

Home is where the shell is: predicting turtle home range sizes

Alex Slavenko^{1*}, Yuval Itescu¹, Flora Ihlow² and Shai Meiri¹

¹Department of Zoology, Tel Aviv University, 6997801 Tel Aviv, Israel; and ²Herpetology Department, Zoologisches Forschungsmuseum Alexander Koenig (ZFMK), 53113 Bonn, Germany

Summary

1. Home range is the area traversed by an animal in its normal activities. The size of home ranges is thought to be tightly linked to body size, through size effect on metabolic requirements. Due to the structure of Eltonian food pyramids, home range sizes of carnivores are expected to exceed those of herbivorous species. The habitat may also affect home range size, with reduced costs of locomotion or lower food abundance in, for example, aquatic habitats selecting for larger home ranges. Furthermore, home range of males in polygamous species may be large due to sexual selection for increased reproductive output.

2. Comparative studies on home range sizes have rarely been conducted on ectotherms. Because ectotherm metabolic rates are much lower than those of endotherms, energetic considerations of metabolic requirements may be less important in determining the home range sizes of the former, and other factors such as differing habitats and sexual selection may have an increased effect.

3. We collected literature data on turtle home range sizes. We used phylogenetic generalized least squares analyses to determine whether body mass, sex, diet, habitat and social structure affect home range size.

4. Turtle home range size increases with body mass. However, body mass explains relatively little of the variation in home range size. Aquatic turtles have larger home ranges than semi-aquatic species. Omnivorous turtles have larger home ranges than herbivores and carnivores, but diet is not a strong predictor. Sex and social structure are unrelated to home range size.

5. We conclude that energetic constraints are not the primary factor that determines home range size in turtles, and energetic costs of locomotion in different habitats probably play a major role.

Key-words: body size, chelonians, energetic constraints, home range size, macroecology, phylogenetic generalized least square

Introduction

Home range is ‘...that area traversed by the individual in its normal activities of food gathering, mating, and caring for the young’ (Burt 1943). Many studies, on various taxa, have tried to estimate the sizes of home ranges (e.g. Ihlow *et al.* 2014; Zhang *et al.* 2014) and to determine the factors that affect them (e.g. McNab 1963; Tucker, Ord & Rogers 2014). Body size is considered to be a crucial factor in determining home range size and is tightly correlated with it in mammals (McNab 1963; Milton & May 1976; Harestad & Bunnell 1979; Lindstedt, Miller & Buskirk

1986; Tucker, Ord & Rogers 2014), birds (Schoener 1968) and lizards (Turner, Jennrich & Weintraub 1969; Christian & Waldschmidt 1984; Perry & Garland 2002).

This relationship is thought to reflect a process whereby metabolic requirements dictate an individual’s home range size. McNab (1963) noted that the slope of the regression of home range size against body mass did not differ significantly from the 0.75 allometric slope of the regression of (log) basal metabolic rate against (log) body mass. He therefore hypothesized that home range size is proportional to basal metabolic rate, and is dictated primarily by energetic constraints – larger animals have higher energetic requirements, and therefore need to traverse larger foraging areas to meet said requirements. Later findings have shown that empirical slopes tend to be roughly

*Correspondence author. E-mail: slavenko@mail.tau.ac.il

isometric (Peters 1983, p. 173). This is thought to be due to increased home range overlap of larger animals and thus less exclusivity of food resources (Jetz *et al.* 2004). The role of energetic requirements in determining home range size, however, is still widely accepted.

This hypothesis is further supported by the findings that home range size, in several taxa, varies with diet, with carnivores generally having larger home ranges than herbivores or omnivores of similar size (McNab 1963; Schoener 1968; Harestad & Bunnell 1979; Perry & Garland 2002). The lower abundance of animal relative to plant food, due to the nature of Eltonian food pyramids (Elton 1927), means carnivores must range farther to acquire sufficient sustenance than do herbivores.

Other factors that are thought to affect home range size include sex, the mating system and habitat preferences. In animals with a polygynous mating system, male home range sizes may be under sexual selection as males need to secure a large number of females and defend them from other males. Male lizards, for example, generally have larger home ranges than do females of the same size (Perry & Garland 2002). While female home range size may be dictated primarily by metabolic needs, male home range is structured to increase their reproductive success rate, by overlapping as many female home ranges as possible (Schoener & Schoener 1982). Polygynous and promiscuous species are thus expected to have larger home ranges than solitary and monogamous species, as well as larger sexual dimorphism in range size (Gaulin & FitzGerald 1988). Despite these findings, social structure and mating systems of the studied taxa have widely been neglected in comparative studies of home range sizes.

The effect of habitat use on home range size is probably substantial, but has rarely been examined (but see Herfindal *et al.* 2005; Nilsen, Herfindal & Linnell 2005). Marine mammals, for example, have larger home ranges than terrestrial mammals (Tucker, Ord & Rogers 2014). Marine species live in environments with mobile food resources, and marine and aquatic species may also have lower energetic costs of locomotion than their terrestrial counterparts (Gleeson 1979; Baudinette, Miller & Sarre 2000). Both factors may allow aquatic species to have larger home ranges than terrestrial species (Tucker, Ord & Rogers 2014), but the absolute speed of locomotion could have a larger effect on home range size than its energetic expenditure (Tamburillo, Côté & Dulvy 2015), and mobility of food resources can have an opposite effect. River fishes have smaller home ranges than lake fishes (Minns 1995), a fact attributed to food resources being carried downstream by rivers and reducing the need of fish to forage widely.

Turtles are a well-studied taxon, comprising of 327 extant species (Turtle Taxonomy Working Group 2014). They vary in size from ~140 g (Nama padloper, *Homopus solus*) to ~900 kg (leatherback turtle, *Dermochelys coriacea*) (Depecker *et al.* 2006). Turtles are found on all continents, barring Antarctica, in various habitats. Some turtles are terrestrial, but most species are aquatic or semiaquatic, and

seven species are marine (Bonin, Devaux & Dupré 2006). Some turtles are herbivores, whereas others are omnivorous or carnivorous (Bonin, Devaux & Dupré 2006).

