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Home range in freshwater turtles and tortoises: implications for conservation

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Abstract. Use of space refers to the quantity and quality of habitat exploitation by animals in a certain locality. While quantity is the area of space used by the animal for its activities, quality refers to the locale and manner in which the animal selects its home range. Both parameters are of crucial importance in driving species distribution and abundance. Testudines are distributed across diverse regions, including areas under severe anthropogenic pressure, and many species are threatened, mainly due to habitat loss and overexploitation. We reviewed scientific literature published between 1995 and 2016 to assess taxonomic and geographic patterns in home ranges of freshwater and terrestrial chelonians based on biological and ecological characteristics and conservation status. We examined the trait "home range size", as well as its relationships with intrinsic and extrinsic factors (sex, diet, carapace size, habitat and study zone) and species-specific conservation status. Many of the reviewed studies focus on the Nearctic region, and Emydidae is the most commonly studied family. We found great variation in the home range sizes of species within the same family. Diet was identified as the main driver of home range size. Sex, carapace size, habitat and study zone were not significant as predictors of home range size. Conservation status does not seem to represent a factor driving the assessed studies since the number of investigations concerning threatened and non-threatened species was similar. Home range sizes of threatened species were significantly lower than those of non-threatened species. We recommend priority be applied on information gathering and defining conservation strategies for species in undersampled areas threatened by habitat loss.

Key words. Testudines, conservation status, home range size, movement, non-marine turtles, spatial ecology.

Introduction

Physical space is one of the major dimensions of ecological niches, because the manner in which it is used has implications on fundamental ecological processes such as habitat use (Akins et al. 2014) and species abundance (Gautestad & Mysterud 2005). Studies on spatial ecology facilitate the evaluation of space overlap and sharing, home range size, patterns of use within specific environments, abundance and spatial distribution of target species, aggregation patterns, reproductive strategies, dispersion, and migration (Forero-Medina et al. 2011, Attum et al. 2013). Home range is an important parameter in the field of spatial ecology, corresponding to the physical space used by an individual to execute daily activities, such as foraging, mating, nesting and parental care (Börger et al. 2008, Powell & Mitchell 2012). Studies generally assume that all habitats within a given area are accessible to all animals (Arthur et al. 1996) and their use of space may be shaped by exogenous factors (biotic and abiotic) and individual characteristics (e.g., sex, diet and life stage) (Lagard et al. 2003). However, space use patterns may be not related to individual preference in cases in which resource availability and/or accessibility are restricted (Mathipoulos 2003).

Diet is one of the most commonly studied factors related to home range (e.g., Xiao et al. 2017). For example, carnivores often need a larger home range size than herbivores because energy loss between trophic levels can reach approximately 80 to 90%. Available scientific studies generally support this prediction (McNab 1963, Mcloughlin & Ferguson 2000, Kelt & Van Vuren 2001, Perry & Garland 2002). Specific food type or foraging style may also affect home range size within trophic levels. For example, browsing ungulates have larger home ranges than grazers (Mysterud et al. 2001, Ofstad et al. 2016). As for turtles, diet is not a strong predictor of home range size (Slavenko et al. 2016). However, the effects of other factors, such as season, life stage, sex, habitat and activity pattern, that can affect home range size, might be mediated by diet and food availability.

Aquatic environments (lentic and lotic), differ from terrestrial landscapes in access to resources and their distribution across the landscape. For instance, larger home ranges have been reported for aquatic species, suggesting that habitat influences it (Slavenko et al. 2016). Furthermore, the availability and accessibility of nesting sites (Micheli-Campbell et al. 2013) may strongly influence the use of space by turtles. Landscape features influence home range size, since they impact on important individual traits, such as life stage, sex, and body shape and size (Rivera 2008, Carriére et al. 2009, Viana et al. 2018). Their impacts may result in different movement patterns in individuals within the same environment – e.g., adult turtles may be able to access areas that are inaccessible to younger or smaller individuals (Carriére et al. 2009). Additionally, some authors have already demonstrated intersexual differences in home range size to exist within populations due to divergent reproductive behaviour between sexes (e.g., Litzgus & Mousseau 2004, Carriére et al. 2009).

