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

2 Alex Slavenko<sup>\*a</sup>, Yuval Itescu<sup>a</sup>, Flora Ihlow<sup>b</sup>, Shai Meiri<sup>a</sup>

3 <sup>a</sup> Department of Zoology, Tel Aviv University, 6997801, Tel Aviv, Israel,

4 +97236409811

5 <sup>b</sup> Herpetology Department, Zoologisches Forschungsmuseum Alexander Koenig

6 (ZFMK), 53113, Bonn, Germany, +492289122253

7

8 \*Corresponding author: [slavenko@mail.tau.ac.il](mailto:slavenko@mail.tau.ac.il)

9

10 Running headline: **Predictors of home range sizes of turtles**

11

12 **Summary**

- 13 1. Home range is the area traversed by an animal in its normal activities. The size of  
14 home ranges is thought to be tightly linked to body size, through size effect on  
15 metabolic requirements. Due to the structure of Eltonian food pyramids, home  
16 range sizes of carnivores are expected to exceed those of herbivorous species. The  
17 habitat may also affect home range size, with reduced costs of locomotion or  
18 lower food abundance in e.g., aquatic habitats selecting for larger home ranges.  
19 Furthermore, home range of males in polygamous species may be large due to  
20 sexual selection for increased reproductive output.
- 21 2. Comparative studies on home range sizes have rarely been conducted on  
22 ectotherms. Because ectotherm metabolic rates are much lower than those of  
23 endotherms, energetic considerations of metabolic requirements may be less  
24 important in determining the home range sizes of the former, and other factors  
25 such as differing habitats and sexual selection may have an increased effect.
- 26 3. We collected literature data on turtle home range sizes. We used phylogenetic  
27 generalised least squares analyses to determine whether body mass, sex, diet,  
28 habitat and social structure, affect home range size.
- 29 4. Turtle home range size increases with body mass. However, body mass explains  
30 relatively little of the variation in home range size. Aquatic turtles have larger  
31 home ranges than semiaquatic species. Omnivorous turtles have larger home  
32 ranges than herbivores and carnivores, but diet is not a strong predictor. Sex and  
33 social structure are unrelated to home range size.

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

37

38 **Key-words** Body size, chelonians, energetic constraints, home range size, macroecology,

39 PGLS

40

Pre-Print

## 41 **Introduction**

42 Home range is "...that area traversed by the individual in its normal activities of  
43 food gathering, mating, and caring for the young" (Burt 1943). Many studies, on various  
44 taxa, have tried to estimate the sizes of home ranges (e.g., Ihlow et al. 2014; Zhang et al.  
45 2014), and to determine the factors that affect them (e.g., McNab 1963; Tucker, Ord &  
46 Rogers 2014). Body size is considered to be a crucial factor in determining home range  
47 size and is tightly correlated with it in mammals (McNab 1963; Milton & May 1976;  
48 Harestad & Bunnell 1979; Lindstedt, Miller & Buskirk 1986; Tucker, Ord & Rogers  
49 2014), birds (Schoener 1968), and lizards (Turner, Jennrich & Weintraub 1969; Christian  
50 & Waldschmid 1984; Perry & Garland 2002).

51 This relationship is thought to reflect a process whereby metabolic requirements  
52 dictate an individual's home range size. McNab (1963) noted that the slope of the  
53 regression of home range size against body mass did not differ significantly from the 0.75  
54 allometric slope of the regression of (log) basal metabolic rate against (log) body mass.  
55 He therefore hypothesised that home range size is proportional to basal metabolic rate,  
56 and is dictated primarily by energetic constraints – larger animals have higher energetic  
57 requirements, and therefore need to traverse larger foraging areas to meet said  
58 requirements. Later findings have shown that empirical slopes tend to be roughly  
59 isometric (Peters 1983, p173). This is thought to be due to increased home range overlap  
60 of larger animals and thus less exclusivity of food resources (Jetz et al. 2004). The role of  
61 energetic requirements in determining home range size, however, is still widely accepted.

62 This hypothesis is further supported by the findings that home range size, in several  
63 taxa, varies with diet, with carnivores generally having larger home ranges than

64 herbivores or omnivores of similar size (McNab 1963; Schoener 1968; Harestad &  
65 Bunnell 1979; Perry & Garland 2002). The lower abundance of animal relative to plant  
66 food, due to the nature of Eltonian food pyramids (Elton 1927), means carnivores must  
67 range farther to acquire sufficient sustenance than do herbivores.

