home range patterns. Carnivores, omnivores and herbivores have differences in their foraging costs (i.e. food acquisition and processing costs) due to their reliance on different food resources, which also have temporally and spatially different distributions. Carnivores feed on resources that are sparsely distributed, mobile and unpredictable across the landscape, and so they require a large home range (Kelt & van Vuren, 2001; Carbone *et al.*, 2007a). There are also additional costs for carnivores such as the time and energy required to hunt for food (Carbone *et al.*, 1999). In contrast, herbivores tend to have the smallest home ranges because they feed on vegetation which is fixed in time and space and is generally abundant. However, there are additional energetic costs associated with processing plant material (e.g. Clauss *et al.*, 2003), which limit the ability of herbivores to forage widely. Omnivores have an intermediate-sized home range that reflects their mixed diet (meat and vegetation) (Kelt & van Vuren, 2001) and the intermediate costs associated with processing these foods (McNab, 1986).

Despite the large body of work on the physiological and ecological variables that might affect the size of an animal's home range (e.g. body mass and diet), gaps remain in our understanding of which factors (or combination of factors) actually drive mammalian home range patterns. While it is clear that diet and body mass are important, past studies have examined these factors separately (e.g. Kelt & van Vuren, 2001; Jetz *et al.*, 2004) and we have little idea of the relative contribution each makes to mammalian home range size. Furthermore, home range data have been historically biased towards terrestrial mammals, resulting in the exclusion of the larger mammals (> 4000 kg). Marine mammals represent a prominent group of large carnivores. It is also unclear whether the factors driving home range size in mammals are the same in terrestrial and marine environments. Furthermore, previous studies have failed to consider the phylogeny of the species being studied. On methodological grounds, not incorporating information on the phylogenetic relatedness among species violates the statistical assumption that data points are independent of one another. This results in inflated Type I error rates and correlations between variables that may not actually exist (Stone *et al.*, 2011). On biological grounds, while closely related species are more likely to share characteristics through common ancestry (and are therefore not independent of one another), variation among species can also be generated through the inherently stochastic process of evolutionary differentiation (e.g. drift) or phenotypic correlations that track the phylogeny and indirectly affect home range rather than through adaptation in the home range specifically. That is, variation in home range size among mammals may have little adaptive significance and might simply reflect a history of stochastic differentiation or other factors associated with phylogeny.

In this study, we set out to clarify these issues by conducting inclusive analyses across both terrestrial and marine mammals to test the diet and the body mass hypotheses alongside each other (i.e. that home ranges will increase with increasing proportion of meat in the diet in addition to, and independently of, increasing body mass) and against an evolutionary null model (stochastic variation). As part of these analyses, we examined if when the relative contribution of these factors is the same it has affected the evolution of home range in the same way in terrestrial and marine mammals.

Colonization of the marine environment has been accompanied by fundamental shifts in physiology and ecology that may have changed the way in which body mass and diet affect home range size in marine species. One example of this is the ability of marine mammals to utilize buoyancy. Marine mammals have evolved various mechanisms to achieve neutral buoyancy, such as increases in bone density and large blubber stores (Wall, 1983). Buoyancy is a key strategy for marine mammals to minimize the costs associated with diving. An example of this is the North Atlantic right whale (*Eubalaena glacialis*) which utilizes positive buoyancy when ascending (Nowacek *et al.*, 2001). Marine mammals have also evolved other adaptations that allow them to survive in the ocean and decrease their cost of transport (COT) per unit weight (Williams, 1999). These include a mixture of adaptations that are physiological (e.g. increased globin levels for more efficient oxygen transfer; Williams *et al.*, 2008) and behavioural (e.g. alternative forms of locomotion during diving; Williams, 1999). The subsequent decrease in COT per unit weight, combined with passive movement via oceanic currents (Tremblay *et al.*, 2006), results in the relaxation of energetic costs in marine environments compared with the terrestrial environment. Given that marine COT is approximately half that of land COT, e.g. COT for a Californian sea lion is 2.5 J kg^{-1} m^{-1} (Williams, 1999) versus COT for a grey wolf of 4.6 J kg^{-1} m^{-1} (Pontzer, 2007), marine mammals on average should have home ranges at least twice as large as terrestrial mammals for any given body mass. Moreover, as the marine system is fluid with few boundaries to limit movement, food resources tend to be highly mobile across the ecosystem (Sims *et al.*, 2008). In response, marine mammals are highly mobile, and this should result in further increases in home range size. Therefore, we anticipated that a regression of home range size on body mass should give a higher intercept for marine mammals (larger home ranges) than for terrestrial mammals. However, as the COT per unit weight decreases with body mass at a similar rate in both marine and terrestrial mammals (Hildebrand & Goslow, 1995; Pontzer, 2007), the scaling relationship of home range size and body mass should remain the same across both environments.