Chelonians (order Testudines) are considered one of the most ancient recent groups of tetrapods, with the first known records from the Triassic being around 230 million years old (Bour 2008). Currently, 356 species are recognized, classified in 14 families. Eleven families are consolidated in the suborder Cryptodira while three are allocated to the suborder Pleurodira (Turtle Taxonomy Working Group 2017). The majority of species are predominantly freshwater turtles and smaller proportions include marine turtles and terrestrial tortoises, respectively. Pleurodira, the side-necked freshwater turtles, are distributed in the southern hemisphere (Neotropical, Afrotropical and Australasian biogeographic regions). Cryptodira, the hidden-necked turtles, occur in all biogeographic regions (van Dijk et al. 2014).

Chelonians are amongst the most threatened vertebrates, due mainly to human impacts such as hunting, trading, and habitat destruction (Gibbons et al. 2000). From this view, the investigation of relationships between home range size and the conservation status of species can reveal trends that may be a useful indicator of their proneness to extinction. However, an as yet unexplored aspect is whether home range sizes of threatened species differ from those of non-threatened species. Is there any pattern associated with a species' conservation status? May home range size act as a predictor of future conservation trends in chelonian species?

The lack of information on basic aspects of chelonian ecology and biology hinders management and conservation efforts (Forero-Medina et al. 2016). Reviewing the existing literature and some analyses we therefore here investigate the following topics: 1) patterns of home range size of freshwater turtles and terrestrial tortoises; 2) the relationships between home range size and intrinsic and extrinsic factors (sex, diet, size, environment and climatic domains); and 3) the relationship between home range size and conservation status.

Materials and Methods

Data sampling

We performed a search for scientific publications indexed in widely used global web search services and databases (Web of Science, Scopus, Science Direct, and Academic Google) applying the following strings of keywords: "home range AND turtle or freshwater turtle or tortoise"; "use of habitat AND turtle or freshwater turtle or tortoise"; "use of space AND turtle or freshwater turtle or tortoise"; "movement patterns AND turtle or freshwater turtle or tortoise". Only papers on home range published between 1995 and 2016 were considered for this assessment.

The following information was obtained from each paper: species and its respective family studied; location of study area(s) (biogeographic region, continent and country); data sampling methods; estimated home range sizes (if available) of adult males, adult females, juveniles and hatchlings; conservation status (if available) of the studied species according to IUCN Red List.

We compiled data on mean carapace length for both males and females in order to test for its possible relationship to home range size (grouped by species). We also compiled data on diet and environment (habitat and study zone) to test for the possible influences exerted by ecological factors. Three trophic levels were defined regarding diet, i.e., carnivorous, herbivorous, and omnivorous. Habitat was categorized per animal into lentic, lotic, semiaquatic, and terrestrial. Study zone was divided into subtropical, temperate, and tropical. Carapace size and diet data were adopted from the sampled studies if available. If no such information was contained, then it was extracted from other publications on either the same or a population nearby (for example, the carapace length for *Kinixys nogueyi* was extracted from Segniagbeto et al. 2015). Habitat type categories were defined using information about the study sites across the sampled literature. All selected papers contained information on, or descriptions of, the studied habitat.

Data analysis

Linear mixed-effects models (LMM) were used to analyse the factors affecting home range size (Bates et al. 2014). Explanatory variables included body size (carapace length), diet (carnivorous, herbivorous, omnivorous), habitat type (lentic, lotic, semiaquatic, terrestrial), sex, and study zone (subtropical, temperate, tropical). Species identity was included as a random factor (Zuur et al. 2009). We performed model comparisons, so that complete models containing all predictor variables were compared to models with excluded factors. The best-fit model was selected by comparing AICc scores with the AICctab (package bbmle) function. We considered the least complex model within a 0–2 ΔAICc range as the most parsimonious model (Burnham et al. 2011). Model estimation and selection were performed with the R packages "lme4" (Bates et al. 2015) and "bmle" (Dorie 2013).

The evaluated species were ordered as per the IUCN categories for threatened (Vulnerable, Endangered, Critically Endangered) and non-threatened species (Least Concern, Near Threatened), respectively, according to their current status. A Mann-Whitney U-test was used to assess differences between the home range sizes of threatened and non-threatened species.

All statistical analyses were performed considering only the dimensional values of home range size obtained by telemetry and estimated using the Minimum Convex Polygon (MCP) method (Powell 2000) (number of selected studies = 86). All values were converted to hectares and log-transformed using base 10.