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

80 The effect of habitat use on home range size is probably substantial, but has rarely  
81 been examined (but see Herfindal et al. 2005; Nilsen, Herfindal & Linell 2005). Marine  
82 mammals, for example, have larger home ranges than terrestrial mammals (Tucker, Ord  
83 & Rogers 2014). Marine species live in environments with mobile food resources, and  
84 marine and aquatic species may also have lower energetic costs of locomotion than their  
85 terrestrial counterparts (Gleeson 1979; Baudinette, Miller & Sarre 2000). Both factors  
86 may allow aquatic species to have larger home ranges than terrestrial species (Tucker,

87 Ord & Rogers 2014), but the absolute speed of locomotion could have a larger effect on  
88 home range size than its energetic expenditure (Tamburello, Côté & Dulvy 2015), and  
89 mobility of food resources can have an opposite effect. River fishes have smaller home  
90 ranges than lake fishes (Minns 1995), a fact attributed to food resources being carried  
91 downstream by rivers and reducing the need of fish to forage widely.

92 Turtles are a well-studied taxon, comprising of 327 extant species (Turtle Taxonomy  
93 Working Group 2014). They vary in size from ~140g (Nama padloper, *Homopus solus*)  
94 to ~900kg (leatherback turtle, *Dermochelys coriacea*) (Depecker et al. 2006). Turtles are  
95 found on all continents, barring Antarctica, in various habitats. Some turtles are  
96 terrestrial, but most species are aquatic or semiaquatic, and seven species are marine  
97 (Bonin, Devaux & Dupré 2006). Some turtles are herbivores, whereas others are  
98 omnivorous or carnivorous (Bonin, Devaux & Dupré 2006).

99 Turtles are defined by their unique synapomorphic trait - the bony shell. The shell  
100 severely restricts turtle locomotion on land and precludes them from adopting arboreal  
101 habits (Rivera et al. 2006). During their evolutionary history, turtles have shifted from  
102 aquatic to terrestrial environments and back several times (Claude et al. 2003; Gerlach  
103 2012). This variability in diet, habitat use and size makes them an interesting case study  
104 to examine the factors that control home range size. Such a study could also have  
105 important implications for conservation, as it allows us to understand how turtles make  
106 use of space. With more than half the living species threatened with extinction, turtles are  
107 among the most endangered taxa on earth (Turtle Taxonomy Working Group 2014).  
108 Identifying the underlying determining factors of space use for turtles could vastly  
109 improve future conservation planning of this highly endangered taxon.

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

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

126

## 127 **Materials and methods**

### 128 Data collection

129 We collected home range size estimates for different species of turtles from  
130 published sources (Appendix S1 in Supporting Information) by searching online  
131 databases such as Google Scholar. As sample sizes used to estimate home range sizes of



132 marine turtles were uniformly very low, and owing to their unique biology and movement  
133 patterns, we omitted marine turtle species from the study.

134 We collected data on home range size for 64 species, with data for males (37 species)  
135 and females (46 species) separately, when available. We used the published mean home  
136 range size of adults of both sexes, or calculated the mean of individual published home  
137 range sizes. If several estimates from different sources for the same species were  
138 available, we calculated the overall mean of these estimates. If means were unavailable,  
139 we calculated the average of reported male and female estimates (i.e., if male estimate is  
140  $x$  and female estimate is  $y$ , then the species estimate is  $[x + y]/2$ ). When neither species  
141 means, means of sexed animals, or home range sizes of individuals were available, we  
142 calculated the midpoint between published minimum and maximum estimates (i.e., if the  
143 home range size ranges between  $m$  and  $n$ , then the species estimate is  $[m + n]/2$ ). Data on  
144 mean straight carapace length (from Itescu 2012) were collected for each species, using  
145 the same method as the collection of home range sizes. We converted the length data to  
146 mass using family-specific allometric equations developed by Itescu (2012).