Our study was conducted in two parts. First, we revisited the relationship between diet, body mass and home range size in terrestrial mammals within an explicit phylogenetic framework and assessed the relative contribution of each factor to shaping home range size. Second, we combined data on marine and terrestrial species to examine the effect of diet and body mass on the evolution of home range size across all mammals, while also

evaluating the role of the environment (marine versus terrestrial). Each of the factors – diet, environment and body mass – was formulated into mathematical functions and tested against an evolutionary null model. This null model provides a biological benchmark to establish the extent to which 'neutral' evolutionary differentiation in home range evolution can be excluded. In this second part of our study we tested two main hypotheses: (1) diet type underpins home range patterns in mammals because of differences in the distribution and assimilation of food types; and (2) the home range–body mass relationship differs between marine and terrestrial mammals because of differences in the physiology of species and the physical properties of the two environments. However, we predicted that body mass would be the primary variable determining the evolution of home range size across all species. This is due to the metabolic and energetic costs associated with body mass driving the food requirements of individuals, which are a key determinant of spatial movements in mammals (Kelt & van Vuren, 2001). Given this overarching effect of body mass, we then predicted that the environment would have an important secondary effect on home range size because it influences both the physiology of animals and the distribution of resources. Finally, within a given environment (e.g. terrestrial), we predicted that diet type would generate additional variation in home range size among species, reflecting the interaction of diet with the metabolic and energetic costs associated with a given body mass.

MATERIALS AND METHODS

Database

A database of 462 mammalian species, representing 293 genera, 89 families and 24 orders, was collated. We collected information on body mass and home range values, physical environment (marine versus terrestrial) and diet (carnivore, omnivore or herbivore). The home range values for individual species were calculated as weighted averages which included both sexes, but did not incorporate sex ratios or averaged population densities. All body mass and home range data for terrestrial mammals was obtained from Kelt & van Vuren (2001) and the PanTHERIA database (Jones et al., 2009). Body mass and home range data for marine species were collected from published literature and unpublished empirical data (Appendix S1 in Supporting Information). Home range was defined as the area covered by an animal during its daily activities such as mating and foraging (Burt, 1943), and was used across the marine and terrestrial environments. Marine mammals were defined as species that rely upon the ocean to survive (e.g. foraging etc.). Carnivores were defined as those species with diets comprising at least 90% meat, herbivores at least 90% vegetation and omnivores between 10 and 90% vegetation (Kelt & van Vuren, 2001). Insectivores were classified as 'carnivores', while frugivores and folivores were classified as 'herbivores'. Home range and body mass data were log_{10}-transformed prior to analysis.

To supplement data for six species that were not well represented in the published literature, we calculated home range size from satellite tracking data. These species were *Hydrurga leptonyx*, *Leptonychotes weddellii*, *Lobodon carcinophaga*, *Mirounga leonina*, *Arctocephalus tropicalis* and *Arctocephalus gazella*. For information on sample size, data collection and sampling protocols see Appendix S2. The satellite tracking data were filtered using a speed–distance–angle filter (Freitas & Lydersen, 2008), resulting in the use of location classes A, B, 1, 2, 3. These classes represent the accuracy of the positional data where 3 has an accuracy of 0.49 km, 2 of 1.01 km, 1 of 4.18 km, A of 6.19 km and B of 10.28 km (Costa et al., 2010). The average daily position was calculated for each individual based upon all location data for a given day and only adult individuals were used. Home range was calculated via the fixed kernel density estimation (KDE) method (Seaman & Powell, 1996) using the ARcGIS extension Hawth's Tools (Beyer, 2004). We chose KDE to calculate home range size, as reviews into the benefits and biases of home range methods, including kernels and minimum convex polygons (Laver & Kelly, 2008), suggest that kernels are preferable to polygons which are biased by outliers and low numbers of location fixes (Börger et al., 2006).