Turtles are defined by their unique synapomorphic trait – the bony shell. The shell severely restricts turtle locomotion on land and precludes them from adopting arboreal habits (Rivera *et al.* 2006). During their evolutionary history, turtles have shifted from aquatic to terrestrial environments and back several times (Claude *et al.* 2003; Gerlach 2012). This variability in diet, habitat use and size makes them an interesting case study to examine the factors that control home range size. Such a study could also have important implications for conservation, as it allows us to understand how turtles make use of space. With more than half the living species threatened with extinction, turtles are among the most endangered taxa on earth (Turtle Taxonomy Working Group 2014). Identifying the underlying determining factors of space use for turtles could vastly improve future conservation planning of this highly endangered taxon.

We examine the following predictors of home range size in turtles: body mass, sex, habitat, diet and social structure, and hypothesize that turtle home range size is determined, in part, by their metabolic needs, as per the energetic constraints hypothesis (McNab 1963). We therefore predict that

- 1 Turtle home range size will increase with body mass, with a slope ~ 0.75 .
- 2 Home ranges of carnivores will be larger than those of omnivores, and home ranges of omnivores will be larger than those of herbivores.
- 3 Aquatic species will have larger home ranges than terrestrial species, due to their lower energetic costs of locomotion facilitating increased mobility.
- 4 Males in polygynous species will have larger home ranges than females, due to the effects of sexual selection on home range size.
- 5 Home range sizes of polygamous and social species will exceed those of solitary species, reflecting the greater metabolic needs of groups relative to individuals (Gaulin & FitzGerald 1988) – however, we also expect this relationship to decrease with body mass, as overlap in home range increases as a function of body size (Jetz *et al.* 2004).

Materials and methods

DATA COLLECTION

We collected home range size estimates for different species of turtles from published sources (Appendix S1, Supporting information) by searching online data bases such as Google Scholar. As sample sizes used to estimate home range sizes of marine turtles were uniformly very low and owing to their unique biology and movement patterns, we omitted marine turtle species from the study.

We collected data on home range size for 64 species, with data for males (37 species) and females (46 species) separately, when

available. We used the published mean home range size of adults of both sexes, or calculated the mean of individual published home range sizes. If several estimates from different sources for the same species were available, we calculated the overall mean of these estimates. If means were unavailable, we calculated the average of reported male and female estimates [i.e. if male estimate is x and female estimate is y , then the species estimate is $(x + y)/2$]. When neither species means, means of sexed animals, or home range sizes of individuals were available, we calculated the midpoint between published minimum and maximum estimates [i.e. if the home range size ranges between m and n , then the species estimate is $(m + n)/2$]. Data on mean straight carapace length (from Itescu 2012) were collected for each species, using the same method as the collection of home range sizes. We converted the length data to mass using family specific allometric equations developed by Itescu (2012).

The most commonly used application in the past to estimate home range size is the minimum convex polygon (MCP) method, whereby one connects all the peripheral locality points of an individual to form the smallest convex polygon, and subsequently calculates the area encompassed by this polygon (Powell 2000). Of the 64 species we collected data for, 50 species' home range sizes have been estimated using the MCP method (including all the sex-specific estimates). Home range sizes of five species were estimated using other methods [linear home range multiplied by river width for the pig-nosed turtle, *Carretochelys insculpta* (Doody, Young & Georges 2002), alligator snapping turtle, *Macrochelys temminckii* (Moore 2011) and Geoffroy's toadhead turtle, *Phrynops geoffroanus* (Souza *et al.* 2008); circle using half of movement range as radius for the western Caspian turtle, *Mauremys rivulata* (Sidis 1983); and fixed kernel for the Madagascan tortoise, *Astrochelys yniphora* (Pedrono & Sarovy 2000)]. For the other nine species, the method used to estimate home range size was not specified (Appendix S1).

We obtained data on turtle habitat use from the literature (Bonin, Devaux & Dupré 2006; Ernst, Altenburg & Barbour 2006; Buhlmann, Gibbons & Jackson 2008; Berry & Iverson 2011; Bertolero *et al.* 2011). Species were designated as aquatic (spend most of their time in bodies of water), semiaquatic (spend substantial time both in water and on land) or terrestrial (spend the majority of their time on land). We further obtained literature data on diet (carnivores, herbivores and omnivores; Vetter 2004, 2005, 2011; Vetter & Van Dijk 2006; Cann 2008). We derived data on social structure from Vetter (2004, 2005, 2011), Vetter & Van Dijk (2006), Cann (2008) and Myers *et al.* (2014). We assigned turtle species to one of three distinct categories of social structure; 'solitary', 'harem' (groups composed of one male and several females) or 'social' (groups composed of several males and several females).

To account for the effects of phylogenetic nonindependence in our data, we used the complete phylogenetic tree of extant turtles compiled by Itescu *et al.* (2014), which we pruned to match the species included in this study (Appendix S2).

STATISTICAL ANALYSES

We performed a phylogenetic generalized least square (PGLS) regression (Freckleton, Harvey & Pagel 2002), after log-transforming the home range size and body mass data to linearize the relationship, normalize residuals and reduce heteroscedasticity. We used the 'caper' package for R (Orme *et al.* 2012) to estimate

the maximum likelihood value of the scaling parameter λ . λ ranges from 0 to 1 and is a measure of the strength of the phylogenetic signal in the data (0 representing no signal, and 1 representing evolution by Brownian motion). If λ was found to be 0, we fitted an ordinary least squares (OLS) regression. We included body mass, diet, habitat and social structure, and their two-way interactions, as possible predictors of turtle home range size. We selected all models with $\Delta\text{AIC}_c < 2$ of the model with the lowest score, unless a model with a lower AIC score was nested within them (so if a model with parameters a , b and c has a $\Delta\text{AIC}_c < 2$ than a model with only parameters a and b , we did not use the more complicated model; Arnold 2010). We averaged the best competing models to arrive at the global model and calculated the relative importance of predictors in the averaged variable, calculated as the sum of Akaike weights over all the models in which the predictor appears [so if models a , b and c were averaged, with Akaike weights x , y and z , respectively (the sum of all three being 1), a predictor that appeared in all three models would have a relative importance of 1, while a predictor that appeared only in, for example models a and b would have a relative importance of $x + y$; Burnham & Anderson 2002, p. 168].

