JOURNAL OF Evolutionary Biology

doi: 10.1111/jeb.13223

Macroecological patterns of sexual size dimorphism in turtles of the world

M. AGHA*, J. R. ENNEN†, A. J. NOWAKOWSKI*, J. E. LOVICH‡, S. C. SWEAT† & B. D. TODD*

*Department of Wildlife, Fish, and Conservation Biology, University of California, Davis, Davis, CA, USA
†Tennessee Aquarium Conservation Institute, Chattanooga, TN, USA
‡Southwest Biological Science Center, U.S. Geological Survey, Flagstaff, AZ, USA

Keywords:

body size evolution;
differential selection;
ecological divergence;
interspecific growth;
morphological variation.

Abstract

Sexual size dimorphism (SSD) is a well-documented phenomenon in both plants and animals; however, the ecological and evolutionary mechanisms that drive and maintain SSD patterns across geographic space at regional and global scales are understudied, especially for reptiles. Our goal was to examine geographic variation of turtle SSD and to explore ecological and environmental correlates using phylogenetic comparative methods. We use published body size data on 135 species from nine turtle families to examine how geographic patterns and the evolution of SSD are influenced by habitat specialization, climate (annual mean temperature and annual precipitation) and climate variability, latitude, or a combination of these predictor variables. We found that geographic variation, magnitude and direction of turtle SSD are best explained by habitat association, annual temperature variance and annual precipitation. Use of semi-aquatic and terrestrial habitats was associated with male-biased SSD, whereas use of aquatic habitat was associated with female-biased SSD. Our results also suggest that greater temperature variability is associated with female-biased SSD. In contrast, wetter climates are associated with male-biased SSD compared with arid climates that are associated with female-biased SSD. We also show support for a global latitudinal trend in SSD, with females being larger than males towards the poles, especially in the families Emydidae and Geoemydidae. Estimates of phylogenetic signal for both SSD and habitat type indicate that closely related species occupy similar habitats and exhibit similar direction and magnitude of SSD. These global patterns of SSD may arise from sex-specific reproductive behaviour, fecundity and sex-specific responses to environmental factors that differ among habitats and vary systematically across latitude. Thus, this study adds to our current understanding that while SSD can vary dramatically across and within turtle species under phylogenetic constraints, it may be driven, maintained and exaggerated by habitat type, climate and geographic location.

Introduction

Sexual size dimorphism (SSD) is a widespread phenomenon among plants and animals that often results from differential selection operating on body sizes of males and females (Fairbairn *et al.*, 2007). The underlying mechanisms that drive and maintain SSD and the resulting macroecological patterns across large spatial scales (i.e. continental and global) remain understudied among ectotherms. The evolution of SSD is often predicted by adaptive significance or nonadaptive significance hypotheses, including genetic constraints (Fairbairn *et al.*, 2007). When nonadaptive, sexual size

Correspondence: Mickey Agha, Department of Wildlife, Fish, and Conservation Biology, University of California, Davis, One Shields Avenue, Davis, CA 95616, USA.
Tel.: +1 530 752 1140; fax: +1 530 752 4154;
e-mail: magha@ucdavis.edu

dimorphism in reptiles generally results from body size scaling, genetic correlations between male and female body size, and evolutionary inertia (Fairbairn, 1990; Blanckenhorn, 2005; Lovich *et al.*, 2014). Alternatively, when adaptive, SSD evolution is often influenced by at least one of three general forces – sexual selection for larger male body size, fecundity selection for larger female body size, or primary and secondary ecological divergence resulting from intraspecific competition (Darwin, 1871; Ghiselin, 1974; Cox *et al.*, 2007; Stephens & Wiens, 2009).

In an adaptive context, sexual selection can drive mating success of males (i.e. male–male competition for female insemination, or female preference for larger males), whereas fecundity selection can lead to increased reproductive potential by favouring increased female body size (Blanckenhorn, 2005). Additionally, ecological divergence from competition can be attributed to intraspecific competition between males and females in which foraging success is related to body size of each sex (Stephens & Wiens, 2009). The strength and influence of these adaptive forces on SSD can be strongly affected by several environmental and ecological variables, such as food availability and foraging success, climate, ecological mode and habitat type (Blanckenhorn, 2005; Stephens & Wiens, 2009). For instance, proximate environmental factors like temperature, precipitation and their variability across a species' range may contribute to differences in selection on male vs. female body size (Stillwell & Fox, 2007), enhance the degree of pre-existing SSD, drive geographic patterns of SSD (Litzgus & Smith, 2010; Friedman & Remeš, 2016), or drive differential rates of growth and development among males and females (Cox *et al.*, 2006).

Previous studies have noted that ecological divergence results from differences in overall selection on males and females of the same species and that the level of differential selection can vary by habitat type (Berry & Shine, 1980; Ceballos *et al.*, 2013). For instance, in semi-aquatic turtles, male-biased SSD can be driven by sexual selection acting on male body size and frequency of male–male combat (Berry & Shine, 1980), or predation pressure during terrestrial habitat movements. In terrestrial turtles, male-biased SSD may be determined predominantly by male–male combat (Berry & Shine, 1980). In contrast, aquatic turtles more commonly show precoital courtship displays such as elaborate signalling and nuptial coloration, and thus, male body size may be related to female choice and male courtship abilities (Berry & Shine, 1980). Furthermore, smaller male body sizes in aquatic habitats might be advantageous during mate searching or male dispersal (Ghiselin, 1974; Lindeman, 2008), and to create early mating opportunities (Gibbons & Lovich, 1990). Specifically, male dispersal may favour agile males that divert their energy towards finding and inseminating many females, possibly reflecting adaptation for greater mobility by decreasing size. Additionally, female-biased SSD could occur presumably because reproductive success and fecundity depend on female body size (reviewed by Andersson (1994); see Iverson (1992) for turtles). Conversely, in terrestrial habitats, larger body size is thought to decrease predation and desiccation risk (Lindeman, 2008). These hypotheses suggest that the direction of SSD can depend on the mating system within a population, niche divergence, habitat type and ecological mode (e.g. terrestrial, semi-aquatic, benthic moving and aquatic swimming), as well as female mate selection (Berry & Shine, 1980; Fairbairn *et al.*, 2007; Keevil *et al.*, 2017), among other factors.