We made an attempt to minimize any effects from different tracking methods (e.g. GPS, satellite and radiotelemetry), analysis methodologies (kernels and polygons) and environments (terrestrial and marine) (Börger et al., 2006; Frair et al., 2010), yet published studies differ in the methods used, meaning that our final database included mixed home range values by necessity. However, these types of methodological effects are minimal at the scale of our study (Appendix S3), which aims to investigate large-scale home range patterns across 462 species from across the globe.

Phylogeny construction

Due to the absence of a single phylogeny including all species of interest, a composite tree was created by combining information from several sources (see Fig. S1). The majority of the phylogeny was based on the mammalian supertree from Fritz et al. (2009) in which branch lengths were proportional to time since divergence. The following species were added to the Fritz et al. (2009) supertree using MESQUITE version 2.74 (Maddison & Maddison, 2010) and species were positioned based on the topologies of the following sources: *Callosciurus erythraeus* (Steppan et al., 2004), *Canis familiaris* (Agnarsson et al., 2010), *Eremitalpa granti* (Kuntner et al., 2011), *Orcaella heinsohni* (McGowen, 2011), *Sciurus aberti* (Grill et al., 2009) and *Sotalia guianensis* (Caballero et al., 2008). The Fritz et al. (2009) supertree included polytomies, which are defined as a node where more than two species diverge at a single point in time (multifurcations). In this instance, these are soft polytomies due to insufficient phylogenetic information. To resolve the branch lengths and the polytomies present, we randomly generated 1000 alternative branch lengths using the 'randomly resolve polytomies' function in MESQUITE version 2.74 (Maddison & Maddison, 2010). This produced 1000 alternative phylogenies and provided the basis for all of the phylogenetic comparative analyses.

Analysis

We applied a model selection approach to test the level of support for alternative models of home range evolution. The best model was selected using the second-order Akaike information criterion with a correction for sample size (AICc; 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 the lowest AICc value was also considered to be a likely candidate (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), to each of the 1000 trees (see Phylogeny construction). Computed log-likelihood estimates from these analyses were converted into AICc values using equations presented in Burnham & Anderson (2002). PGLS regression also computes an α parameter using maximum likelihood that estimates the extent to which phenotypic variation among species (e.g. mean body mass and associated home range size) 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 evolution. 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).

First, we assessed the level of support for the relationship between diet and home range among 429 species of terrestrial mammals relative to the level of variation in home range size generated solely by body mass or the evolutionary null model. These models were formulated as: (1) $\beta_0 + \beta_{mass} + \beta_{diet\_H} + \beta_{diet\_O}$, where diet was scored as binary dummy variables with the resulting parameters β_0, β_{diet_H} and β_{diet_O} corresponding to carnivores, herbivores and omnivores, respectively (this was effectively a phylogenetic ANCOVA); (2) $\beta_0 + \beta_{mass}$, which predicted that differences in home range size among species were exclusively explained by body mass; and (3) β_0, the evolutionary null model in which no predictor variable was included, and which therefore modelled variance in species home range size as the outcome of Brownian evolution and stochastic factors associated with evolutionary differentiation.

Second, we expanded our analyses to cover both marine and terrestrial species in order to examine the relationship between environment and home range, and the extent to which environment overrides the influence of diet. This analysis included new empirical data on several marine species (see Database) and covered 462 species. Models were formulated as: (1) $\beta_0 + \beta_{mass} + \beta_{environment}$, where environment was entered as a binary variable in which species were coded as living in either a terrestrial (0) or marine (1) environment; (2) $\beta_0 + \beta_{mass} + \beta_{diet\_H} + \beta_{diet\_O}$, the diet model which is described above for the terrestrial mammal analysis; (3) $\beta_0 + \beta_{mass} + \beta_{diet\_H} + \beta_{diet\_O} + \beta_{environment}$, where both diet and environment were included together in the same model; (4) $\beta_0 + \beta_{mass}$, which assumed body mass was the only variable predicting home range size; and (5) β_0, the evolutionary null model described above for the terrestrial mammal analysis.

Table 1 Level of support for explanatory models of evolution of home range size in land mammals. Results are from phylogenetic generalized least squares (PGLS) regression computed for 1000 alternative resolutions of the mammalian phylogeny. Model terms include herbivores (diet_H), omnivores (diet_O), body mass (mass) and intercept (0).