Results

Our search for available literature found 179 studies of use for our investigated subject, published between 1995 and 2016. A total of 67% of these had been conducted in the Nearctic region (Fig. 1), and the majority of these were published in the United States. We amassed a total of 101 North American publications, representing more than 50% of all compiled scientific output. Results for other biogeographic regions amounted to between 6 and 22 studies per region. These numbers show that research effort is greatly biased towards a single biogeographic region, the Nearctic (Fig. 2), which also encompasses approximately five times the number of species studied in other regions (Table 1).

Table 1. Numbers of freshwater and terrestrial chelonian species studied between 1995 and 2016 per biogeographic region, numbers of native species, and numbers of endemic species, according to Turtle Conservation Coalition (2017). $_a$ = One of the studied species is exotic.

Geographic region	No. of studied species	No. of occurring species	No. of endemic species
Nearctic	29	53	40
Neotropics	9	93	74
Afrotropics	10	48	46
Asia (Oriental + Eastern Palaearctic)	8_a	77	77
Australasia	6	35	35
Western Palaearctic	6_a	14	12

We found four types of methodologies employed in the studies: Spool-and-line, Capture-mark-recapture (CMR), Telemetry, and Visual Localisation. In some studies, these methods were used in combination or associated with auxiliary methods: CMR and Datalogger, CMR and Telemetry, CMR and Visual Localisation, Telemetry and Photography,