Few studies have examined macroecological patterns of reptile SSD at global scales (Cox *et al.*, 2003; Stephens & Wiens, 2009). In reptiles, SSD may vary spatially among populations (e.g. Lovich *et al.*, Pearson *et al.*, 2002; Litzgus & Smith, 2010), among habitat types or ecological niches (e.g. Berry & Shine, 1980; Ceballos *et al.*, 2013), and along environmental gradients (e.g. Lovich *et al.*, 2010; Blanckenhorn *et al.*, 2006). Environmental gradients (e.g. temperature and precipitation) have been suggested as a possible explanation of geographic variation of SSD in snakes, turtles and lizards (Cox *et al.*, 2009; Amarello *et al.*, 2010; Michael *et al.*, 2014; Joos *et al.*, 2017) and could explain interspecific variation in growth, development and timing of maturation (Stillwell & Fox, 2009). For instance, growth rates and maturation may be determined by optimal sex-specific developmental temperatures or amount of precipitation during development (St. Clair, 1998; Cox *et al.*, 2009; Ceballos *et al.*, 2013), thereby benefitting one sex more than the other across latitudinal or environmental gradients, or in different ecological niches. Additionally, SSD driven by climate or climate variability could be correlated with resistance to desiccation, survival and fitness-related phenotypic traits in certain species, thereby reinforcing sex-specific differences among ecological niches. However, no study has yet examined how SSD in a reptile group may covary with climate and habitat at the global scale in a spatial and phylogenetic framework.

Reptiles exhibit variable morphology and life-history traits, as pointed out in several reviews of general patterns of SSD within the group (Berry & Shine, 1980; Fitch, 1981; Gibbons & Lovich, 1990; Cox *et al.*, 2007). In addition, chelonians are one of the best-studied reptile superorders in terms of geographic distribution, fossil record and phylogeny (Lovich & Ennen, 2013; Rödder *et al.*, 2013). Consequently, turtles offer a unique opportunity to test the generality of SSD hypotheses across large spatial extents (i.e. latitudinal gradients). Here, we use published body size data on 135 species from nine turtle families (Ceballos *et al.*, 2013) to examine macroecological patterns of SSD at the global scale. We revisit the effects of habitat type (e.g. terrestrial, aquatic and semi-aquatic) on turtle SSD previously addressed by Ceballos *et al.* (2013) and we test these patterns in unison with latitude and climate effects while controlling for expected trait covariation between taxa that results from their common ancestry (Kamilar & Cooper, 2013). Specifically, we examined potential correlations among climate and climate variability and turtle SSD across latitudinal gradients in combination with the effects of habitat type. We expected that differences in habitat type would directly influence sex bias and magnitude of SSD because there may be different optimal body sizes associated with reproductive behaviours in different habitat types (Berry & Shine, 1980; Jaffe *et al.*, 2011; Ceballos *et al.*, 2013). For instance, the cost of increasing female body size may be more severe in terrestrial habitats than in aquatic or semi-aquatic habitats due to constraints imposed by locomotion. Alternatively, the benefit of increasing male body size for combat may be greater in terrestrial environments where avoiding being upended can mean the difference between life or death (Golubović *et al.*, 2013). Additionally, because body size increases with latitude in many turtle species (Ashton & Feldman, 2003; Angielczyk *et al.*, 2015; Tesche & Hodges, 2015), and because the fecundity advantage hypothesis predicts larger females at higher latitudes (Iverson *et al.*, 1993; Cox *et al.*, 2003; Litzgus & Smith, 2010), we expected that SSD magnitude would increase and would be female-biased towards the poles. To further examine the underlying mechanisms driving latitudinal variation in SSD, we expected that climatic factors such as precipitation and temperature that vary systematically with latitude would be linked to body size variation (Blanckenhorn *et al.*, 2006; Litzgus & Smith, 2010). Because temperature and precipitation are critical to growth and development in turtles (Gibbons *et al.*, 1981), we expected that these environmental factors would influence spatial trends in turtle SSD and alter the magnitude of difference between male and female body size at maturity. Finally, we expected that SSD differences among turtle families would be highly constrained by phylogeny because ecological similarity can often be related to phylogenetic relatedness (Losos, 2008).

Materials and methods

To examine global geographic patterns of SSD in turtles, we first georeferenced and digitized turtle species' distributions using ArcMap v10.3 (ESRI, Redlands, CA, USA), excluding the two families of sea turtles (Cheloniidae and Dermochelyidae). In addition, the geographic centre of distributions (centre latitude) was calculated from the distribution polygons. These spatial data were acquired from maps generated by the Turtle Taxonomy Working Group (TTWG) (Van Dijk *et al.*, 2014). These data represent the most complete study of turtle distributions in the literature that are readily available. Range maps from TTWG were generated by data from Buhlmann *et al.* (2009), International Union for Conservation of Nature (IUCN) Red List and numerous species accounts published in Conservation Biology of Freshwater Turtles and Tortoises (Rhodin *et al.*, 2008).

We also recorded the general habitat preference type (i.e. ecological mode: aquatic, semi-aquatic and terrestrial), for each species in our data set using descriptions from Ernst & Lovich (2009), Ernst *et al.* (2007), Joyce & Gauthier (2004), TTWG and the IUCN Red List. In addition, some of our habitat classifications are modified or updated from previous studies (Berry & Shine, 1980; Ceballos *et al.*, 2013). Finally, we obtained annual mean temperature, annual temperature variance (i.e. standard deviation of annual temperature), annual precipitation and annual precipitation variance (i.e. standard deviation of annual precipitation) data, averaged across each turtle species' entire distribution using WorldClim 30 arc-second resolution data (available from http://www.worldclim.org/) with ESRI Spatial Analyst Extension. These variables were selected because they have previously been found to predict turtle species richness patterns at the continental scale (Ennen *et al.*, 2016), and thus may be associated with other macroecological patterns in turtles.

To quantify SSD, we used average adult male and female body size (i.e. straight-line carapace length; 135 species) from multiple sources – Ceballos *et al.* (2013), Rostal *et al.* (2014), and Gibbons & Lovich (1990), which included references from over 450 individual published papers. Straight-line carapace length is a standard measurement taken in turtle field studies and is a common measurement used to examine survival, growth and maturation in turtles (Ernst & Lovich, 2009). The most commonly used and accepted indicator of SSD in turtles is the sexual dimorphism index (SDI) (Lovich & Gibbons, 1992; Smith, 1999; Cox *et al.*, 2003; Fairbairn *et al.*, 2007; Lovich *et al.*, 2014). Thus, for our study, we used SDI, which generates sexual dimorphism indices that are continuous around zero. Lovich & Gibbons (1992) generate SDI values as follows:

1. If female is the larger sex then $\mathrm{SDI} = (L/S) - 1$
2. If male is the larger sex then $\mathrm{SDI} = -(L/S) + 1$

where L is the average size of the larger sex for the species, and S is the average size of the smaller sex for the species. As a result, a positive SDI value represents female-biased SSD, whereas a negative value represents male-biased SSD (Lovich & Gibbons, 1992). Using this calculation, we produced SDIs for all 135 species for which data were available in the families Carettochelyidae (1), Chelidae (20), Chelydridae (3), Emydidae (33), Geoemydidae (24), Kinosternidae (13), Podocnemididae (7), Testudinidae (26) and Trionychidae (8).