Model	ΔAICc	ΔAICc 95% CI (upper, lower)	PGLS α	Effect size (r)
$\beta_0 + \beta_{mass} + \beta_{diet\_H} + \beta_{diet\_O}$	0.0	n.a.	14.8	0.82
$\beta_0 + \beta_{mass}$	40.6	34.8, 51.0	8.4	0.72
β_0	281.5	268.5, 298.4	2.9	–

AICc, Akaike information criterion with a correction for sample size; n.a., not applicable.

RESULTS

We found that diet and body mass together accounted for a portion of the variation in home range size observed among terrestrial mammals (Table 1, Fig. 1). Carnivores, omnivores and herbivores demonstrated the predicted difference in intercept values. Carnivores showed the predicted large home ranges with an intercept that was significantly higher than omnivores and herbivores. Omnivores had intermediate home range sizes that were significantly larger than those of herbivores, and herbivores had the smallest home ranges across the three dietary categories (Fig. 1). However, whereas body mass accounted for 52% of the variance in home range size among terrestrial species ($r = 0.72$), the inclusion of diet improved the explanatory power of the model by 15% ($r = 0.82$). There was also a substantial improvement in the computed AICc value between the diet model and the body mass only model (ΔAICc = 40.6). The inclusion of phylogeny was important for these analyses as the estimated phylogenetic signal in home range size among species was high (the null model, α = 2.9; note that values approaching 0 indicate a high phylogenetic signal in species data). That is, closely related species tended to share similar home range sizes and this could not be explained by phylogenetic inertia in body mass (i.e. α is a combined estimate of phylogenetic signal across all the variables entered into the model, and when body mass was included α was 8.36, suggesting that the level of phylogenetic signal exhibited by body mass was potentially lower than for home range size, otherwise the estimate would be similar to or even lower than that estimated by the null model).

When the analysis was expanded to all mammals in both terrestrial and marine environments, the model that included environment, diet and body mass was by far the best-supported model and explained 74% of the variance in home range size among species ($r = 0.86$; Table 2). There was virtually no support for any of the alternative models (ΔAICc > 10), although it was noteworthy that the second best model of diet and body mass provided a similarly high level of explanatory power (72% variance explained; $r = 0.85$; Table 2). The majority of marine species are large and carnivorous (*c.* 95% carnivorous
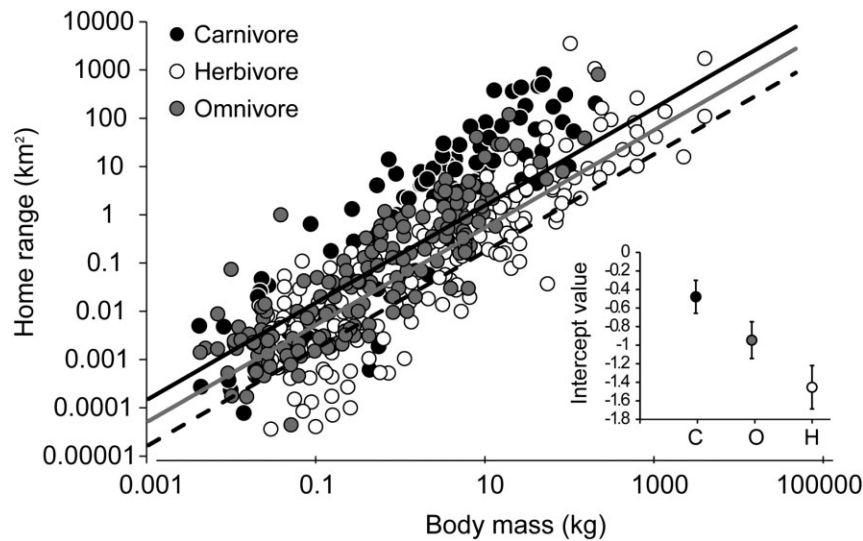
Figure 1 Home range size as a function of species body mass compared for terrestrial carnivorous (black circles), herbivorous (white circles) and omnivorous (grey circles) species. Each datum represents a species mean value ($n = 429$ species). The solid black line is the phylogenetic regression of carnivorous mammals: $\log Y = 1.12 \log X – 0.48$. The dashed black line is the phylogenetic regression of omnivorous mammals: $\log Y = 1.12 \log X – 0.94$. The solid grey line is the phylogenetic regression of herbivorous mammals: $\log Y = 1.12 \log X – 1.45$. Bottom right insert: intercept values and confidence intervals for terrestrial herbivores (H), omnivores (O) and carnivores (C). Values were calculated from phylogenetic least squares regression analyses applied to 1000 alternative resolutions of the mammalian phylogeny.