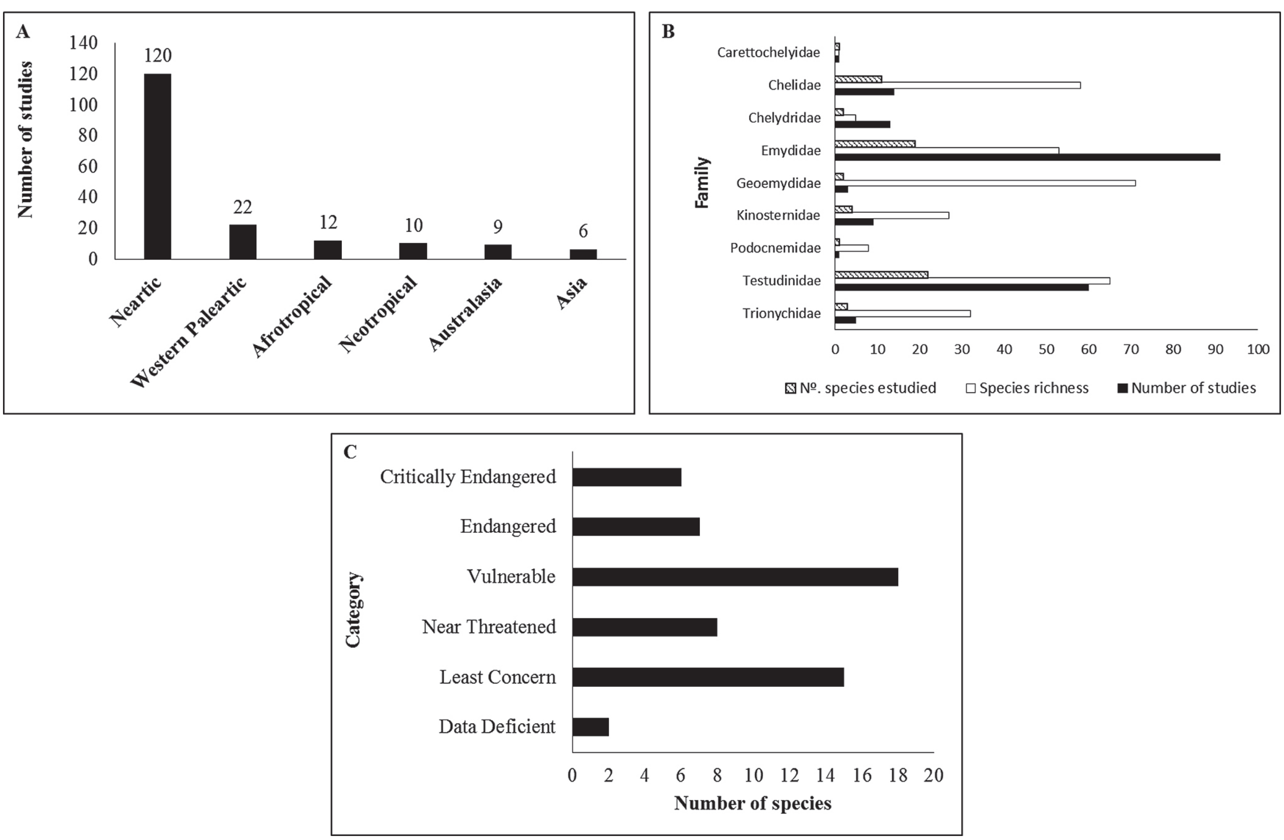

Figure 1. A) Number of studies conducted per biogeographic region. Asia = Oriental + Eastern Palaearctic. B) Number of examined species, species richness, and number of revised studies per family. C) Conservation status of species investigated in the revised studies, according to IUCN.

Telemetry and Datalogger, Telemetry and Spool-and-line. Telemetry was the most frequently used technique, applied in > 80% (n = 151) of the studies.

Only 65 of the 356 recognized freshwater and terrestrial chelonian species (Turtle Taxonomy Working Group 2017) (18.25%) were examined in the sampled studies, encompassing nine families (Fig. 1). The highest study counts per suborder were for the families Chelidae (Pleurodira) and Emydidae (Cryptodira). Most sampled studies (n = 138) focused on only two families, Emydidae and Testudinidae. Testudinidae was the most commonly investigated family, with around 50% of its species (n = 22) being represented in the sampled studies. The number of studies concerning other families varied between 1 and 14 (Fig. 1). We also detected a high variation in the number of studies per species, again ranging from 1 to 14. *Emys blandingii* (Emydidae) and *Gopherus agassizii* (Testudinidae) were the most intensely investigated species, tallying 14 studies in total.

Minimum Convex Polygon (MCP) was the most widely used estimator, employed in 90 of these studies (72.58%). Home range was estimated for 55 of the 65 species through MCP or other estimators, including Kernel and Linear methods. From the studies with home range estimates, 66.13% (n = 82) assessed this parameter for both females and males, while nine calculated it only for females. Furthermore, the authors of 16 studies estimated home range size by grouping males and females together, or without considering sex, giving their estimates as "total home range". Nine studies dealt with both adult and juvenile home ranges. Only one study was restricted to juveniles (*Astrochelys yniphora;* Pedrono & Sarovy 2000). Three studies estimated home ranges of hatchlings, investigating the species *Glyptemys insculpta* (Tuttle & Carroll 2005), *Gopherus polyphemus* (Pike 2006), and *Testudo graeca* (Keller et al. 1997). Four studies did not provide estimates.

We found data on females of 38 species and on males of 34 species considering only the MCP estimator. The mean home range size was 68.932 ha (min.: 0.040, max.: 3206.000) for females, and 21.758 ha (min.: 0.070, max.: 275.00) for males (Table 2). The mean for carnivores was 268.926 ha (min.: 0.980, max.: 3206.000), while for herbivores it was 21.094 ha (min.: 0.170, max.: 167.250), and 14.430 ha (min.: 0.040, max.: 3206.000) for omnivores (Table 2). The most parsimonious model explaining variation in home range size included the factor 'diet' (Table 3). Carapace size, habitat, sex, and study zone were no significant predictors of home range sizes (Fig. 3). Most of the models presented higher AICc values and AICc delta values above 2, indicating that none of the alternative models fit better than the selected one (Table 4).

Thirty-one of the 64 species investigated by the sampled studies are included in one of the three IUCN threat categories (Vulnerable, Endangered or Critically Endangered) (Fig. 1). Two species were listed as "Deficient Data", and nine others have not yet been evaluated. The Mann-Whitney U-test revealed significant differences between the home range sizes of threatened and non-threatened species (U = 226, P = 0.0002). The mean home range size of threatened species was 9.632 ha (SD = 12.898 ha), while that of non-threatened species was 117.379 ha (SD = 467.289 ha).