To evaluate SSD variation in turtles at the global scale, we used both nonphylogenetic and phylogenetic methods. First, we examined multiple *a priori* hypotheses about mechanisms driving geographic variation in SSD by analysing the effect of absolute mean centre latitude of species range (latitude), habitat type (aquatic, semi-aquatic and terrestrial) and environmental factors (i.e. annual precipitation and annual mean temperature, and their respective variances) on SDI using linear mixed-effects models (LMMs) in R fit with maximum likelihood (Pinheiro & Bates, 2000). To account for broad phylogenetic associations among species, we fit turtle family as a random effect. As a complementary approach to account for nonindependence among species (i.e. phylogenetic relatedness), we obtained branch lengths from a phylogeny of 288 turtle species (Thomson, RC, PQ Spinks, HB Shaffer. in prep. Toward a turtle tree of life: phylogeny and diversification of the extant Testudines). Seven species in our SDI data set were missing from this phylogeny (5% of species in the SDI data set). Therefore, we added these species to the phylogeny by randomly placing branches within the subtree corresponding to the genus of each missing species. Our analyses should be robust to random branch placement because of the small number of missing taxa and because most branch length variation among species should be attributable to variation among clades corresponding to genera and families (i.e. higher order classifications). Subsequently, we examined the effect of latitude, habitat type and environmental factors on SDI by fitting phylogenetic generalized least squares (PGLS) models (Purvis, 2008; Paradis, 2011). We accounted for phylogenetic nonindependence by fitting models with a correlation structure generated from branch lengths. We evaluated model fit with corrected Akaike information criterion (AICc; Akaike, 1974) using multiple correlation structures derived from alternative models of trait evolution; we fit final models using the ‘corGrafen’ function of package ‘ape’ (Paradis *et al.*, 2004) in Program R. Because of heterogeneity in global model residuals, we also incorporated a fixed variance structure into the models (Zuur *et al.*, 2009). We compared models for each modelling approach (LMMs and PGLS) separately using AICc weighting adjusted for variance inflation (Burnham & Anderson, 2004), and we generated model-averaged parameter estimates across all additive subsets (i.e. 95% confidence set) using the ‘MuMin’ package (Bartoń, 2013). To infer relative strength of the different ecological and environmental factors with respect to one another, we present relative variable importance weights (RIW). These RIWs are the sum of all AIC weights from models that contain that variable in the 95% confidence model sets (Burnham & Anderson, 2004). In addition, to determine whether a specific turtle family drives spatial variation in SDI across latitude, we separately analysed the data with a generalized least squares (GLS) model framework in which we set SDI as the response variable and an interaction between latitude and family as predictor variables.

Finally, we tested for phylogenetic signal in SDI and habitat type using the ‘phylosig’ function in package ‘phytools’ (Revell, 2012) and the ‘fitDiscrete’ function in package ‘geiger’ (Harmon *et al.*, 2008), respectively. These functions compute Pagel’s λ, which represents the degree to which the phylogeny is transformed to best fit the expected trait distribution under a Brownian motion model of trait evolution. Values of λ near 1 signify strong phylogenetic signal (e.g. trait has evolved according to Brownian motion divergence model of evolution; Kamilar & Cooper, 2013), whereas values of λ near 0 indicate that the expected trait distribution is independent of phylogeny (e.g. close relatives are not more similar than distant relatives; Kamilar & Cooper, 2013). We assessed significance of phylogenetic signal using a likelihood ratio test comparing the λ-transformed tree to a star phylogeny (where $\lambda = 0$). All statistical analyses and graphs were generated using Program R version 3.2.3 (R Development Core Team, 2015), and statistical significance was established at $\alpha < 0.05$.

Results

Turtles displayed a range of SDI (−0.41 to 1.54), with females larger than males in approximately 73% of turtle species in our study. A predominant pattern of female-biased SSD occurred in the families Trionychidae, Podocnemidae, Geoemydidae, Emydidae, Chelidae and Carettochelyidae, whereas a predominant pattern of males being larger than females occurred in the families Kinosternidae and Chelydridae (Fig. 1). Turtles in the family Testudinidae were evenly spread between male- and female-biased cases of SSD (Fig. 1). Emydid species showed some of the most wide-ranging cases of male- and female-biased SSD (i.e. largest variance) globally. Additionally, the most disproportionate levels of male- and female-biased SSD occurred in the southeastern USA (Fig. 2).

Using model-averaged estimates from our LMMs (Table S1), we found that habitat type was a significant predictor of SSD. Use of semi-aquatic and terrestrial habitats was associated with male-biased SSD (Table 1). Use of aquatic habitat, in contrast, was associated with female-biased SSD (Table 1). In addition, latitude was positively correlated with SSD, meaning that females were increasing larger relative to males towards the poles. Furthermore, relative variable importance values suggest that habitat type is the most important predictor variable, followed by latitude (Table 2). Our GLS coefficient that estimated the interaction between family and latitude suggested that, specifically, the families Emydidae and Geoemydidae were strongly female-biased towards the poles.

In our complementary PGLS model set that controlled for phylogenetic relatedness (Table S2), our model-averaged estimates showed that habitat type predicted the direction of SSD (Table 1, Figs 3 and 4). We also found support for a positive relationship between annual temperature variance and SSD, suggesting that environments with greater temperature variability were correlated with female-biased SSD. Conversely, we found support for a negative relationship between annual precipitation and SSD, suggesting that wetter locales are male-biased (Table 1). Furthermore, relative variable importance values suggest that habitat type is the most important predictor variable, followed by annual precipitation (Table 2). Additionally, SSD showed high phylogenetic signal ($\lambda = 0.84$, $P < 0.001$), and habitat type also showed high phylogenetic signal ($\lambda = 0.91$, $P < 0.001$).