Table 2 Level of support for explanatory models of home range size evolution in mammals. Results are from phylogenetic generalized least squares (PGLS) regression computed for 1000 alternative resolutions of the mammalian phylogeny. Model terms include herbivores (diet_H), omnivores (diet_O), environment (marine or terrestrial), body mass (mass) and intercept (0).

Model	ΔAICc	ΔAICc 95% CI (upper, lower)	PGLS α	Effect size (r)
$\beta_0 + \beta_{mass} + \beta_{diet\_H} + \beta_{diet\_O} + \beta_{environment}$	0.0	n.a.	14.6	0.86
$\beta_0 + \beta_{mass} + \beta_{diet\_H} + \beta_{diet\_O}$	21.3	7.0, 44.3	14.1	0.85
$\beta_0 + \beta_{mass} + \beta_{environment}$	43.9	24.2, 61.8	8.9	0.79
$\beta_0 + \beta_{mass}$	77.9	58.8, 100.8	7.2	0.73
β_0	322.9	302.3, 354.2	2.4	–

AICc, Akaike information criterion with a correction for sample size; n.a., not applicable.

species) and this led us to question whether the environment specifically influenced the best-supported model or whether it was due to the inclusion of larger carnivores in the data set. To explore this, we examined the parameter estimates for the second best-supported model which included only diet and body mass. These estimates confirmed the expected positive relationship between home range and body mass and showed that all the diet categories were significantly different from one

another: carnivores had the largest home ranges, omnivores had intermediate home ranges and herbivores had the smallest home ranges (Fig. 2). That is, with the inclusion of the marine mammals, the primary effect seems to have been a divergence in intercept values between the carnivores and omnivores (compare Figs 1 & 2).

To examine whether the environment has had any impact on home range size, we restricted our analyses to only carnivorous marine and terrestrial mammals and refitted the environment and body mass model ($\beta_0 + \beta_{mass} + \beta_{environment}$), the body mass only model ($\beta_0 + \beta_{mass}$) and the evolutionary null model (β_0). The environment model was the best-supported model of the three, but only explained an additional 1.7% of the variance in home range size above the 72% explained by body mass only (Table 3). In general, however, marine carnivores have home ranges that are 1.2 times larger than those of terrestrial species of a similar mass (Fig. 3).

Overall, our results confirmed the overarching effect of body mass on mammalian home range size. In addition to body mass, diet and the physical environment, both explained additional variance in home range size among species, but their influence was less than that of body mass. There was evidence to suggest that diet might have had a greater impact on home range size than the physical environment (19% additional variance explained for diet compared with 9% for the environment). In no instance was the evolutionary null model a compelling alternative explanation for differences in home range size among species, but home range size was found to exhibit a strong phylogenetic signal in all analyses ($\alpha = 1.50$–2.90; Tables 1–3).
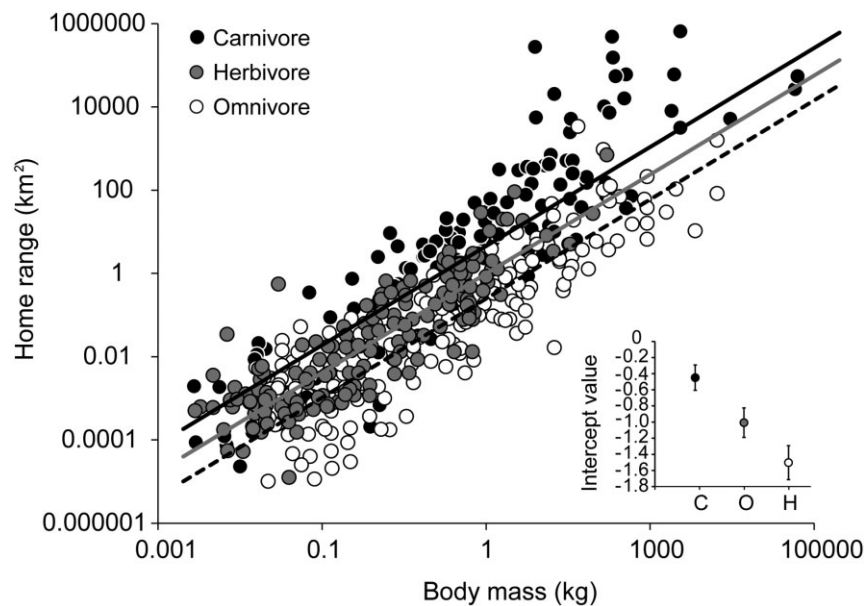
Figure 2 Home range size as a function of species body mass compared for carnivorous (black circles), herbivorous (white circles) and omnivorous (grey circles) species. Each datum represents a species mean value ($n = 462$ species). The solid black line is the phylogenetic regression of carnivorous mammals: $\log Y = 1.19 \log X - 0.29$. The dashed black line is the phylogenetic regression of omnivorous mammals: $\log Y = 1.19 \log X - 0.91$. The solid grey line is the phylogenetic regression of herbivorous mammals: $\log Y = 1.19 \log X - 1.47$. Bottom right insert: intercept values and confidence intervals for carnivores (C), omnivores (O) and herbivores (H). Values were calculated from phylogenetic least squares regression analyses applied to 1000 alternative resolutions of the mammalian phylogeny.