147 The most commonly used application in the past to estimate home range size is the  
148 minimum convex polygon (MCP) method, whereby one connects all the peripheral  
149 locality points of an individual to form the smallest convex polygon, and subsequently  
150 calculates the area encompassed by this polygon (Powell 2000). Of the 64 species we  
151 collected data for, 50 species' home range sizes have been estimated using the MCP  
152 method (including all the sex-specific estimates). Home range sizes of five species were  
153 estimated using other methods (Linear home range multiplied by river width for the pig-  
154 nosed turtle, *Carretochelys insculpta* [Doody, Young & Georges 2002], alligator

155 snapping turtle, *Macrochelys temminckii* [Moore 2011] and Geoffroy's toadhead turtle,  
156 *Phrynops geoffroanus* [Souza et al. 2008]; circle using half of movement range as radius  
157 for the western Caspian turtle, *Mauremys rivulata* [Sidis 1983]; and fixed kernel for the  
158 Madagascan tortoise, *Astrochelys yniphora* [Pedrono & Sarovy 2000]). For the other nine  
159 species, the method used to estimate home range size was not specified (Appendix S1).

160 We obtained data on turtle habitat use from the literature (Bonin, Devaux & Dupré  
161 2006; Ernst, Altenburg & Barbour 2006; Buhlmann, Gibbons & Jackson 2008; Berry &  
162 Iverson 2011; Bertolero et al. 2011). Species were designated as aquatic (spend most of  
163 their time in bodies of water), semiaquatic (spend substantial time both in water and on  
164 land) or terrestrial (spend the majority of their time on land). We further obtained  
165 literature data on diet (carnivores, herbivores and omnivores; Vetter 2004, 2005, 2011;  
166 Vetter & Van Dijk 2006; Cann 2008). We derived data on social structure from Vetter  
167 (2004; 2005; 2011), Vetter & Van Dijk (2006), Cann (2008) and Myers et al. (2014). We  
168 assigned turtle species to one of three distinct categories of social structure; "solitary",  
169 "harem" (groups composed of one male and several females) or "social" (groups  
170 composed of several males and several females).

171 To account for the effects of phylogenetic non-independence in our data, we used the  
172 complete phylogenetic tree of extant turtles compiled by Itescu et al. (2014), which we  
173 pruned to match the species included in this study (Appendix S2 in Supporting  
174 Information).

175

#### 176 Statistical analyses

177 We performed a phylogenetic generalised least square (PGLS) regression  
178 (Freckelton, Harvey & Pagel 2002), after log-transforming the home range size and body

179 mass data to linearize the relationship, normalise residuals, and reduce heteroscedasticity.  
180 We used the 'caper' package for R (Orme et al. 2012) to estimate the maximum likelihood  
181 value of the scaling parameter  $\lambda$ .  $\lambda$  ranges from 0 to 1 and is a measure of the strength of  
182 the phylogenetic signal in the data (0 representing no signal, and 1 representing evolution  
183 by Brownian motion). If  $\lambda$  was found to be 0, we fitted an ordinary least squares (OLS)  
184 regression. We included body mass, diet, habitat and social structure, and their two-way  
185 interactions, as possible predictors of turtle home range size. We selected all models with  
186  $\Delta AICc < 2$  of the model with the lowest score, unless a model with a lower AIC score was  
187 nested within them (so if a model with parameters  $a$ ,  $b$  and  $c$  has a  $\Delta AICc < 2$  than a  
188 model with only parameters  $a$  and  $b$ , we did not use the more complicated model; Arnold  
189 2010). We averaged the best competing models to arrive at the global model, and  
190 calculated the relative importance of predictors in the averaged variable, calculated as the  
191 sum of Akaike weights over all the models in which the predictor appears (so if models  $a$ ,  
192  $b$  and  $c$  were averaged, with Akaike weights  $x$ ,  $y$  and  $z$ , respectively [the sum of all three  
193 being 1], a predictor that appeared in all three models would have a relative importance  
194 of 1, while a predictor that appeared only in e.g. models  $a$  and  $b$  would have a relative  
195 importance of  $x + y$ ; Burnham & Anderson 2002, p168).

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

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

207 We performed all statistical analyses in R v3.0.2 (The R Foundation for Statistical  
208 Computing 2013), using the RStudio v0.98.978 (RStudio Inc. 2013) interface.