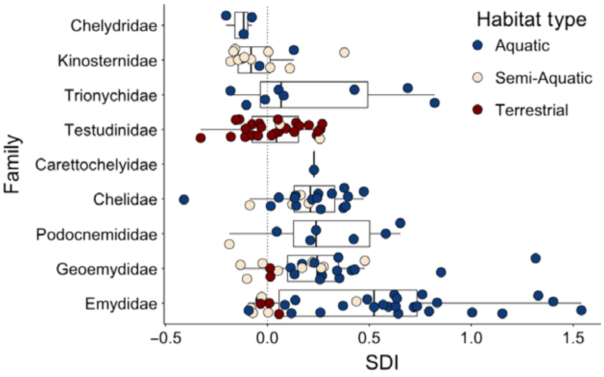

Fig. 1 Sexual size dimorphism indices (SDI) for 135 turtle species in nine families. Vertical lines denote mean and standard deviation of SDI, and horizontal lines denote range of SDI. Dotted vertical line denotes the general division between male-biased (negative SDI) and female-biased (positive SDI) sexual size dimorphism (SSD). Colour codes denote habitat type, blue: aquatic; cream: semi-aquatic; and red: terrestrial.

Discussion

Our results support the idea that the evolution of SSD within turtles is explained, in part, by environmental and ecological factors that likely influence adaptive significance mechanisms in a spatial and phylogenetic framework. In particular, we found that habitat type, latitude, temperature variability and annual precipitation are associated with SSD in turtles at the global scale, suggesting that ecological and environmental variables may drive, maintain and/or intensify the degree of body size divergence between the sexes in turtles of the world. These macroecological patterns may arise from underlying factors that could include sex-specific reproductive behaviour (i.e. mating strategy, male–male combat), fecundity and sex-specific responses to environmental factors (i.e. growth rates and timing of maturity) that differ between habitats and systematically across latitudes. However, phylogenetic signal in SSD suggests that these patterns are not random with respect to phylogeny and that a portion of the variation in SSD results from the shared evolutionary history of closely related turtle species.

Intra- and interspecific variation in turtle SSD among habitat types can result from sex-specific differences in growth rates and timing of maturation or male and female reproductive behaviour and strategies, all of which are uniquely tied with and intensified by environmental attributes such as temperature and precipitation (Berry & Shine, 1980; Gibbons *et al.*, 1981; Gibbons & Lovich, 1990; Stamps, 1993; Mushinsky *et al.*, 1994; Lindeman, 2003; John-Alder *et al.*, 2007; Lubcke & Wilson, 2007). In addition, species living in different habitat types may experience different

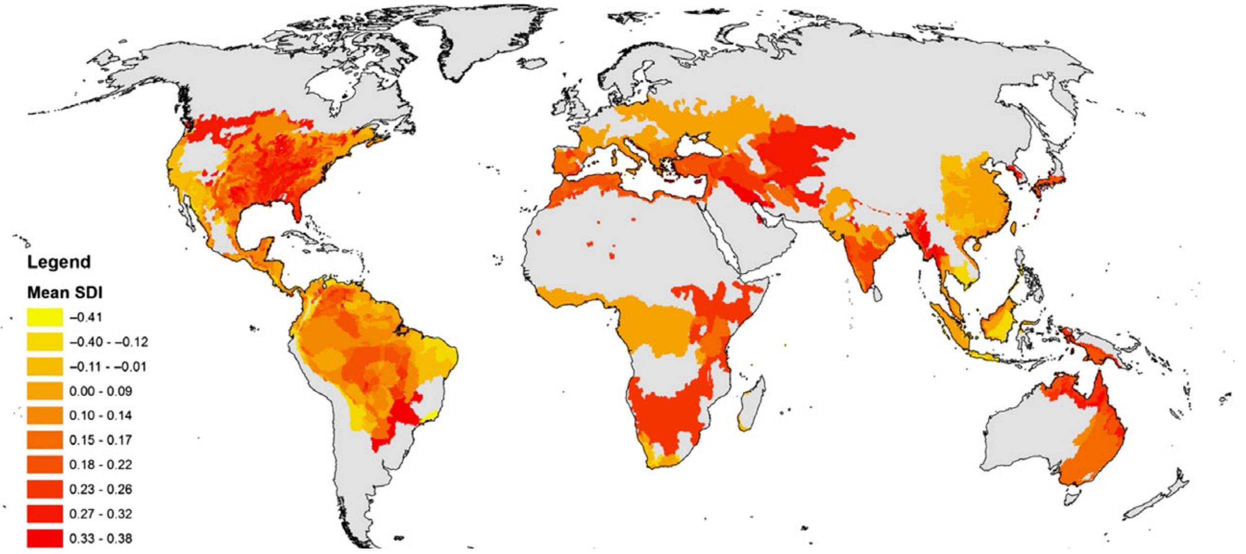

Fig. 2 Mean sexual size dimorphism index (SDI) for 135 turtle species across the globe (0.25 square degrees). For SDI, points are on colour ramp from negative SDI values (i.e. male-biased), yellow, to positive SDI values (i.e. female-biased), red.

Table 1 Summary of significant and suggestive conditional, model-averaged coefficients related to the direction of sexual size dimorphism in turtles for both LMM and PGLS 95% confidence model sets. Sex bias is denoted by a positive (female) or negative (male) coefficient, and significance is based on 95% confidence levels that did not overlap 0 (significant at $P < 0.05$).

Model-averaged coefficients	LMM estimate and SE	LMM confidence level	PGLS estimates and SE	PGLS confidence level
Habitat type: Terrestrial	−0.48 ± 0.04	**−0.59 to −0.38**	−0.23 ± 0.06	**−0.34 to −0.11**
Habitat type: Aquatic	0.034 ± 0.07	**0.21 to 0.47**	0.20 ± 0.07	**0.06 to 0.34**
Habitat type: Semi-aquatic	−0.39 ± 0.04	**−0.47 to −0.31**	−0.24 ± 0.05	**−0.34 to −0.15**
Annual mean temperature	0.01 ± 0.04	−0.08 to 0.16	−0.02 ± 0.04	−0.11 to 0.07
Annual temperature variance	0.02 ± 0.03	−0.01 to 0.09	0.05 ± 0.02	**0.003 to 0.09**
Annual precipitation	−0.01 ± 0.02	−0.08 to 0.02	−0.04 ± 0.02	**−0.08 to −0.001**
Annual precipitation variance	−0.001 ± 0.01	−0.05 to 0.04	−0.004 ± 0.02	−0.05 to 0.04
Latitude	0.05 ± 0.03	**0.01 to 0.11**	0.001 ± 0.03	−0.05 to 0.06

Bold sets of confidence levels denote significant at $P < 0.05$.