Discussion

Approximately 356 extant species of freshwater and terrestrial chelonians are distributed around the world, except Polar regions (Bour 2008). Some regions are considered hot spots for this group. Asia stands out, harbouring 77 endemic species (Buhlmann et al. 2009), including the Oriental and Eastern Palaearctic regions. Although it is considered a region of exceptional diversity and endemism for the group, only six studies investigating home range and habitat use by chelonian species were conducted in it in the last twenty years. The species distributed in this region

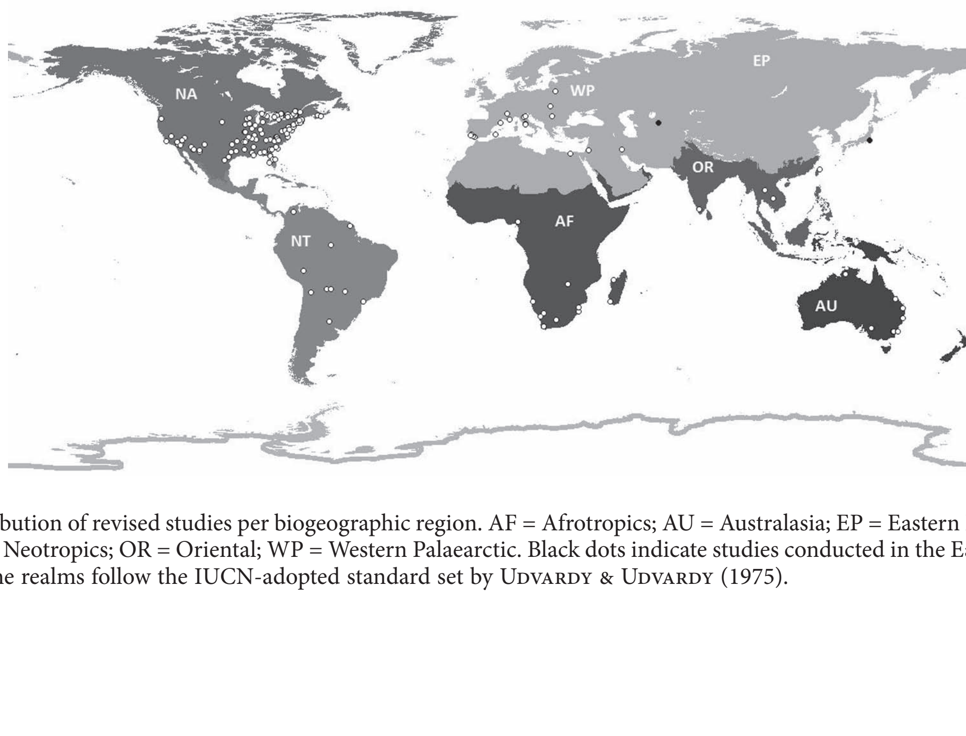

Figure 2. Distribution of revised studies per biogeographic region. AF = Afrotropics; AU = Australasia; EP = Eastern Palaearctic; NA = Nearctic; NT = Neotropics; OR = Oriental; WP = Western Palaearctic. Black dots indicate studies conducted in the Eastern Palaearctic region (EP). The realms follow the IUCN-adopted standard set by Udvardy & Udvardy (1975).

Table 2. Variation in home range size (MCP in ha) of of freshwater turtles and tortoises. Standard error (S.E), Min (minimum) and Max (maximum).

Groups	Mean	S.E.	Min	Max	N
General (Females and Males)	47.338	272.012	0.040	3206.000	142
Females	68.932	367.090	0.040	3206.000	77
Males	21.758	41.981	0.070	275.000	65
Carnivorous	268.926	762.703	0.980	3206.000	17
Herbivorous	21.094	35.129	0.170	167.250	52
Omnivorous	14.430	39.554	0.040	327.600	73
Lentic	24.687	55.468	0.040	327.600	48
Lotic	202.866	693.632	0.980	3206.000	21
Semiaquatic	3.084	1.852	0.530	6.450	15
Terrestrial	21.217	33.490	0.170	167.250	58
Subtropical	10.912	16.006	0.170	72.200	42
Temperate	75.117	380.016	0.040	3206.000	72
Tropical	30.545	42.899	0.670	167.250	28
Threatened	9.632	12.898	0.040	72.200	85
Non-threatened	117.379	467.289	1.410	3206.000	47

Table 3. Estimated coefficients of generalized linear mixed models for home range size (MCP in ha on a log scale) of freshwater turtles and tortoises. S.E. = standard error.