To account for the possible bias caused using different methods for calculating home range size (Nilsen, Pedersen & Linnell 2008), we ran the analyses on two data sets: one including only the 50 species for which we were sure home range size was estimated using MCP, and another with all 64 species. When analysing the full data set, we added the method (MCP for the 50 species or 'other' for the remaining 14) as a predictor.

We further examined the effect of sex on home range sizes of turtles. However, we had fewer home range estimates for sexed individuals (all estimated using MCP) than estimates of unsexed ones. We therefore fitted separate models, following the same methods and model selection process as the global models, for the sexed 37-species subset of the MCP data set and included sex and its two-way interactions with the other variables as predictors.

We performed all statistical analyses in R v3.0.2 (R Development Core Team 2013), using the RSTUDIO v0.98.978 (RStudio Inc. 2013) interface.

Results

Home range sizes of nonmarine turtles span four orders of magnitude, from 0.013 ha [Tabasco mud turtle, *Kinosternon acutum* (mean mass = 235g; Iverson & Vogt 2011)] to 327.6 ha [red-eared slider, *Trachemys scripta* (mean mass = 933 g; Jaeger & Cobb 2012)], with a mean range size of 23.35 ha and a median range size of 6.82 ha (Table 1). There is also much intraspecific variability in home range sizes, often with great differences between populations of the same species [e.g. estimates of 3.7 ha (Haxton & Berrill 1999) and 15 ha (Litzgus & Mousseau 2004) for different populations of spotted turtles, *Clemmys guttata*] and between adult individuals within the same population [e.g. home range sizes spanning from 2.1 to 628.9 ha for individuals from a single population of red-footed tortoises, *Chelonoidis carbonaria* in Bolivia (Montaño *et al.* 2013)], albeit these differences are on a smaller scale than the interspecific variation. This variation obviously undermines the ability of comparative studies such as ours, using a single value per species, to

Table 1. Summary table with descriptive statistics of mean home range sizes of turtles in each of the three habitat (aquatic, semiaquatic, terrestrial), diet (carnivorous, herbivorous, omnivorous) and sociality (harem, social, solitary) categories, along with sample sizes

Dataset	Habitat			Diet			Sociality			
	All	Aquatic	Semiaquatic	Terrestrial	Carnivorous	Herbivorous	Omnivorous	Harem	Social	Solitary
Complete										
Mean (ha)	23	32.19	8.51	20.06	21.46	19.7	26.06	34.05	18.83	17.94
Median (ha)	6.13	13.19	2.28	7	3.61	5.1	10.56	8.46	6.91	3.61
SE (ha)	5.3	10.05	5.28	7.52	9.35	11.37	7.93	14.26	4.97	7.17
Minimum (ha)	0.01	0.01	0.05	0.28	0.01	0.28	0.23	0.01	0.24	0.04
Maximum (ha)	195	177.87	60.25	195	141.05	195	177.87	195	75.4	141.05
Sample size	64	26	11	27	19	17	28	19	20	25
MCP-only										
Mean (ha)	24.21	41.29	12.08	14.21	35.22	9.6	27.53	31.81	22	20.71
Median (ha)	8.84	13.87	2.28	7.1	13.55	4.16	12.67	11.89	9.22	5.42
SE (ha)	5.65	13.1	8.18	3.72	15.02	3.63	8.78	14.71	6.11	8.41
Minimum (ha)	0.27	0.94	0.27	0.35	0.94	0.35	0.27	0.94	1.13	0.27
Maximum (ha)	177.87	177.87	60.25	75.4	141.05	50.77	177.87	177.87	75.4	141.05
Sample size	50	19	7	24	11	14	25	14	15	21

fully encompass the plethora of selective forces affecting home range size (although we think it is unlikely to bias the estimates *per se*). This variation is real, and thus in itself offers a fascinating opportunity to study the factors affecting home range sizes.

Phylogenetic affinities do not seem to affect the relationships between our predictors and home range sizes: the maximum likelihood value of λ was 0 in all models. We therefore fitted OLS models for all data sets and report these results.

The two best models for turtle home range sizes (ranked by AIC_c scores) are listed in Appendix S3. The averaged model to predict turtle home range sizes for the entire 64 species data set includes body mass, home range size estimation method and diet as predictors, but diet has a low relative importance (0.56). Surprisingly, omnivores emerged as having the largest home ranges (intercept is 0.39 log units higher than carnivores) and herbivores the smallest (difference in intercepts from omnivores is 0.46). Home range size increases with body mass (slope = 0.67, 95% CI = 0.34–1), and home ranges estimated using MCPs are larger than those estimated with other or unknown methods (difference in intercepts is 0.94 log units, or roughly tenfold; Fig. 1). While R^2 values cannot be calculated for averaged models, they ranged between 31% and 37% in the top-ranked models.

The averaged model for the MCP-only, 50 species data set, includes body mass, habitat and diet as predictors of home range size (Fig. 2). As with the complete data set, diet has low relative importance (0.65), and omnivores have the largest home ranges. Home range size increases with body mass, albeit with an even shallower slope than in the full data set (0.56, 95% CI = 0.25–0.87). In this model, aquatic species have larger home ranges than semiaquatic and terrestrial species (differences in intercepts are 0.75 and 0.41, respectively). R^2 values of the two top-ranked models ranged between 30% and 39%.

Sex and social structure were not retained as predictors in the top-ranked model of the subset of the data set which included data on home range size estimates of males and females separately, and neither were their two-way interactions with each other or with body mass. The resulting model had the same predictors (body mass, habitat and diet) as the best MCP-only model with no data on sex.