Table 2 Relative variable importance weights after model averaging 95% confidence LMM and PGLS model sets that predict the direction of sexual size dimorphism in turtles. Our all-subsets approach included each variable in equal number of models.

Variable	LMM: Importance	LMM: N containing models	PGLS: Importance	PGLS: N containing models
Habitat type	1.00	20	1.00	23
Annual mean temperature	0.32	8	0.27	10
Annual temperature variance	0.58	10	0.72	13
Annual precipitation	0.40	12	0.75	14
Annual precipitation variance	0.25	8	0.29	10
Latitude	0.86	14	0.21	8

conditions, such as variation in resource availability, visibility and competition, all of which are hypothesized to directly influence SSD (Butler *et al.*, 2000; Blanckenhorn, 2005). For instance, habitat and SSD was correlated in *Anolis* lizards, with the link being attributed to variation in intersexual competition with respect to sexual selection pressures created by the structure of the habitat (Butler *et al.*, 2000). Our results reaffirm that adaptation of ectotherms to their proximate environments is more complex than previously known, because there may be sexual selection pressures operating differentially between sexes in different habitats (i.e. aquatic, semi-aquatic and terrestrial).

Our study also shows that the absolute average SSD in species that are female-biased is three times larger than species with male-biased SSD, suggesting that fecundity selection is a common and strong evolutionary force in turtles. Otherwise, one might expect similar absolute average SSD between the male- and female-biased species. Additionally, reproductive behaviours and habitat type could also explain the magnitude of difference in SSD between species with male- and female-biased SSD. Aquatic species displayed the largest disparity in body size between the sexes and their SSD was female-biased (Fig. 4). In these species, female body size can be increasingly larger than male body size because of two opposite evolutionary forces: (i) fecundity selection drives female body size larger to increase maternal volume, which is correlated with fecundity, whereas (ii) natural selection drives smaller male body size to increase movement efficiency in mate searching and earlier mating opportunity (Gibbons & Lovich, 1990; Lindeman, 2008). These great differences in body size between males and females may be maintained as mating may become impossible on land. In terrestrial turtles, the average male-biased SSD magnitude was small compared to that of aquatic and semi-aquatic turtles (Fig. 4). Male body size likely cannot diverge rapidly from female body size to produce a great difference between the sexes in terrestrial turtles for at least three reasons: (i) fecundity selection acting on females remains strong, (ii) natural selection favours larger sizes for both sexes, which limits predation, and thus maintains fecundity selection (Lindeman, 2008) and (iii) the interaction in which sexual selection occurs results primarily from male–male interaction (i.e. male–male combat) and not a male–female interaction.

In many taxa, spatial variation of SSD can be attributed to sex-specific responses of body size to macro-environmental gradients (e.g. differential-plasticity hypothesis; Fairbairn, 2005; Stillwell *et al.*, 2007; Hu *et al.*, 2010). There is often a complex interaction between the environment, body size and natural selection (Blanckenhorn, 2005; Yu *et al.*, 2010), obscuring basic drivers of body size evolution. Moreover, several life-history traits (e.g. age, size of maturity and growth), which often covary with adult body size, can themselves vary along environmental gradients and between the sexes (Andrews, 1982; Congdon *et al.*, 1982; Fairbairn *et al.*, 2007). We found evidence of turtle SSD varying along a latitudinal gradient. For example, latitude was positively associated with turtle SSD; turtles displayed a male-biased SSD at low latitudes and increasingly female-biased SSD at higher latitudes. This pattern has also been noted in the literature for lizards (Fitch, 1981; Cox *et al.*, 2003), and an opposite but

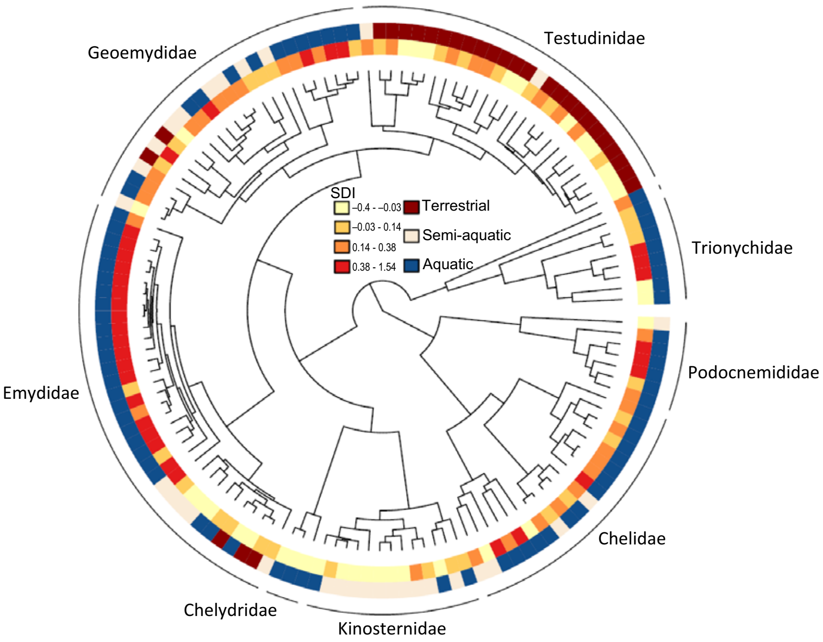

Fig. 3 Phylogeny of 135 turtle species included in phylogenetic least squares (PGLS) analysis. The inside row of colours represents sexual size dimorphism index (SDI) and is denoted by colour scale, and scale goes from male biased (light yellow) to female biased (red). The outside row represents habitat type (terrestrial = red; semi-aquatic = cream; and aquatic = blue).