Variable	Estimate	S.E.	p-value
(Intercept)	2.537	0.318	4.41E-11
Habitat_lotic	-0.136	0.290	0.639
Habitat_semiaquatic	-0.364	0.435	0.409
Habitat_terrestrial	-0.447	0.379	0.245
Diet_herbivorous	-0.587	0.564	0.303
Diet_omnivorous	-0.826	0.397	0.043*
Habitat_terrestrial: diet herbivorous	-0.559	0.634	0.383
Habitat_lotic: diet omnivorous	0.485	0.478	0.314

are amongst the most endangered in the world (Turtle Taxonomy Working Group 2017), and only seven were investigated by the sampled studies. Data on species-specific spatial ecology, such as home range size and patterns of habitat use, are essential for efforts to reintroduce chelonians to their natural environments, especially in the Asiatic region, where they are traditionally collected in the wild (Ihlow et al. 2014, van Dijk et al. 2000, Luiselli et al. 2016). There were few studies about the behavioural ecologies of freshwater turtles and terrestrial tortoises from the Australasian, Asia, Afrotropical and Neotropical regions, where they are exposed to intense over-exploitation and habitat reduction (Rodrigues 2005, Diagne 2014). These threats are particularly great in developing regions like the Brazilian Atlantic Forest and rainforests of West Africa, which have been severely fragmented and reduced (Laurance 2010). In addition, difficult access to some habitats hampers the development of studies on chelonian species (Diagne 2014). Research on spatial ecology usually requires long periods of monitoring, which demand extensive fieldwork and monetary resources. The Western Palaearctic experienced a limited diversification of studies on non-marine chelonians when compared to other regions (Bour 2008, Buhlmann et al. 2009). However, the few studies conducted in the Western Palaearctic can be considered relevant in view of the small radiation of this group in this region.

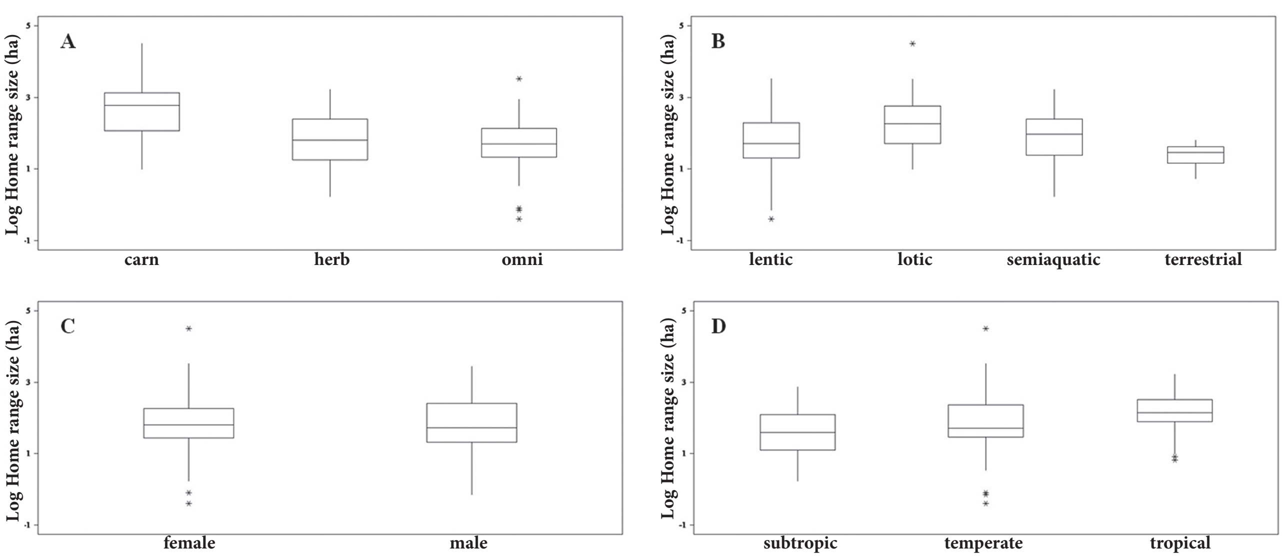

Figure 3. The relationship between home range size (MCP in ha on a log scale) of freshwater turtles and tortoises and A) diet (herbivorous, omnivorous, and carnivorous), B) habitat (lentic, lotic, semiaquatic, and terrestrial), C) sex (females and males) and D) climatic zone (subtropical, temperate and tropical).