209

## 210 **Results**

211 Home range sizes of non-marine turtles span four orders of magnitude, from 0.013  
212 ha (Tabasco mud turtle, *Kinosternon acutum* [mean mass = 235g]; Iverson & Vogt 2011)  
213 to 327.6 ha (red-eared slider, *Trachemys scripta* [mean mass = 933g]; Jaeger & Cobb  
214 2012), with a mean range size of 23.35 ha and a median range size of 6.82 ha (Table 1).  
215 There is also much intraspecific variability in home range sizes, often with great  
216 differences between populations of the same species (e.g., estimates of 3.7 ha [Haxton &  
217 Berrill 1999] and 15 ha [Litzgus & Mousseau 2004] for different populations of spotted  
218 turtles, *Clemmys guttata*) and between adult individuals within the same population (e.g.,  
219 home range sizes spanning from 2.1 ha to 628.9 ha for individuals from a single  
220 population of red-footed tortoises, *Chelonoidis carbonaria* in Bolivia [Montaño et al.  
221 2013]), albeit these differences are on a smaller scale than the interspecific variation. This  
222 variation obviously undermines the ability of comparative studies such as ours, using a  
223 single value per species, to fully encompass the plethora of selective forces affecting

224 home range size (although we think it is unlikely to bias the estimates per se). This  
225 variation is real, and thus in itself offers a fascinating opportunity to study the factors  
226 affecting home range sizes.

227 Phylogenetic affinities do not seem to affect the relationships between our predictors  
228 and home range sizes: the maximum likelihood value of  $\lambda$  was 0 in all models. We  
229 therefore fitted OLS models for all datasets and report these results.

230 The two best models for turtle home range sizes (ranked by AICc scores) are listed in  
231 Appendix S3 in Supporting Information. The averaged model to predict turtle home  
232 range sizes for the entire 64 species dataset includes body mass, home range size  
233 estimation method, and diet as predictors, but diet has a low relative importance (0.56).  
234 Surprisingly, omnivores emerged as having the largest home ranges (intercept is 0.39 log  
235 units higher than carnivores), and herbivores the smallest (difference in intercepts from  
236 omnivores is 0.46). Home range size increases with body mass (slope = 0.67, 95% CI =  
237 0.34-1), and home ranges estimated using minimum convex polygons are larger than  
238 those estimated with other or unknown methods (difference in intercepts is 0.94 log units,  
239 or roughly tenfold; Fig. 1). While  $R^2$  values cannot be calculated for averaged models,  
240 they ranged between 31% and 37% in the top-ranked models.

241 The averaged model for the MCP-only, 50 species dataset, includes body mass,  
242 habitat and diet as predictors of home range size (Fig. 2). As with the complete dataset,  
243 diet has low relative importance (0.65), and omnivores have the largest home ranges.  
244 Home range size increases with body mass, albeit with an even shallower slope than in  
245 the full dataset (0.56, 95% CI = 0.25-0.87). In this model aquatic species have larger  
246 home ranges than semiaquatic and terrestrial species (differences in intercepts are 0.75

247 and 0.41, respectively).  $R^2$  values of the two top-ranked models ranged between 30% and  
248 39%.

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

254

## 255 **Discussion**

256 Few of the factors we examine seem to affect turtle home range size, but the  
257 measuring method does. We found that home range sizes estimated using minimum  
258 convex polygons were about ten times larger than estimates based on other methods, or  
259 on unreported methods. The MCP method has been criticised for introducing a sample  
260 size-based bias and is sensitive to extreme outlying localities, could cause either over- or  
261 under-estimation of actual home range size when compared to other methods (Powell  
262 2000; Börger et al. 2006), and may affect the results of comparative studies (Laver &  
263 Kelly 2008, but see Nilsen, Pedersen & Linnell 2008). However, as most of the home  
264 range sizes we considered in the “other” category did not have the method of estimation  
265 specified, it is possible and even likely, considering the popularity of the MCP method,  
266 that many of them were also estimated using MCPs. Whether the method of estimation  
267 matters or our result is a statistical artefact is therefore difficult to determine. It appears  
268 that the method used to estimate home range size can affect the results of comparative  
269 studies, and should be accounted for when mixing studies that estimated home range

270 sizes with different methods, at least until a larger dataset of home range sizes estimated  
271 using more robust methods (such as the kernel density estimator; Börger et al. 2006) can  
272 be established. However, the MCP method by itself does not seem to introduce a  
273 systematic bias in large-scale macroecological analyses, and therefore viable conclusions  
274 can be drawn from analyses based solely on MCP estimates (Nilsen, Pedersen & Linnell  
275 2008; Signer et al. 2015). Therefore, in order to ensure comparability of results, we only  
276 consider the results gained from the MCP-only dataset (without data on sex – which did  
277 not emerge as important) for further interpretation.