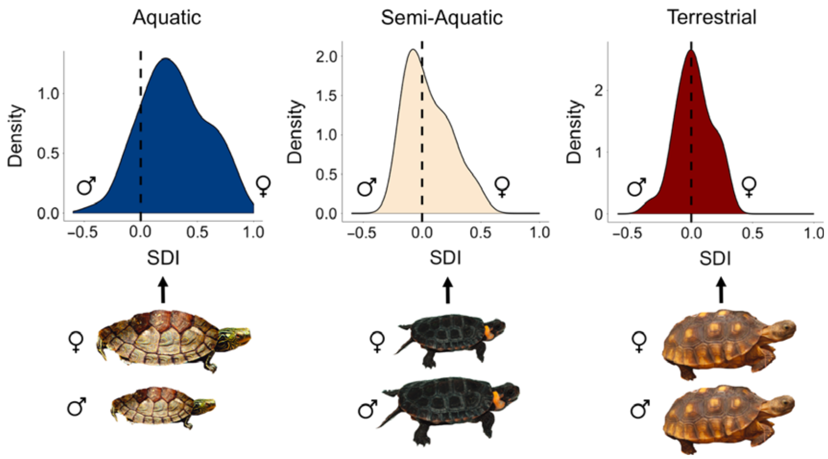

Fig. 4 Turtle sexual dimorphism index (SDI) variation among habitats. For habitat type, colour codes are denoted as follows, blue: aquatic; cream: semi-aquatic; and red: terrestrial. Relative size of the turtles in the figure represents the general sexual size dimorphism (SSD) trend in each of the habitat types presented.

strong latitudinal pattern was found among populations of painted turtles (Litzgus & Smith, 2010).

The latitudinal trend found in our study (i.e. larger females towards the poles) may result from at least two potential factors: fecundity advantage and environmental factors. Fecundity advantage, where female-biased SSD is related to higher latitudes, involves more offspring per reproductive bout during a short reproductive season (Cox *et al.*, 2003). Additionally, proximate environmental factors such as temperature and precipitation have sex-specific effects on selection, growth and potential timing of maturation within and among turtle species (Gibbons & Lovich, 1990). For instance, higher incubation temperatures may influence body size by affecting age at first reproduction (i.e. gonadal development; St. Clair, 1998). Conversely, geographic variation could be primarily influenced by phylogenetic conservatism, as some turtle species are associated with male-biased SSD at higher latitudes.

Latitudinal gradients are often systematically accompanied by strong environmental gradients, which can be the underlying forces driving body size variation among and within species (Cox *et al.*, 2007; Friedman & Remeš, 2016). Localized environmental conditions may differentially interact with each sex, thus influencing the development of SSD (Gibbons & Lovich, 1990), and generating geographic variation (Iverson, 1985). Multiple studies have noted that SSD variation is associated with environmental gradients (e.g. temperature, Stillwell & Fox (2007), Amarello *et al.* (2010), Lovich *et al.*, 2010, and Snover *et al.*, 2015, seasonality, Dobson & Wigginton (1996) and moisture, Stillwell *et al.* (2007)). Turtle SSD variation in our study was associated with precipitation and annual temperature variance, such that males were larger than females in wetter regions, and the opposite was true in areas with less temperature variability. Conversely, our models suggested that females were larger than males in arid regions and areas with greater temperature variability. Thus, a potential explanation that remains to be further investigated in turtles is that relatively wetter, more productive environments cause enhanced growth in males, and greater temperature variability causes enhanced growth in females. Interestingly, in sugar gliders (*Petaurus breviceps*), the degree of male-biased SSD increased along a precipitation and productivity gradient (Quin *et al.*, 1996), similar to our analyses here in turtles. The authors attributed the pattern to selection favouring males allocating the extra resources to growth and body size for greater success in male–male combat, whereas females may direct more energy towards reproduction – and not body size – to minimize energy costs during a reproduction event. Other examples of sex-specific climate-related responses in body size could be associated with resistance to desiccation (Stillwell *et al.*, 2007). In turtles, larger body sizes do equate to a lower surface-to-volume ratio and higher total water content (Finkler, 2001). Additionally, in aquatic turtle species with unique sex-specific movement ecology where one sex exhibits more frequent, longer, terrestrial movements, male-biased SSD could have evolved to increase the resistance to desiccation in the more mobile sex (usually males in turtles; Blanckenhorn, 2005; Lindeman, 2008). Finally, other taxa have also shown a relationship between SSD and precipitation and humidity, similar to the findings we report in turtles (e.g. frogs, Schauble, 2004 and beetles, Stillwell *et al.*, 2007).

The evolution of SSD in turtles may also be constrained by mechanisms such as allometry and traits shared by both males and females (Fairbairn, 1990; Fairbairn *et al.*, 2007; Kuntner & Elgar, 2014). For turtles, some families appear to follow an adaptive significance explanation for SSD (male–male combat or increased fecundity with female body size), whereas others (e.g. Emydids) may be constrained by allometry or nonadaptive significance (Fairbairn, 1990; Stephens & Wiens, 2009; Ceballos & Iverson, 2014). However, the extent to which the evolutionary history of a species influences SSD is poorly known (Fairbairn *et al.*, 2007), and only recently have studies examined nonadaptive mechanisms like differential timing of maturity while controlling for phylogenetic effects on SSD (Lovich *et al.*, 2014).

In conclusion, our study provides evidence that spatial variation of turtle SSD is primarily influenced and magnified by a combination of habitat type and proximate climatic factors (i.e. annual temperature variability and precipitation), and is constrained by phylogeny. Furthermore, our study reveals that the magnitude and direction of SSD covary with latitude prominently in Emydids and Geoemydids (i.e. increased female-biased SSD towards the poles), which suggests that the degree and direction of SSD may be plastic for turtles. While our study reaffirms the complexity of SSD evolution in turtles, it also supports the view that SSD variation among turtle species and across latitudinal gradients is most likely affected by sex-specific reproductive behaviour, fecundity advantage and sex-specific responses to environmental factors that differ among habitat types, species and systematically across latitude.

Acknowledgments

We thank Shannon Skalos, Andy Sih and Evan Eskew for comments on earlier drafts of the manuscript. We also thank Karen Estes and Todd Staley of the Tennessee Aquarium for their photos and/or assistance with Fig. 4. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

References

Akaike, H. 1974. A new look at the statistical model identification. *IEE Trans. Autom. Control* **19**: 716–723.

Amarello, M., Nowak, E.M., Taylor, E.N., Schuett, G.W., Repp, R.A., Rosen, P.C. *et al.* 2010. Potential environmental influences on variation in body size and sexual size dimorphism among Arizona populations of the western diamond-backed rattlesnake (*Crotalus atrox*). *J. Arid Environ.* **74**: 1443–1449.

Andersson, M. 1994. *Sexual Selection*. Princeton University Press, Princeton, NJ.

Andrews, R.M. 1982. Patterns of growth in reptiles. In: *Biology of the Reptilia* (C. Gans, ed.), pp. 273–320. Academic Press, New York, NY.