Table 3 Level of support for explanatory models of home range size evolution in carnivorous mammals. Results are from phylogenetic generalized least squares (PGLS) regression computed for 1000 alternative resolutions of the mammalian phylogeny. Model terms include environment (marine or terrestrial), body mass (mass) and intercept (0).

Model	ΔAICc	ΔAICc 95% CI (upper, lower)	PGLS α	Effect size (r)
$\beta_0 + \beta_{mass} + \beta_{environment}$	0.0	n.a.	11.6	0.86
$\beta_0 + \beta_{mass}$	4.0	3.6, 4.6	11.0	0.85
β_0	93.7	90.3, 101.5	1.5	–

AICc, Akaike information criterion with a correction for sample size; n.a., not applicable.

DISCUSSION

Body mass was the principal predictor of home range size in mammals, accounting for 53–85% of the observed variation in home range size among species. The evolution of home range size appears to have been driven, for the most part, by the energetic requirements and costs or benefits associated with a given body mass. Energetic requirements, such as metabolic rate (kJ day^{-1}), are positively correlated with body mass (Nagy, 2005). As large species have higher absolute energy needs, they must consume more resources and cover larger areas in order to be able to meet their energetic demands (McNab, 1963). By con-

trast, the energetic costs associated with movement are greater in smaller species (Pontzer, 2007), which tends to constrain their movements and results in smaller home range sizes. In addition to the effects of body mass, we found that the amount of meat included in diets was a second-order predictor of home range, followed closely by the physical environment (terrestrial versus marine).

However, while providing significant improvements in the level of support for models, there were varying effects of diet and physical environment on home range size. Both could only explain a further 1–19% of the variation in home range size among species beyond the effect of body mass. Such a small effect was surprising for diet because several past studies have concluded diet to be the key determinant of the home range–body mass relationship in terrestrial mammals (Swihart *et al.*, 1988; Kelt & van Vuren, 2001). This seems reasonable considering that what species eat has a direct impact on both their energetic requirements and the types of costs incurred in obtaining and processing food resources. However, while our results confirm that diet has been a factor in shaping mammalian home ranges (support was high for models that included a parameter for diet) it has nevertheless been far less influential than body mass. Previous studies of diet and home range use were based on datasets with limited species coverage across physical environments (i.e. marine and terrestrial), which can result in model bias and cause issues when these models are extrapolated over a broader range of species (Sibly *et al.*, 2012). Furthermore, phylogenetic information was not incorporated into previous analyses and our results showed that home range
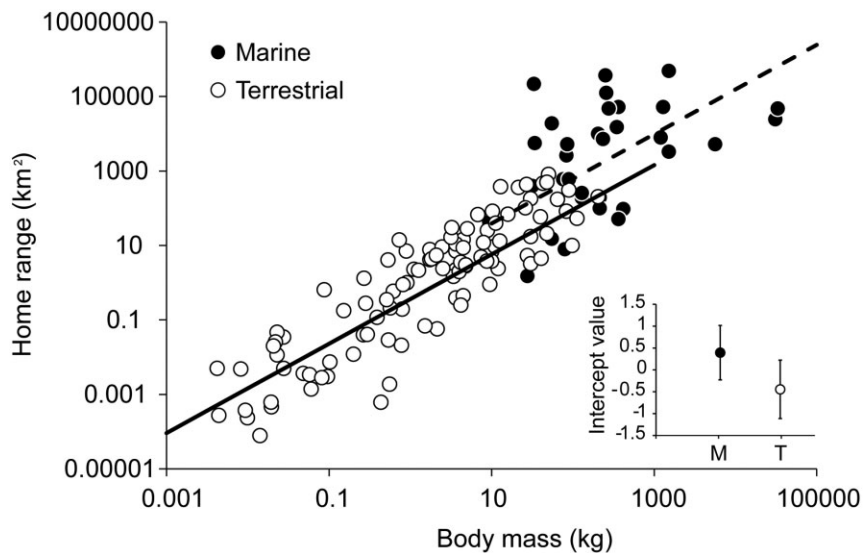
Figure 3 Carnivore home range size as a function of species body mass compared for species occupying terrestrial (white circles) and marine (black circles) environments. Each datum represents a species mean value ($n = 134$ species). The solid black line is the phylogenetic regression of terrestrial mammals: $\log Y = 1.2 \log X + 0.39$. The dashed black line is the phylogenetic least squares (PGLS) regression line of marine mammals: $\log Y = 1.2 \log X - 0.44$. The river otter (9 kg) and southern humpback whale (32,000 kg) are the smallest and largest marine mammals, while the masked shrew (4.2 g) and lion (204 kg) are the smallest and largest terrestrial mammals. Bottom right insert: intercept values and confidence intervals for terrestrial (T) and marine (M) mammals. Values were calculated from PGLS regression analyses applied to 1000 alternative resolutions of the mammalian phylogeny.