278 Home range size of turtles increases with body mass. While our slope (0.57) is not  
279 significantly different than the slope of 0.75 predicted by McNab's (1963) energetic  
280 constraints hypothesis (95% CI of 0.22-0.85 for the slope of the MCP-only dataset), it is  
281 shallower than many empirical slopes that are roughly isometric (Peters 1983, p173; but  
282 see Nilsen & Linnell 2006) and is similar to the slope calculated for freshwater lake  
283 fishes (0.58; Minns 1995). The scaling of home range size to body mass is still debated,  
284 as several studies report slopes steeper than those predicted by metabolic rates, with  
285 varying explanations (Peters 1983; Reiss 1988; Kelt & Van Vuren 2001; Haskell, Ritchie  
286 & Olf 2002). Our finding suggests that, in turtles, body mass explains relatively little  
287 variation in home range size, with wide confidence intervals for the regression slope (it  
288 should be noted that a model with only body mass included as a predictor explains only  
289 12% of the variation in home range size). The claim that home range size is dictated by  
290 energetic requirements and scales to metabolic rate is therefore difficult to evaluate.  
291 Indeed, while many life history and ecological traits are thought to scale with metabolic  
292 rate (West, Brown & Enquist 1997) this concept has come under much scrutiny (e.g.,

293 Dodds, Rothman & Weitz 2001; Kozłowski & Konarzewski 2004; da Silva, Garcia &  
294 Barbosa 2006).

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

304 The effect of diet on turtle home range size is somewhat ambiguous, as models with  
305 diet included as a predictor fared generally well, but model averaging revealed this effect  
306 to be weak. Furthermore, contrary to the energetic constraints hypothesis' (McNab 1963),  
307 we found omnivores had the largest home ranges, and not carnivores. It is possible that  
308 our dietary categories are too coarse, as they do not distinguish between different  
309 foraging strategies (e.g., sit-and-wait predators such as the alligator snapping turtle,  
310 *Macrochelys temminckii* vs. active foragers such as Dahl's toadhead turtle, *Mesoclemmys*  
311 *dahli*) or diet specialists (e.g., the impressed tortoise, *Manouria impressa*, which feeds  
312 exclusively on mushrooms) vs. generalists (e.g., the leopard tortoise, *Stigmochelys*  
313 *pardalis*). However, studies with similarly broad categories have found diet to have a  
314 strong effect on home range size in various taxa (e.g., McNab 1963; Perry & Garland  
315 2002; Tucker, Ord & Rogers 2014), which strengthen our conclusion that diet is at least



316 not a strong driver of home range size in turtles, while its effects cannot be discounted  
317 entirely.

318 Ectotherms have lower metabolic rates than similar-sized endotherms (Gillooly et al.  
319 2001), and therefore lower energetic demands. We find that turtles have smaller home  
320 ranges than do endotherms such as mammals – a terrestrial mammal weighing 1kg is  
321 predicted to have a home range of 245.47 ha (calculated using the equations in Tucker,  
322 Ord & Rogers 2014), whereas we predict from our relationship a terrestrial turtle of the  
323 same weight to have a home range of 6.22 ha. However, thermoregulation strategy might  
324 not strongly affect home range size, as there do not seem to be consistent differences in  
325 home range size between ectotherms and endotherms (Tamburello, Côté & Dulvy 2015).  
326 Indeed, turtles appear to have small home range sizes even for terrestrial ectotherms, with  
327 home ranges smaller than those of either frogs or snakes (Smelitsch & Bodie 2003;  
328 Tamburello, Côté & Dulvy 2015), and with home range allometry more comparable to  
329 those of fishes (see Minns 1995; Nash et al. 2015; Tamburello, Côté & Dulvy 2015). The  
330 reduced energetic requirements of turtles possibly result in a greater weight to other  
331 factors that affect home range size – a turtle’s home range also needs to include basking  
332 sites, egg deposition sites (for females), as well as suitable hibernation and aestivation  
333 sites (Ultsch 2006). The availability of such sites may determine the home range sizes of  
334 turtles. Whether or not small ranges that are only weakly affected by energetic demands  
335 are a turtle-specific pattern, or a more general one for ectotherms, remains to be  
336 examined.