Angielczyk, K.D., Burroughs, R.W. & Feldman, C. 2015. Do turtles follow the rules? Latitudinal gradients in species richness, body size, and geographic range area of the world's turtles. *J. Exp. Zool. B Mol. Devel. Evol.* **324**: 270–294.

Ashton, K.G. & Feldman, C.R. 2003. Bergmann's rule in nonavian reptiles: turtles follow it, lizards and snakes reverse it. *Evolution* **57**: 1151–1163.

Bartoń, K. 2013. *MuMIn: Multi-model Inference*. R package version 1.9.13. The Comprehensive R Archive Network (CRAN), Vienna, Austria.

Berry, J.F. & Shine, R. 1980. Sexual size dimorphism and sexual selection in turtles (order Testudines). *Oecologia* **44**: 185–191.

Blanckenhorn, W.U. 2005. Behavioral causes and consequences of sexual size dimorphism. *Ethology* **111**: 977–1016.

Blanckenhorn, W.U., Stillwell, R.C., Young, K.A., Fox, C.W. & Ashton, K.G. 2006. When Rensch meets Bergmann: does sexual size dimorphism change systematically with latitude? *Evolution* **60**: 2004–2011.

Buhlmann, K.A., Akre, T.S., Iverson, J.B., Karapatakis, D., Mittermeier, R.A., Georges, A. *et al.* 2009. A global analysis of tortoise and freshwater turtle distributions with identification of priority conservation areas. *Chelonian Conserv. Biol.* **8**: 116–149.

Burnham, K.P. & Anderson, D.R. 2004. Multimodel inference understanding AIC and BIC in model selection. *Social. Method Res.* **33**: 261–304.

Butler, M.A., Schoener, T.W. & Losos, J.B. 2000. The relationship between sexual size dimorphism and habitat use in Greater Antillean Anolis lizards. *Evolution* **54**: 259–272.

Ceballos, C.P. & Iverson, J.B. 2014. Patterns of sexual dimorphism in Chelonia: revisiting Kinosternidae. *Biol. J. Linn. Soc.* **111**: 806–809.

Ceballos, C.P., Adams, D.C., Iverson, J.B. & Valenzuela, N. 2013. Phylogenetic patterns of sexual size dimorphism in turtles and their implications for Rensch's rule. *Evol. Biol.* **40**: 194–208.

Congdon, J.D., Dunham, A.E. & Tinkle, D.W. 1982. Energy budgets and life histories of reptiles. In: *Biology of the Reptilia* (C. Gans, ed.), pp. 233–271. Academic Press, New York, NY.

Cox, R.M., Skelly, S.L. & John-Alder, H.B. 2003. A comparative test of adaptive hypotheses for sexual size dimorphism in lizards. *Evolution* **57**: 1653–1669.

Cox, R.M., Zilberman, V. & John-Alder, H.B. 2006. Environmental sensitivity of sexual dimorphism: laboratory common garden removes effects of sex and castration on lizard growth. *Funct. Ecol.* **20**: 880–888.

Cox, R.M., Butler, M.A. & John-Adler, H.B. 2007. Sexual size dimorphism in reptiles. In: *Sex, Size, and Gender Roles: Evolutionary Studies of Sexual Size Dimorphism* (D.J. Fairbairn, W.U. Blanckenhorn & T. Szekely eds), pp. 38–49. Oxford University Press, Oxford, UK.

Cox, R.M., Stenquist, D.S. & Calsbeek, R. 2009. Testosterone, growth and the evolution of sexual size dimorphism. *J. Evol. Biol.* **22**: 1586–1598.

Darwin, C. 1871. *The Descent of Man and Selection in Relation to Sex*, 1st edn. John Murray, London, UK.

Development Core Team, R. 2015. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna.

Dobson, F.S. & Wigginton, J.D. 1996. Environmental influences on the sexual dimorphism in body size of western bobcats. *Oecologia* **108**: 610–616.

Ennen, J.R., Agha, M., Matamoros, W., Hazzard, S.C. & Lovich, J.E. 2016. Using climate, energy, and spatial-based hypotheses to interpret macroecological patterns of North America chelonians. *Can. J. Zool.* **94**: 453–461.

Ernst, C.H. & Lovich, J.E. 2009. *Turtles of the United States and Canada*. John Hopkins University Press, Baltimore, MD.

Ernst, C.H., Altenburg, R.G.M. & Barbour, R.W. 2007. Turtles of the world. http://wbd.etibioinformatics.nl/bis/turtles.php?menuentry=inleiding.

Fairbairn, D.J. 1990. Factors influencing sexual size dimorphism in temperate waterstriders. *Am. Nat.* **136**: 61–86.

Fairbairn, D.J. 2005. Allometry for sexual size dimorphism: testing two hypotheses for Rensch's rule in the water strider *Aquarius remigis*. *Am. Nat.* **166**: 69–84.

Fairbairn, D.J., Blanckenhorn, W.U. & Székely, T. (eds.). 2007. *Sex, Size, and Gender Roles: Evolutionary Studies of Sexual Size Dimorphism (Vol. 266)*. Oxford University Press, Oxford, UK.

Finkler, M.S. 2001. Rates of water loss and estimates of survival time under varying humidity in juvenile snapping turtles (*Chelydra serpentina*). *Copeia* **2**: 521–525.

Fitch, H.S. 1981. *Sexual Differences in Reptiles*. Misc. Publ. No. 70. University of Kansas Museum of Natural History, Lawrence, KS.

Friedman, N.R. & Remeš, V. 2016. Global geographic patterns of sexual size dimorphism in bird: support for a latitudinal trend? *Ecography* **39**: 17–25.

Ghiselin, M.T. 1974. *The Economy of Nature and the Evolution of Sex*. University of California Press, Berkeley, CA.

Gibbons, J.W. & Lovich, J.E. 1990. Sexual dimorphism in turtles with emphasis on the slider turtle (*Trachemys scripta*). *Herpetological Monographs* **1990**: 1–29.

Gibbons, J.W., Semlitsch, R.D., Greene, J.L. & Schubauer, J.P. 1981. Variation in age and size at maturity of the slider turtle (*Pseudemys scripta*). *Am. Nat.* **117**: 841–845.

Golubović, A., Bonnet, X., Djordjević, S., Djurakic, M. & Tomović, L. 2013. Variations in righting behaviour across Hermann's tortoise populations. *J. Zool.* **291**: 69–75.