Discussion

Few of the factors we examine seem to affect turtle home range size, but the measuring method does. We found that home range sizes estimated using MCPs were about ten times larger than estimates based on other methods, or on unreported methods. The MCP method has been criticized for introducing a sample size-based bias and is sensitive to extreme outlying localities, could cause either over- or under-estimation of actual home range size when compared to other methods (Powell 2000; Börger *et al.* 2006), and may affect the results of comparative studies (Laver & Kelly 2008; but see Nilsen, Pedersen & Linnell 2008). However, as most of the home range sizes we considered in the 'other' category did not have the method of estimation specified, it is possible and even likely, considering the popularity of the MCP method, that many of them were also estimated using MCPs. Whether the method of estimation matters or our result is a statistical artefact is therefore difficult to determine. It appears that the method used to estimate home range size can affect the results of comparative studies and should be accounted for when mixing studies that estimated home range sizes with different methods, at least until a larger data set of home range sizes estimated using more robust methods (such as the kernel density estimator; Börger *et al.* 2006) can be established. However, the MCP method by itself does not seem to introduce a systematic bias in large-scale macroecological analyses, and there-

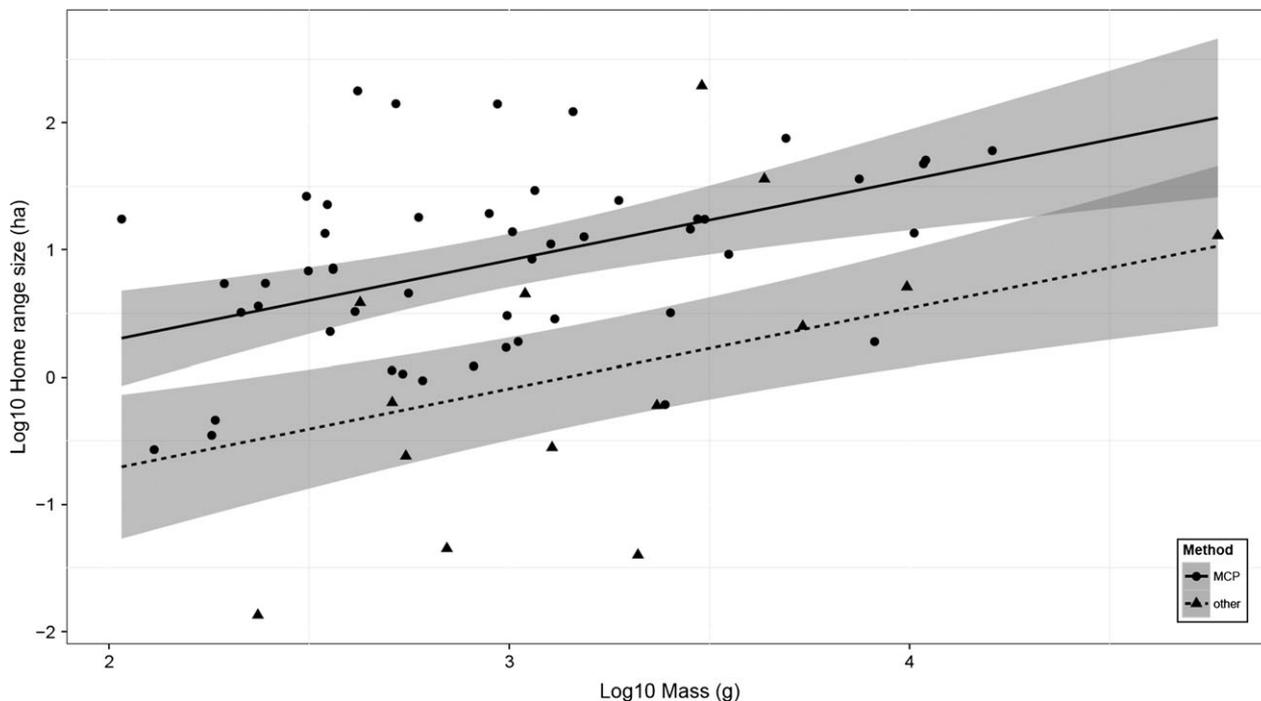


Fig. 1. Log-loglinear regression of home range size against body mass in the unsexed (complete) data set. Circles and solid line represent home range sizes estimated using minimum convex polygons (MCPs), while triangles and dashed line represent home range sizes estimated using other or unreported methods. 95% confidence intervals are represented by the shaded areas.

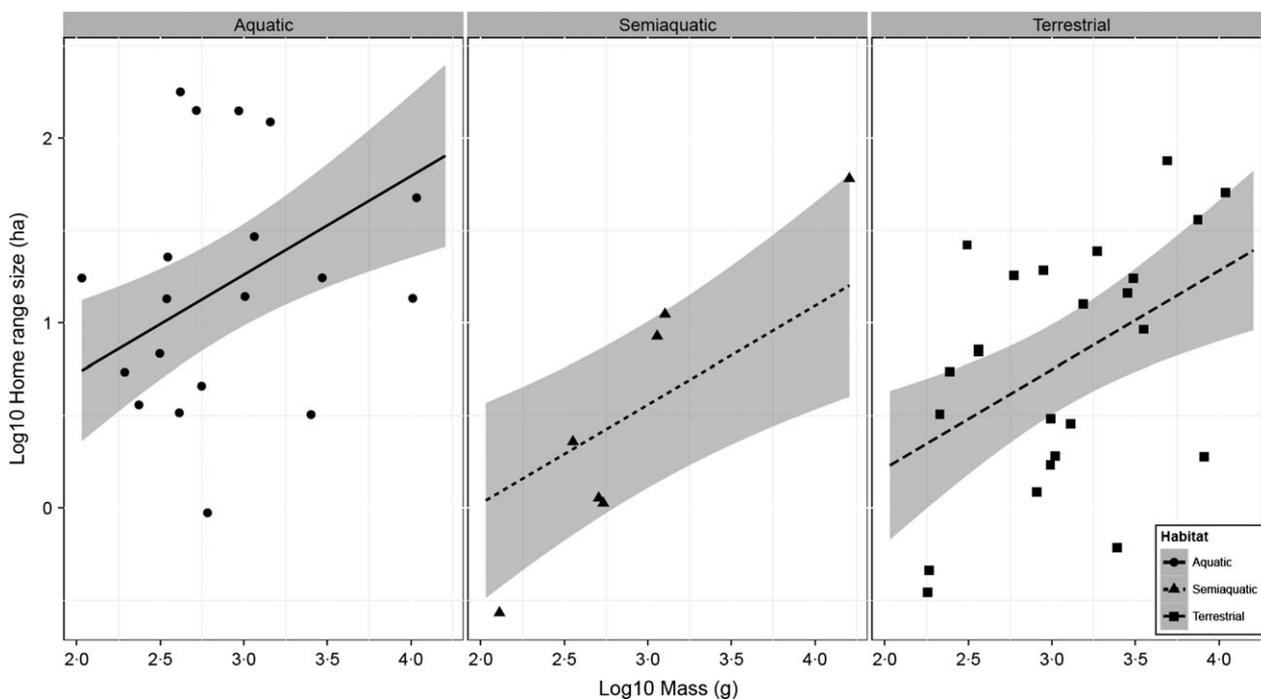


Fig. 2. Log-loglinear regression of home range size against body mass in the unsexed (MCP-only) data set. Home range size increases with body mass, and aquatic turtles have larger home ranges than terrestrial or semiaquatic turtles. 95% confidence intervals are represented by the shaded areas.