337 The exact effect of habitat on home range size can be difficult to interpret – aquatic  
338 species’ home range size estimates could be conservative because their three-dimensional

339 use of space is poorly accounted for by common methods for estimating home range size  
340 (Perry & Garland 2002; Tucker, Ord & Rogers 2014). Of the species we examine, aquatic  
341 turtles have the largest home ranges. This is likely due to the reduced costs of locomotion  
342 in aquatic environments (Baudinette, Miller & Sarre 2000; Tucker, Ord & Rogers 2014),  
343 especially when aquatic turtles are compared to cumbersome animals such as terrestrial  
344 tortoises. While swimming is generally a slower mode of locomotion than running and  
345 therefore should result in smaller home ranges (Tamburello, Côté & Dulvy 2015),  
346 terrestrial tortoises are extremely cumbersome animals, and move slowly (Jayes &  
347 Alexander 1980). The effect of habitat, however, is only true for the MCP-only dataset,  
348 and habitat use is uncorrelated with home range size in the complete dataset. In keeping  
349 with the concerns we raise here regarding home range size estimation methods, we  
350 cannot, as yet, determine whether this difference between the complete and MCP-only  
351 datasets is a true difference or merely an artefact.

352       Although we excluded them from this study, it should be noted that marine turtles  
353 have extremely large home ranges. The smallest estimate we found is of 1,662 ha for the  
354 green turtle, *Chelonia mydas* (Seminoff, Resendiz & Nichols 2002), and even that is five  
355 times larger than the largest home range in our entire dataset. The largest home range is  
356 840,750 ha for the loggerhead, *Caretta caretta* (Renaud & Carpenter 1994), about 2500  
357 times larger than the largest estimate for a non-marine turtle (327.6 ha for the aquatic red-  
358 eared slider, *Trachemys scripta*; Jaeger & Cobb 2012). It is also interesting to note that  
359 the smallest of the sea turtle home ranges belongs to *Chelonia mydas*, a herbivore of  
360 roughly similar size to the omnivorous, closely related *Caretta caretta*. Barring further

361 information on marine turtles, however, these data remain anecdotal, and the debate as to  
362 whether the plural of anecdote is or is not data still rages on.

363 Home range size is an important animal trait, describing how they use space. As  
364 such, it has many important implications, including as a predictor of extinction risk, with  
365 e.g. wide-ranging species considered to be more vulnerable to habitat loss (Woodroffe &  
366 Ginsberg 1998). We have data for only 64 out of the ~320 extant non-marine species  
367 (Turtle Taxonomy Working Group 2014), and these data are geographically biased.

368 North American turtles are over-represented in our dataset (36% of species in our dataset  
369 are North American. However, only 17% out of all non-marine turtle species are found in  
370 North America), probably due to easier accessibility facilitating more research than in  
371 other regions of the world. Furthermore, the average number of different home range size  
372 estimates for a North American species in our dataset is 2.6, while it is 1.3 for turtles  
373 from other regions (e.g., 1.5 for European turtles). We were especially surprised to  
374 discover that some of the most charismatic, big, and well-known turtle species do not  
375 have home range size estimates (e.g., the various *Chelonoidis* species of the Galápagos  
376 Islands and the giant *Aldabrachelys* tortoises of the Indian Ocean). This bias places an  
377 emphasis on the need for further research on home range sizes in heretofore unexamined  
378 turtle species, and the standardisation of reliable methods across studies to estimate these  
379 home range sizes. Our study helps to define predictors of home range sizes in turtles and  
380 suggests a surprisingly reduced role for metabolic requirements in dictating range size.  
381 However, further basic research on home range sizes of turtles will allow us to expand  
382 the scope of our analyses, and gain a better understanding of space use by members of

383 this unique and endangered taxon, as well as by ectotherms in general. Such  
384 understanding of space use could prove vital in future conservation planning for turtles.