size does exhibit a large amount of phylogenetic signal (and this was not likely to be the by-product of phylogenetic inertia in body mass).

When our analyses were applied to all species, an apparent dual role of both diet and the environment seemed to be supported (Table 2). However, the precise relationship with the physical environment was unclear because the majority of marine mammals were large carnivores with very large home ranges. The specific relevance of the marine environment to home range evolution was therefore unclear. When the effect of diet was controlled for by focusing on carnivorous mammals across terrestrial and marine environments, we found that home ranges were significantly larger in marine environments for a given body mass than they were on land (Table 3), but the effect was arguably smaller than that of diet (environment only accounted for an additional 1.7% of the variation in home range size among species over body mass). The combination of living in an open environment, feeding on mobile resources and lower transport costs has resulted in the evolution of large home range sizes in marine carnivorous mammals (roughly 1.2 times larger than those of terrestrial carnivorous mammals), but the impact of these factors has been minimal compared with the energetic requirements/costs driven by body mass. Unfortunately we were unable to examine the relationship between home range, diet and environment more closely for herbivores and omnivores due to the predominance of carnivory within the marine environment.

Large carnivorous mammals have high daily energy requirements, and one strategy for meeting these requirements is to utilize pack hunting (Carbone *et al.*, 2007a). Pack hunting enables prey with a large body mass to be hunted whilst mini-

mizing energy expended during the hunt. There is the potential that pack hunting may alter home range size due to the increased density of individuals within an area. Our data did not suggest any difference in home range size between carnivores that utilize pack hunting and those that do not (Appendix S3). It would be ideal to have more complete home range information on whales. With the addition of more whale species, we would expect to see a different home range relationship with body mass, such as an increase in the scaling of home range size with body mass, resulting in extreme home range sizes with large body mass. This would especially be the case with the inclusion of the various whale migrations, which cover a large area, for example the length of a migration (i.e. one direction, single track) can be greater than 5000 km, without accounting for the 'width' of the home range (Alerstam *et al.*, 2003). At present, there are a limited number of tracking data available for whales, especially long-term data that also include their migration.

Like mammals, birds provide an interesting comparison with the home range size of marine mammals. Birds also live within a three-dimensional environment (excluding the flightless species) and home range sizes in non-migratory birds tend to be larger than those of mammals for their size (Haskell *et al.*, 2002). The literature suggests that body mass and food resources are the main drivers of home range size in birds, similar to mammals. Body mass was attributed to energy requirements, as large birds 'require more food per unit area than smaller birds' (Schoener, 1968). Also, birds with an increasing amount of vertebrate prey in their diet will have larger home range sizes due to lower densities of their prey compared with that of herbivores and omnivores (Schoener, 1968).