fore, viable conclusions can be drawn from analyses based solely on MCP estimates (Nilsen, Pedersen & Linnell 2008; Signer *et al.* 2015). Therefore, to ensure comparability of results, we only consider the results gained from the

MCP-only data set (without data on sex – which did not emerge as important) for further interpretation.

Home range size of turtles increases with body mass. While our slope (0.57) is not significantly different than

the slope of 0.75 predicted by McNab's (1963) energetic constraints hypothesis (95% CI of 0.22–0.85 for the slope of the MCP-only data set), it is shallower than many empirical slopes that are roughly isometric (Peters 1983, p. 173; but see Nilsen & Linnell 2006) and is similar to the slope calculated for freshwater lake fishes (0.58; Minns 1995). The scaling of home range size to body mass is still debated, as several studies report slopes steeper than those predicted by metabolic rates, with varying explanations (Peters 1983; Reiss 1988; Kelt & Van Vuren 2001; Haskell, Ritchie & Olf 2002). Our finding suggests that, in turtles, body mass explains relatively little variation in home range size, with wide confidence intervals for the regression slope (it should be noted that a model with only body mass included as a predictor explains only 12% of the variation in home range size). The claim that home range size is dictated by energetic requirements and scales to metabolic rate is therefore difficult to evaluate. Indeed, while many life-history and ecological traits are thought to scale with metabolic rate (West, Brown & Enquist 1997), this concept has come under much scrutiny (e.g. Dodds, Rothman & Weitz 2001; Kozłowski & Konarzewski 2004; da Silva, Garcia & Barbosa 2006).

Surprisingly, we found no phylogenetic signal in the relationships between home range size and our examined predictors, meaning that the similarity in home range size is not proportional to the phylogenetic distance between species, despite closely related species being similar in body size, social structure, diet, habitat preferences and other ecological traits. This could reflect the large variability in home range size (see 'Results') and suggests that home range size is less dictated by intrinsic, phylogenetically conserved animal traits, and more by extrinsic factors such as environmental productivity (e.g. Herfindal *et al.* 2005; Nilsen, Herfindal & Linnell 2005) or the topography and size of the available habitat.

The effect of diet on turtle home range size is somewhat ambiguous, as models with diet included as a predictor fared generally well, but model averaging revealed this effect to be weak. Furthermore, contrary to the energetic constraints hypothesis (McNab 1963), we found omnivores had the largest home ranges and not carnivores. It is possible that our dietary categories are too coarse, as they do not distinguish between different foraging strategies (e.g. sit-and-wait predators such as the alligator snapping turtle, *M. temminckii* vs. active foragers such as Dahl's toadhead turtle, *Mesoclemmys dahl*) or diet specialists (e.g. the impressed tortoise, *Manouria impressa*, which feeds exclusively on mushrooms) vs. generalists (e.g. the leopard tortoise, *Stigmochelys pardalis*). However, studies with similarly broad categories have found diet to have a strong effect on home range size in various taxa (e.g. McNab 1963; Perry & Garland 2002; Tucker, Ord & Rogers 2014), which strengthen our conclusion that diet is at least not a strong driver of home range size in turtles, while its effects cannot be discounted entirely.

Ectotherms have lower metabolic rates than similar-sized endotherms (Gillooly *et al.* 2001), and therefore lower energetic demands. We find that turtles have smaller home ranges than do endotherms such as mammals – a terrestrial mammal weighing 1 kg is predicted to have a home range of 245.47 ha (calculated using the equations in Tucker, Ord & Rogers 2014), whereas we predict from our relationship a terrestrial turtle of the same weight to have a home range of 6.22 ha. However, thermoregulation strategy might not strongly affect home range size, as there do not seem to be consistent differences in home range size between ectotherms and endotherms (Tamburello, Côté & Dulvy 2015). Indeed, turtles appear to have small home range sizes even for terrestrial ectotherms, with home ranges smaller than those of either frogs or snakes (Semlitsch & Bodie 2003; Tamburello, Côté & Dulvy 2015), and with home range allometry more comparable to those of fishes (see Minns 1995; Nash *et al.* 2015; Tamburello, Côté & Dulvy 2015). The reduced energetic requirements of turtles possibly result in a greater weight to other factors that affect home range size – a turtle's home range also needs to include basking sites, egg deposition sites (for females), as well as suitable hibernation and aestivation sites (Ultsch 2006). The availability of such sites may determine the home range sizes of turtles. Whether or not small ranges that are only weakly affected by energetic demands are a turtle-specific pattern, or a more general one for ectotherms, remains to be examined.

The exact effect of habitat on home range size can be difficult to interpret – aquatic species' home range size estimates could be conservative because their three-dimensional use of space is poorly accounted for by common methods for estimating home range size (Perry & Garland 2002; Tucker, Ord & Rogers 2014). Of the species we examine, aquatic turtles have the largest home ranges. This is likely due to the reduced costs of locomotion in aquatic environments (Baudinette, Miller & Sarre 2000; Tucker, Ord & Rogers 2014), especially when aquatic turtles are compared to cumbersome animals such as terrestrial tortoises. While swimming is generally a slower mode of locomotion than running and therefore should result in smaller home ranges (Tamburello, Côté & Dulvy 2015), terrestrial tortoises are extremely cumbersome animals, and move slowly (Jays & Alexander 1980). The effect of habitat, however, is only true for the MCP-only data set, and habitat use is uncorrelated with home range size in the complete data set. In keeping with the concerns, we raise here regarding home range size estimation methods, we cannot, as yet, determine whether this difference between the complete and MCP-only data sets is a true difference or merely an artefact.