385

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392

## 393 **Data Accessibility**

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

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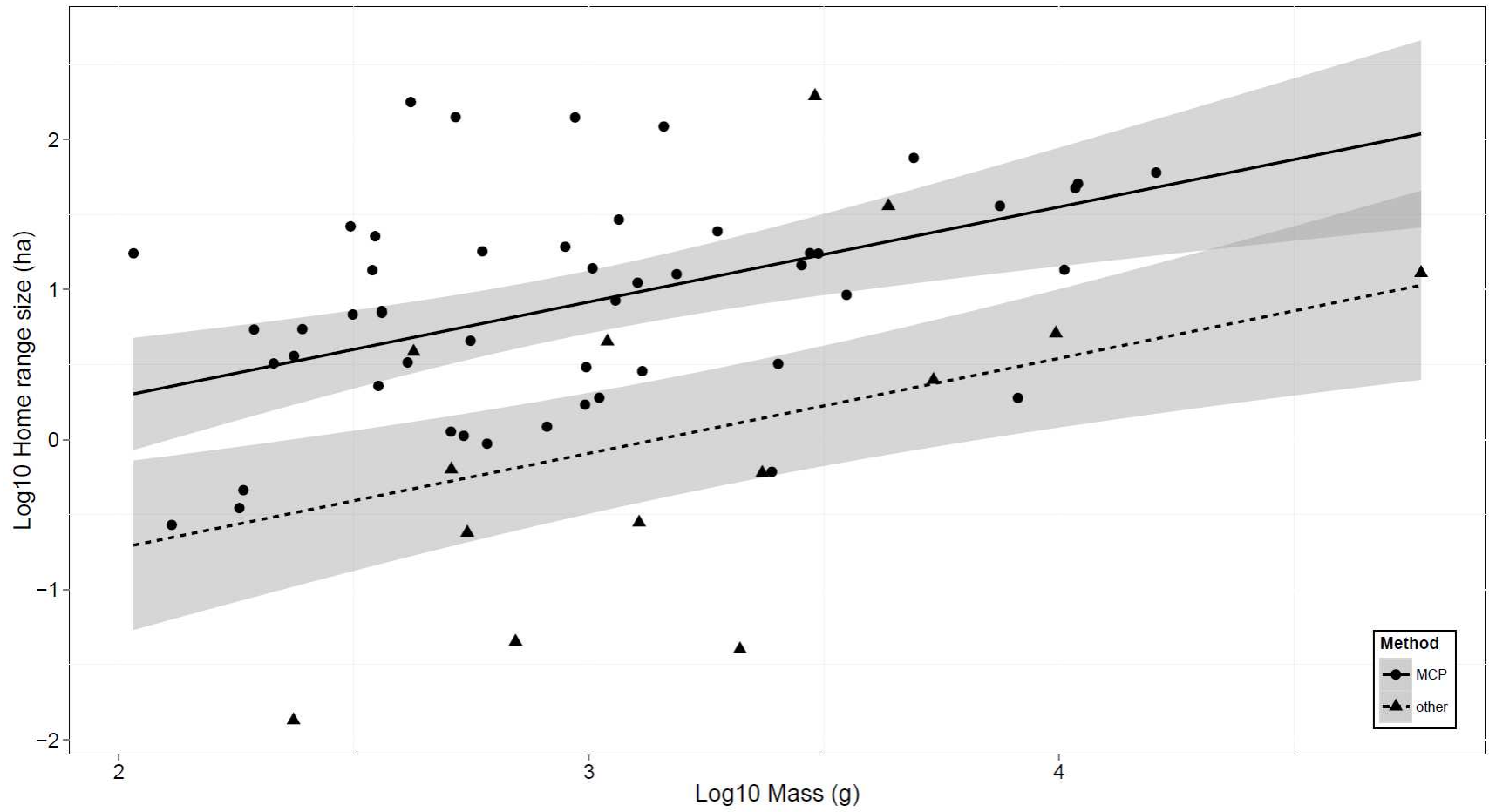
574 **Figure 1.** Log-log linear regression of home range size against body mass in the  
575 unsexed (complete) dataset. Circles and solid line represent home range sizes estimated  
576 using minimum convex polygons (MCP), while triangles and dashed line represent home  
577 range sizes estimated using other or unreported methods. 95% confidence intervals are  
578 represented by the shaded areas.

579 **Figure 2.** Log-log linear regression of home range size against body mass in the  
580 unsexed (MCP-only) dataset. Home range size increases with body mass, and aquatic  
581 turtles have larger home ranges than terrestrial or semiaquatic turtles. 95% confidence  
582 intervals are represented by the shaded areas.

583

Figure 1.