Table 4. Candidate models (five with lesser AICc values) and subsequent selections (in bold) examining the influence of diet (Diet), habitat (Habitat), sex (Sex), and carapace length (CL) on estimates of home range size (ha). Random effects include group ID (ID). Models are ranked from lowest AICc to highest. AICc Akaike's information criterion, ΔAICc difference in AICc compared to the best model, wj = Akaike weigh.

Test	Response variable	Model	df	AICc	ΔAICc	wj
LMM	Home range size (ha)	Diet × Habitat × CL + (1 | ID)	18	211.8	0	0.978
		Diet × CL + (1 | ID)	8	221.4	9.5	0.009
		CL + (1 | ID)	4	223.7	11.9	0.003
		Diet × Habitat × Sex × CL + (1 | ID)	34	225.2	13.4	0.001
		Diet + CL + (1 | ID)	6	225.4	13.6	0.001

Our results reveal that studies in the Nearctic region keep increasing in number, contrasting with all other regions. This may be associated with the distribution of research effort focusing on chelonians. A large portion of research on this topic stems from institutions in the United States (e.g., Chelonian Research Foundation, Conservation, Turtle Conservation Found, Turtle Survival Alliance), a country with high economic capacity for supporting longer-term programmes. Few studies were conducted on Chelidae, likely due to its distribution, likely because its populations often live far from research centres specializing in Testudines (Forero-Medina et al. 2016). For instance, Chelidae is widely distributed in South America, however, in this region there is little investment into turtle research. Additionally, we expected a higher number of scientific publications on Podocnemidae, regardless of its low diversity, because this family encompasses high-density populations living in accessible locations, and thus presents a greater chance of being found and studied than those of the Chelidae family (Forero-Medina et al. 2016).

True tortoises, i.e., members of the Testudinidae family (60 species), are widely distributed in all biogeographic regions except Australasia (van Dijk et al. 2014). Factors such as a wide geographic distribution and high diversity may have contributed to the standing of this group as the family with the second highest number of studies and the highest number of studied species.

The distribution of the families and the number of species vary between geographical regions (Table 1, Fig. 1). For example, unlike Geoemydidae, Emydidae stood out both in the number of works and the number of studied species. The geographic distribution and species richness of this family has probably determined these results, since its diversity is highest in the southeastern United States (Ernst & Barbour 1989, Ernst & Lovich 2009). In addition, the financial resources available in the USA may contribute to this finding. However, some species were considerably more intensely investigated than others (see Results).

Intraspecific or even intrapopulation variation between the home range sizes of males and females, as well as form and intensity of habitat use are well documented (e.g., Litzgus & Mousseau 2004, Carriére et al. 2009). This differentiation occurs mainly due to the differences in behaviour typically associated with each sex during the reproduction period. More specifically, females travel longer distances than males during that period in search of appropriate nesting sites (Schlaepfer et al. 2002, Litzgus & Mousseau 2004, Carriére et al. 2009). Nevertheless, the home range sizes of studied species did not reveal differences between the sexes. Male movement is closely related to the search for sexual partners, while females may prioritise the search for nesting sites (Schlaepfer et al. 2002, Litzgus & Mousseau 2004, Carriére et al. 2009, Millar & Blouin-Demers 2011). In this context, it is recommended that further analyses be made separately for males and females, providing a better understanding of the spatial resource requirements of each sex, even when they have similar home range sizes. Slavenko et al. (2016) analysed the home range sizes of 62 species of different families and found great variation of this variable within families, suggesting that this parameter is likely shaped by external environmental factors and not by phylogeny itself. The large variation in estimated home range sizes between species of the same family (e.g., Jaeger & Cobb 2012) can be attributed to several factors such as habitat type, body size, and feeding habits (Perry & Garland 2002, Slavenko et al. 2016).

Few of the sampled studies evaluated and compared different age classes (hatchlings, juveniles and adults). Some of these found discrepancies between the home range sizes of different age classes (Anthonysamy et al. 2013, Moore et al. 2014). The differentiated use of environments by adults and juveniles is likely a consequence of different habitat requirements. Shallow waters and dense vegetation cover may be of great importance for smaller individuals, since they may provide protection against predators (Sloan et al. 1996, Moore et al. 2014). Studies that evaluate the use of space by hatchlings are still incipient. There is great difficulty in gathering data on hatchlings due to their small size and extreme crypsis in their environments (Pike 2006). The low number of papers found reflects this methodological difficulty.