The effects of diet on the relationship between home range size and body mass found by this study are likely to only be large-scale effects of resource use and distribution constraints across the broad diet categories of carnivores, omnivores and herbivores. This is because resource use and resource distribution constraints have varied effects on home range size. Changes in the type of resources used and their abundance can vary on different temporal scales. For example, resource distribution and availability in the Arctic are highly seasonal, with a distinct set of resources available during winter compared with summer. This would have a strong effect on the home range size of individuals living in this region (e.g. polar bears; Ferguson *et al.*, 1999). However, an individual may also change which resources they use on a much shorter temporal scale, such as on a day to day basis. Shifts in resource use or distribution on this small scale are unlikely to be detected in home range analyses due to home range size being calculated over longer periods (i.e. generally on a seasonal or yearly scale). Small-scale studies with a focus on a single species and a more direct approach, such as state-space models (Bestley *et al.*, 2013), would be ideal for investigating dietary effects over these shorter periods.

Our sample sizes were biased towards terrestrial mammals despite our data including all available information on home range size for marine species (Fig. 1). This partly reflects the difference in the number of mammal species on land versus those in the water that were included in our analyses. Calculating home range for marine species is difficult because of issues associated with tracking marine species (satellite tracking often being required). For example, home ranges are often calculated over shorter tracking periods in marine species compared with those on land. As tracking technology improves, and methodologies for estimating home ranges in marine species become more sophisticated, the number of species for which home range information is available should increase. Nevertheless, mammalian species diversity in marine environments is much lower than on land, so this bias in sampling partly reflects biological reality and this will not change with improved methods of home range estimation.

It should also be noted that the home range values of marine species used in this study may be conservative because they were measured in two dimensions while marine mammals use a three-dimensional environment (Pawar *et al.*, 2012). However, Carbone *et al.* (2007b) investigated abundance scaling in mammals in three-dimensional environments and their models predict a −2/3 scaling similar to abundance scaling within two-dimensional environments. As there is a relationship between animal abundance scaling and home range size (Jetz *et al.*, 2004), we may expect to see a similar pattern in the scaling of home range size in mammals. The effect of the dimensionality of environments would be an interesting concept to examine in a future study, using similar mathematical methods to those used in Carbone *et al.* (2007b).

It is unlikely that differences in home range size across the marine and terrestrial environments are driven by how species are related (i.e. collinearity between environment and relatedness). Marine mammals are interspersed across the mammalian clade (see Fig. S1). For example, within Carnivora there are both marine (e.g. pinnipeds, *Ursus maritimus* and *Enhyrda lutris*) and terrestrial (e.g. Canidae, Mephitidae, Procyonidae) representatives.

Conclusion

Home range is a complex factor influenced by a range of variables, including body mass, diet and environment. Our aim was to clarify the role of these variables and extent to which they affect home range size in mammals. We highlight that across the mammalian radiation the evolution of home range has been driven by a hierachy of variables, but some variables have clearly been more influential than others. The key explanatory variable for home range size was body mass, followed by the secondary variables of diet and then environment. To better understand the evolution of mammalian home range size we need to investigate the proximate mechanisms (here, proximate mechanisms are the physiological and morphological drivers) of its relationship to body size. Furthermore, because the effects of diet and environment on home range use were small, it would be prudent to reconsider past assumptions regarding the influence of differing resource bases (meat versus plant), modes of transport (swimming versus walking and running) and altered physical properties (water versus air) as underlying mechanisms of home range use.

Broad models developed using information from many species, such as the allometric model of home range size (Jetz *et al.*, 2004; this study), are often used to guide conservation and management strategies. It is critical then that the underlying assumptions of these models are biologically appropriate. Previous models have focused exclusively on select groups of species (e.g. terrestrial mammals), and we have developed an important amendment to these models to show that home range drivers once thought to be highly influential are not so. We have demonstrated that by using an integrative model which incorporates an inclusive list of predictor variables, species and phylogenetic information, our knowledge of home range patterns across mammals can be significantly enhanced.

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Additional references to the data sources may be found at the end of Appendices S1 & S2 at [http://onlinelibrary.wiley.com/doi/10.1111/geb.12194/suppinfo].

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Appendix S1 Database of home range and body mass values for 462 species of mammal, including sources.
Appendix S2 Additional information on sample size, data collection and sampling protocols for data used in home range calculation.
Appendix S3 Additional analyses and results.
Figure S1 The phylogeny of 462 extant species of mammal and their home range size.

BIOSKETCHES

Marlee Tucker is a PhD candidate under the supervision of Tracey Rogers. Marlee's research encompasses macroecological patterns in mammals, specifically changes in behaviours and patterns that have occurred with the colonization of the marine environment.

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