Although we excluded them from this study, it should be noted that marine turtles have extremely large home ranges. The smallest estimate we found is of 1662 ha for the green turtle, *Chelonia mydas* (Seminoff, Resendiz & Nichols 2002), and even that is five times larger than the largest

home range in our entire data set. The largest home range is 840 750 ha for the loggerhead, *Caretta caretta* (Renaud & Carpenter 1994), about 2500 times larger than the largest estimate for a nonmarine turtle (327.6 ha for the aquatic red-eared slider, *T. scripta*; Jaeger & Cobb 2012). It is also interesting to note that the smallest of the sea turtle home ranges belongs to *C. mydas*, a herbivore of roughly similar size to the omnivorous, closely related *C. caretta*. Barring further information on marine turtles, however, these data remain anecdotal, and the debate as to whether the plural of anecdote is or is not data still rages on.

Home range size is an important animal trait, describing how they use space. As such, it has many important implications, including as a predictor of extinction risk, with, for example, wide-ranging species considered to be more vulnerable to habitat loss (Woodroffe & Ginsberg 1998). We have data for only 64 of the ~320 extant nonmarine species (Turtle Taxonomy Working Group 2014), and these data are geographically biased. North American turtles are over-represented in our data set (36% of species in our data set are North American). However, only 17% out of all nonmarine turtle species are found in North America), probably due to easier accessibility facilitating more research than in other regions of the world. Furthermore, the average number of different home range size estimates for a North American species in our data set is 2.6, while it is 1.3 for turtles from other regions (e.g. 1.5 for European turtles). We were especially surprised to discover that some of the most charismatic, big and well-known turtle species do not have home range size estimates (e.g. the various *Chelonoidis* species of the Galápagos Islands and the giant *Aldabrachelys* tortoises of the Indian Ocean). This bias places an emphasis on the need for further research on home range sizes in heretofore unexamined turtle species, and the standardization of reliable methods across studies to estimate these home range sizes. Our study helps to define predictors of home range sizes in turtles and suggests a surprisingly reduced role for metabolic requirements in dictating range size. However, further basic research on home range sizes of turtles will allow us to expand the scope of our analyses, and gain a better understanding of space use by members of this unique and endangered taxon, as well as by ectotherms in general. Such understanding of space use could prove vital in future conservation planning for turtles.

Acknowledgements

We would like to thank Maria Novosolov for her assistance with data analysis. We would like to extend our gratitude to two anonymous referees for their helpful comments on a previous draft of this manuscript. Alex Slavenko is funded by a special grant for students in the fast-track PhD programme from the George S. Wise Faculty of Life Sciences.

Data accessibility

Species home range size estimates and body masses: uploaded as online supporting information (Appendix S1).

References

- Arnold, T.W. (2010) Uninformative parameters and model selection using Akaike's information criterion. *The Journal of Wildlife Management*, **74**, 1175–1178.
- Baudinette, R.V., Miller, A. & Sarre, M. (2000) Aquatic and terrestrial locomotory energetics in a toad and a turtle: a search for generalisations among ectotherms. *Physiological and Biochemical Zoology*, **73**, 672–682.
- Berry, J. & Iverson, J. (2011) *Kinosternon scorpioides* (Linnaeus 1766) – Scorpion Mud Turtle. *Chelonian Research Monographs*, **5**, 63.1–63.15.
- Bertolero, A., Cheylan, M., Hailey, A., Livoreil, B. & Willemsem, R. (2011) *Testudo hermanni* (Gmelin 1789) – Hermann's tortoise. *Chelonian Research Monographs*, **5**, 59.1–59.20.
- Bonin, F., Devaux, B. & Dupré, A. (2006) *Turtles of the World*. Johns Hopkins University Press, Baltimore, MD, USA.
- Börger, L., Franconi, N., De Michele, G., Gantz, A., Meschi, F., Manica, A. *et al.* (2006) Effects of sampling regime on the mean and variance of home range size estimates. *Journal of Animal Ecology*, **75**, 1393–1405.
- Buhlmann, K.A., Gibbons, J.W. & Jackson, D.R. (2008) *Deirochelys reticularia* (Latreille 1801)-chicken turtle. *Chelonian Research Monographs*, **5**, 14.1–14.6.
- Burnham, K.P. & Anderson, D.R. (2002) *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. Springer Science & Business Media, New York, NY, USA.
- Burt, W.H. (1943) Territoriality and home range concepts as applied to mammals. *Journal of Mammalogy*, **24**, 346–352.
- Cann, J. (2008) *A wild Australia Guide: Freshwater Turtles*. Steve Parish Publishing, Archerfield, Australia.
- Christian, K.A. & Waldschmidt, S. (1984) The relationship between lizard home range and body size: a reanalysis of the data. *Herpetologica*, **40**, 68–75.
- Claude, J., Paradis, E., Tong, H. & Auffray, J.-C. (2003) A geometric morphometric assessment of the effects of environment and cladogenesis on the evolution of the turtle shell. *Biological Journal of the Linnean Society*, **79**, 485–501.
- Depecker, M., Berge, C., Penin, X. & Renous, S. (2006) Geometric morphometrics of the shoulder girdle in extant turtles (Chelonii). *Journal of Anatomy*, **208**, 35–45.
- Dodds, P.S., Rothman, D.H. & Weitz, J.S. (2001) Re-examination of the “3/4-law” of metabolism. *Journal of Theoretical Biology*, **209**, 9–27.
- Doody, J.S., Young, J.E. & Georges, A. (2002) Sex differences in activity and movements in the pig-nosed turtle, *Carettochelys insculpta*, in the wet-dry tropics of Australia. *Copeia*, **2002**, 93–103.
- Elton, C.S. (1927) *Animal Ecology*. The University of Chicago Press, Chicago, IL, USA.
- Ernst, C.H., Altenburg, R.G.M. & Barbour, R.W. (2006) *Turtles of the World*. DVD-ROM for Windows and Macintosh, version 1.3. Smithsonian Institution Scholarly Press, Washington, DC, USA.
- Freckleton, R., Harvey, P. & Pagel, M. (2002) Phylogenetic analysis and comparative data: a test and review of evidence. *The American Naturalist*, **160**, 712–726.
- Gaulin, S.J.C. & FitzGerald, R.W. (1988) Home-range size as a predictor of mating systems in *Microtus*. *Journal of Mammalogy*, **69**, 311–319.
- Gerlach, J. (2012) *The Great Survivors: 220 Million Years of Turtle Evolution*. Phelsuma Press, Cambridge, UK.
- Gillooly, J.F., Brown, J.H., West, G.B., Savage, V.M. & Charnov, E.L. (2001) Effects of size and temperature on metabolic rate. *Science*, **293**, 2248–2251.
- Gleeson, T.T. (1979) Foraging and transport costs in the Galapagos marine iguana, *Amblyrhynchus cristatus*. *Physiological Zoology*, **52**, 549–557.
- Harestad, A.S. & Bunnell, F. (1979) Home range and body weight – a re-evaluation. *Ecology*, **60**, 389–402.
- Haskell, J.P., Ritchie, M.E. & Olf, H. (2002) Fractal geometry predicts varying body size scaling relationships for mammal and bird home ranges. *Nature*, **418**, 527–530.
- Haxton, T. & Berrill, M. (1999) Habitat selectivity of *Clemmys guttata* in central Ontario. *Canadian Journal of Zoology*, **77**, 593–599.
- Herfindal, I., Linnell, J.D.C., Odden, J., Nilsen, E.B. & Andersen, R. (2005) Prey density, environmental productivity and home-range size in the Eurasian lynx (*Lynx lynx*). *Journal of Zoology*, **265**, 63–71.
- Ihlow, F., Rödder, D., Bochynek, T., Sothanin, S., Handschuh, M. & Böhme, W. (2014) Reinforcement as a conservation tool – assessing site fidelity and movement of the endangered elongated tortoise *Indotestudo elongata* (Blyth, 1854). *Journal of Natural History*, **48**, 2473–2485.