The home ranges of continental turtles tends to be larger for carnivores than for herbivores, similarly to other animal groups (e.g., mammals and lizards) (Perry & Garland 2002). This is possibly due to food resources of plant origin being often more concentrated in a given area (McNab 1963, Mcloughlin & Ferguson 2000). The lack of significant influence of carnivory in our results is probably due to the wide large amplitude in home range size amongst carnivorous turtles. The smaller home ranges of omnivorous species emphasize their ability to exploit a larger spectrum of food items, which can bring about significant energetic benefits.

Our results do not support an influence of habitat on home range size. However, we are not suggesting that habitat is not important for home range size, only that 'habitat' proved not significant in our selected models (semiaquatic, lotic and terrestrial) (Table 3). When we analysed the average values of home range per habitat, we observed that lotic species had larger home range sizes than the other turtles. This result suggests that home range may be influenced by abiotic factors. As has been suggested in some literature (McLoughlin & Ferguson 2000, Lubcke & Wilson 2007, Rivera 2008), physical characteristics of space may influence the size and shape of organisms. Freshwater turtles and tortoises exhibit morphological differences and variation in the build of their carapaces (Claude et al. 2003, Rivera 2008), whereas that of individuals from lotic environments are more uniform. Thus, displacement in lotic habitats may require less energy expenditure than in other environments.

Climatic zones (latitude) also don't influence home range size. We believe that this finding could be based on factors not shaped by latitude. The home ranges of non-turtle vertebrate groups tend to be larger at higher latitudes than at lower ones (Scoular et al. 2011). According to Huston & Wolverton (2009), this pattern forms because productivity is lower at higher latitudes and, consequently, species need larger home ranges, which in turn boosts competition for space and resources.

Home range size is considered a predictor of extinction risk (Woodroffe & Ginsberg 1998). This ecological attribute can be shaped by abiotic factors, such as habitat composition, and be influenced by resource availability and landscape connectivity (Fortin et al. 2012). Habitat loss is another one of the main threats to turtles (Gibbons et al. 2000, Quesnelle et al. 2013). Our results reveal that endangered species have smaller home ranges than expected, likely due to anthropogenic impacts within the target species distribution. Reduction of appropriate habitats increases vulnerability to extinction because it limits both dispersal capacity and access to resources (Sodhi et al. 2009).

The two species around which the higher number of studies was concentrated, *Emys blandingii* and *Gopherus agassizii*, are listed as "Endangered" and "Vulnerable", respectively (IUCN 2017). However, studies evaluating threatened and non-threatened species were very similar in number in the current study. Low accessibility often culminates in neglecting certain species, and geographical knowledge gaps may be related to a lack of state incentives for research and the absence of specialized local research effort – e.g., in certain parts of Asia and Africa (Van Dijk et al. 2000, Böhm et al. 2013). This becomes even more evident when considering that most threatened species are distributed in the Asiatic region (Turtle Conservation Coalition 2017, IUCN 2017), which has been extremely affected by illegal trade and consumption.

The lack of a standardized method to estimate home range size and other information on the use of space makes it impossible to compare many of the studies, hampering the identification of patterns and development of macroecological analyses. We suggest that future investigations into the spatial parameters of continental chelonians calculate home range size using more than one estimator. It is important to consider that there probably is no universal estimator for home range. Therefore, it is necessary to select the estimator / model with the best potential for answering the questions of interest (Powell & Mitchell 2012). Minimum Convex Polygon (MCP) is a widely used method despite its being the subject of criticism (Downs & Horner 2008), as is demonstrated in the present work, and it could facilitate comparisons between past and future studies.

Our results contribute to better understand the ecological determinants of home range-related behaviour. We highlight the importance of habitat and trophic levels for explaining the home range sizes of continental chelonians. This information should be incorporated into management plans to help determine the necessary dimensions of protected areas, especially in projects aimed at conserving threatened chelonians. The present work has identified a deficiency of studies on spatial parameters of chelonians in many regions, especially those that harbour high numbers of endangered species. Scientific research aimed at gathering information/data on the use of space is essential and urgently required to aid the formulation of conservation programmes, especially for threatened species.

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