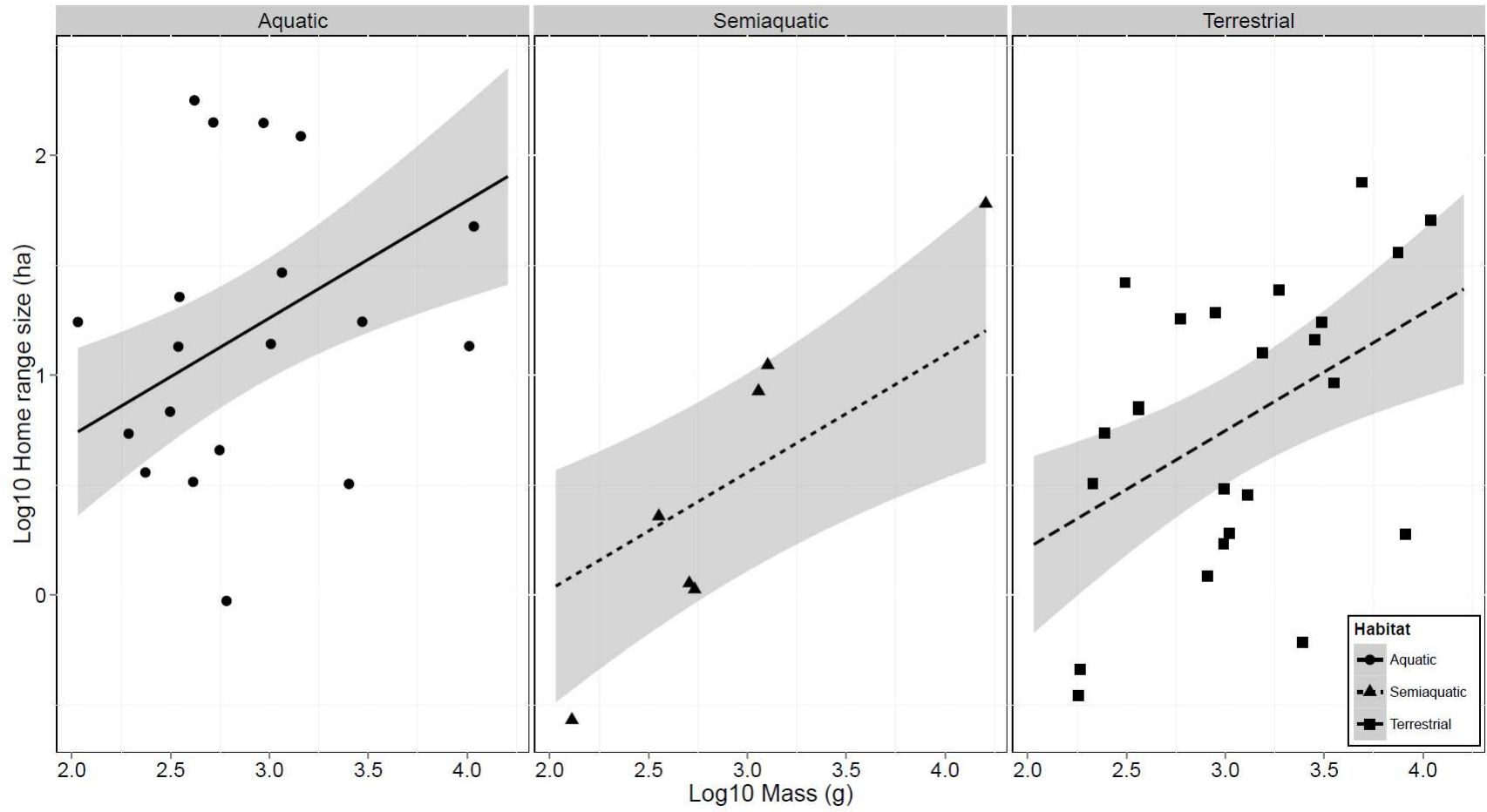
584



585

586

Figure 2.



587

588

589 **Table 1.** Summary table with descriptive statistics of mean home range sizes of turtles in each of the three habitat (Aquatic,  
590 Semiaquatic, Terrestrial), diet (Carnivorous, Herbivorous, Omnivorous) and sociality (Harem, Social, Solitary) categories, along with  
591 sample sizes.

Dataset	All	Habitat			Diet			Sociality			
		Aquatic	Semiaquatic	Terrestrial	Carnivorous	Herbivorous	Omnivorous	Harem	Social	Solitary	
<b>Complete</b>	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
	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	

592

593



594 **Supporting Information**

595 The following supporting information is available for this article online:

596 **Appendix S1.** A full list of species included in this study with species-specific mean  
597 home range size estimates, along with sources and sample sizes. Also listed are mass,  
598 diet, habitat preference, social structure, and method of estimating home range.

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

601 **Appendix S3.** The best models and averaged models (the lowest ranking model by AICc,  
602 and any models with  $\Delta AICc < 2$  of the best model) in the complete and MCP-only dataset.