- Itescu, Y. (2012) *A biogeographic perspective on turtle evolution*. MSc thesis, Tel Aviv University, Tel Aviv, Israel.
- Itescu, Y., Karraker, N.E., Raia, P., Pritchard, P.C.H. & Meiri, S. (2014) Is the island rule general? Turtles disagree. *Global Ecology and Biogeography*, **23**, 689–700.
- Iverson, J.B. & Vogt, R.C. (2011) *Kinosternon acutum* Gray 1831 – Tabasco Mud Turtle, Montero, Chechagua de Monte. *Chelonian Research Monographs*, **5**, 62.1–62.6.
- Jaeger, C.P. & Cobb, V.A. (2012) Comparative spatial ecologies of female painted turtles (*Chrysemys picta*) and red-eared sliders (*Trachemys scripta*) at Reelfoot Lake, Tennessee. *Chelonian Conservation and Biology*, **11**, 59–67.
- Jayes, A.S. & Alexander, R. (1980) The gaits of chelonians: walking techniques for very low speeds. *Journal of Zoology*, **191**, 353–378.
- Jetz, W., Carbone, C., Fulford, J. & Brown, J.H. (2004) The scaling of animal space use. *Science*, **306**, 266–268.
- Kelt, D.A. & Van Vuren, D.H. (2001) The ecology and macroecology of mammalian home range area. *The American Naturalist*, **157**, 637–645.
- Kozłowski, J. & Konarzewski, M. (2004) Is West, Brown and Enquist's model of allometric scaling mathematically correct and biologically relevant? *Functional Ecology*, **18**, 283–289.
- Laver, P.N. & Kelly, M.J. (2008) A critical review of home range studies. *Journal of Wildlife Management*, **72**, 290–298.
- Lindstedt, S.L., Miller, B.J. & Buskirk, S.W. (1986) Home range, time, and body size in mammals. *Ecology*, **67**, 413–418.
- Litzgus, J.D. & Mousseau, T.A. (2004) Home range and seasonal activity of southern spotted turtles (*Clemmys guttata*): implications for management. *Copeia*, **2004**, 804–817.
- McNab, B.K. (1963) Bioenergetics and the determination of home range size. *The American Naturalist*, **97**, 133–140.
- Milton, K. & May, M.L. (1976) Body weight, diet and home range area in primates. *Nature*, **259**, 459–462.
- Minns, C.K. (1995) Allometry of home range size in lake and river fishes. *Canadian Journal of Fisheries and Aquatic Sciences*, **52**, 1499–1508.
- Montaño, R.R., Cuéllar, E., Fitzgerald, L.A., Soria, F., Mendoza, F., Peña, R. et al. (2013) Ranging patterns by the red-footed tortoise – *Geochelone carbonaria* (Testudines: Testudinidae) – in the Bolivian Chaco. *Ecología en Bolivia*, **48**, 17–30.
- Moore, D. (2011) *Monitoring a translocated population of Alligator Snapping Turtles*. MSc, Oklahoma State University, Oklahoma City, OK, USA.
- Myers, P.R., Espinosa, R., Parr, C.S., Jones, T., Hammond, G.S. & Dewey, T.A. (2014) The animal diversity web. Available at: <http://animaldiversity.org> (accessed 10 August 2014).
- Nash, K.L., Welsh, J.Q., Graham, N.A.J. & Bellwood, D.R. (2015) Home-range allometry in coral reef fishes: comparison to other vertebrates, methodological issues and management implications. *Oecologia*, **177**, 73–83.
- Nilsen, E.B., Herfindal, I. & Linnell, J.D.C. (2005) Can intra-specific variation in carnivore home-range size be explained using remote-sensing estimates of environmental productivity? *Ecoscience*, **12**, 68–75.
- Nilsen, E.B. & Linnell, J.D.C. (2006) Intra-specific variation and tax-sampling affects the home range – body mass relationship. *Acta Theriologica*, **51**, 225–232.
- Nilsen, E.B., Pedersen, S. & Linnell, J.D.C. (2008) Can minimum convex polygon home ranges be used to draw biologically meaningful conclusions? *Ecological Research*, **23**, 635–639.
- Orme, D., Freckleton, R., Thomas, G., Petzoldt, T., Fritz, S., Isaac, N. et al. (2012) Caper: comparative analyses of phylogenetics and evolution in R. <http://CRAN.R-project.org/package=caper>.
- Pedrono, M. & Sarovy, A. (2000) Trial release of the world's rarest tortoise *Geochelone yniphora* in Madagascar. *Biological Conservation*, **95**, 333–342.
- Perry, G. & Garland, T. Jr (2002) Lizard home ranges revisited: effects of sex, body size, diet, habitat, and phylogeny. *Ecology*, **83**, 1870–1885.
- Peters, R.H. (1983) *The Ecological Implications of Body Size*. Cambridge University Press, Cambridge, UK.
- Powell, R.A. (2000) Animal home ranges and territories and home range estimators. *Research Techniques in Animal Ecology: Controversies and Consequences* (eds L. Boitani & T.K. Fuller), pp. 65–110. Columbia University Press, New York, NY, USA.
- R Development Core Team (2013) *R: A Language and Environment for Statistical Computing*. The R Foundation for Statistical Computing, Vienna, Austria.
- RStudio Inc. (2013) *RStudio v0.98.978*. RStudio Inc., Boston, MA, USA.
- Reiss, M. (1988) Scaling of home range size: body size, metabolic needs and ecology. *Trends in Ecology & Evolution*, **3**, 85–86.
- Renaud, M.L. & Carpenter, J.A. (1994) Movements and submergence patterns of loggerhead turtles (*Caretta caretta*) in the Gulf of Mexico determined through satellite telemetry. *Bulletin of Marine Science*, **55**, 1–15.
- Rivera, G., Rivera, A.R., Dougherty, E.E. & Blob, R.W. (2006) Aquatic turning performance of painted turtles (*Chrysemys picta*) and functional consequences of a rigid body design. *Journal of Experimental Biology*, **209**, 4203–4213.
- Schoener, T.W. (1968) Sizes of feeding territories among birds. *Ecology*, **49**, 123–141.
- Schoener, T.W. & Schoener, A. (1982) Intraspecific variation in home-range size in some Anolis lizards. *Ecology*, **63**, 809–823.
- Seminoff, J.A., Resendiz, A. & Nichols, W.J. (2002) Home range of green turtles *Chelonia mydas* at a coastal foraging area in the Gulf of California, Mexico. *Marine Ecology Progress Series*, **242**, 253–265.
- Semlitsch, R.D. & Bodie, J.R. (2003) Biological criteria for buffer zones around wetlands and riparian habitats for amphibians and reptiles. *Conservation Biology*, **17**, 1219–1228.
- Sidis, I. (1983) *Ecology of the Caspian terrapin (Mauremys caspica rivulata) in polluted and unpolluted habitats in Israel*. MSc, Tel Aviv University, Tel Aviv, Israel.
- Signer, J., Balkenhol, N., Ditmer, M. & Fieberg, J. (2015) Does estimator choice influence our ability to detect changes in home-range size? *Animal Biotelemetry*, **3**, 1–9.
- da Silva, J.K.L., Garcia, G.J. & Barbosa, L.A. (2006) Allometric scaling laws of metabolism. *Physics of Life Reviews*, **3**, 229–261.
- Souza, F.L., Raizer, J., Da Costa, H.T.M. & Martins, F.I. (2008) Dispersal of *Phrynos geoffroanus* (Chelidae) in an urban river in central Brazil. *Chelonian Conservation and Biology*, **7**, 257–261.
- Tamburello, N., Côté, I.M. & Dulvy, N.K. (2015) Energy and the scaling of animal space use. *The American Naturalist*, **186**, 196–211.
- Tucker, M.A., Ord, T.J. & Rogers, T.L. (2014) Evolutionary predictors of mammalian home range size: body mass, diet and the environment. *Global Ecology and Biogeography*, **23**, 1105–1114.
- Turner, F.B., Jennrich, R.I. & Weintraub, J.D. (1969) Home ranges and body size of lizards. *Ecology*, **50**, 1076–1081.
- Turtle Taxonomy Working Group [van Dijk, P.P., Iverson, J.B., Rhodin, A.G.J., Shaffer, H.B. & Bour, R.] (2014) Turtles of the world, 7th edition: annotated checklist of taxonomy, synonymy, distribution with maps, and conservation status. *Chelonian Research Monographs*, **5**, 329–479.
- Ullsch, G.R. (2006) The ecology of overwintering among turtles: where turtles overwinter and its consequences. *Biological Reviews*, **81**, 339–367.
- Vetter, H. (2004) *TerraLog, Turtles of the World, Vol. 2, North America*. Edition Chimaira, Frankfurt am Main, Germany.
- Vetter, H. (2005) *TerraLog, Turtles of the World, Vol. 3, Central and South America*. Edition Chimaira, Frankfurt am Main.
- Vetter, H. (2011) *TerraLog, Turtles of the World, Vol. 1, Africa, Europe and Western Asia*. Edition Chimaira, Frankfurt am Main, Germany.
- Vetter, H. & Van Dijk, P. (2006) *TerraLog, Turtles of the World, Vol. 4, East and South Asia*. Edition Chimaira, Frankfurt am Main, Germany.
- West, G.B., Brown, J.H. & Enquist, B.J. (1997) A general model for the origin of allometric scaling laws in biology. *Science*, **276**, 122–126.
- Woodroffe, R. & Ginsberg, J.R. (1998) Edge effects and the extinction of populations inside protected areas. *Science*, **280**, 2126–2128.
- Zhang, Z., Sheppard, J.K., Swaisgood, R.R., Wang, G., Nie, Y., Wei, W. et al. (2014) Ecological scale and seasonal heterogeneity in the spatial behaviors of giant pandas. *Integrative Zoology*, **9**, 46–60.

Received 10 November 2014; accepted 14 September 2015
Handling Editor: Luca Börger

Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. A full list of species included in this study with species-specific mean home range size estimates, along with sources and sample sizes.

Appendix S2. The pruned turtle phylogeny used in this study, presented both in newick format and as a figure.

Appendix S3. The best models and averaged models (the lowest ranking model by AIC_c , and any models with $\Delta AIC_c < 2$ of the best model) in the complete and MCP-only data set.