Harmon, L.J., Weir, J.T., Brock, C.D., Glor, R.E. & Challenger, W. 2008. GEIGER: investigating evolutionary radiations. *Bioinformatics* **24**: 129–131.

Hu, Y., Xie, Y., Zhu, F., Wang, C. & Lei, C. 2010. Variation in sexual size dimorphism among populations: testing the differential-plasticity hypothesis. *Entomol. Exp. Appl.* **137**: 204–209.

Iverson, J.B. 1985. Geographic variation in sexual size dimorphism in the mud turtle *Kinosternon hirtipes*. *Copeia* **1985**: 388–393.

Iverson, J.B. 1992. Correlates of reproductive output in turtles (Order Testudines). *Herpetological Monographs* **6**: 25–42.

Iverson, J.B., Balgooyen, C.P., Byrd, K.K. & Lyddan, K.K. 1993. Latitudinal variation in egg and clutch size in turtles. *Can. J. Zool.* **71**: 2448–2461.

Jaffe, A.L., Slater, G.J. & Alfaro, M.E. 2011. The evolution of island gigantism and body size variation in tortoises and turtles. *Biol. Lett.* **7**: 558–561.

John-Alder, H.B., Cox, R.M. & Taylor, E.N. 2007. Proximate developmental mediators of sexual dimorphism in size. *Integr. Comp. Biol.* **47**: 258–271.

Joos, J., Kirchner, M., Vamberger, M., Kaviani, M., Rahimibashar, M.R., Fritz, U. *et al.* 2017. Climate and patterns of body size variation in the European pond turtle, *Emys orbicularis*. *Biol. J. Linn. Soc.* **122**: 351–365.

Joyce, W.G. & Gauthier, J.A. 2004. Palaeoecology of Triassic stem turtles sheds new light on turtle origins. *Proc. R Soc. London B. Biol. Sci.* **271**: 1–5.

Kamilar, J.M. & Cooper, N. 2013. Phylogenetic signal in primate behavior, ecology and life history. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **368**: 20120341.

Keevil, M.G., Hewitt, B.S., Brooks, R.J. & Litzgus, J.D. 2017. Patterns of intraspecific aggression inferred from injuries in an aquatic turtle with male-biased size dimorphism. *Can. J. Zool.* **95**: 393–403.

Kuntner, M. & Elgar, M.A. 2014. Evolution and maintenance of sexual size dimorphism: aligning phylogenetic and experimental evidence. *Front. Ecol. Evol.* **2**: 26.

Lindeman, P.V. 2003. Sexual difference in habitat use of Texas map turtles (*Emydidae: Graptemys versa*) and its relationship to size dimorphism and diet. *Can. J. Zool.* **81**: 1185–1191.

Lindeman, P.V. 2008. Evolution of body size in the map turtles and sawbacks (*Emydidae: Deirochelyinae: Graptemys*). *Herpetologica* **64**: 32–46.

Litzgus, J.D. & Smith, S.E. 2010. Geographic variation in sexual size dimorphism in painted turtles (*Chrysemys picta*). *J. Herpetol.* **44**: 320–326.

Losos, J.B. 2008. Phylogenetic niche conservatism, phylogenetic signal and the relationship between phylogenetic relatedness and ecological similarity among species. *Ecol. Lett.* **11**: 995–1003.

Lovich, J.E. & Ennen, J.R. 2013. A quantitative analysis of the state of knowledge of turtles of the United States and Canada. *Amphibia-Reptilia* **34**: 11–23.

Lovich, J.E. & Gibbons, J.W. 1992. A review of techniques for quantifying sexual size dimorphism. *Growth Dev. Aging* **56**: 269–281.

Lovich, J.E., Ernst, C.H., Zappalorti, R.T. & Herman, D.W. 1998. Geographic variation in growth and sexual size dimorphism of Bog Turtles (*Clemmys muhlenbergii*). *Am. Midl. Nat.* **139**: 69–78.

Lovich, J.E., Znari, M., Baamrane, M.A.A., Naimi, M. & Mostalih, A. 2010. Biphasic geographic variation in sexual size dimorphism of turtle (*Mauremys leprosa*) populations along an environmental gradient in Morocco. *Chelonian Conserv. Biol.* **9**: 45–53.

Lovich, J.E., Gibbons, J.W. & Agha, M. 2014. Does the timing of attainment of maturity influence sexual size dimorphism and adult sex ratio in turtles? *Biol. J. Linn. Soc.* **112**: 142–149.

Lubcke, G.M. & Wilson, D.S. 2007. Variation in shell morphology of the Western Pond Turtle (*Actinemys marmorata*) from three aquatic habitats in Northern California. *J. Herpetol.* **41**: 107–114.

Michael, D.R., Banks, S.C., Piggott, M.P., Cunningham, R.B., Crane, M., MacGregor, C. *et al.* 2014. Geographical variation in body size and sexual size dimorphism in an Australian Lizard, Boulenger's Skink (*Morethia boulengeri*). *PLoS ONE* **9**: e109830.

Mushinsky, H.R., Wilson, D.S. & McCoy, E.D. 1994. Growth and sexual dimorphism of *Gopherus polyphemus* in central Florida. *Herpetologica* **50**: 119–128.

Paradis, E. 2011. *Analysis of Phylogenetics and Evolution with R.* Springer Science & Business Media, New York, NY.

Paradis, E., Claude, J. & Strimmer, K. 2004. APE: Analyses of Phylogenetics and Evolution in R language. *Bioinformatics* **20**: 289–290.

Pearson, D., Shine, R. & Williams, A. 2002. Geographic variation in sexual size dimorphism within a single snake species (*Morelia spilota, Pythonidae*). *Oecologia* **131**: 418–426.

Pinheiro, J.C. & Bates, D.M. 2000. Linear mixed-effects models: basic concepts and examples. In: *Mixed-effects Models in S and S-Plus* (J. Chambers, W. Eddy, W. Härdle, S. Sheather & L. Tierney, eds), pp. 1–271. Springer, New York.

Purvis, A. 2008. Phylogenetic approaches to the study of extinction. *Annu. Rev. Ecol. Evol. Syst.* **39**: 301–319.

Quin, D.G., Smith, A.P. & Norton, T.W. 1996. Eco-geographic variation in size and sexual dimorphism in sugar gliders and squirrel gliders (Marsupialia: Petauridae). *Aust. J. Zool.* **44**: 19–45.

Revell, L.J. 2012. phytools: an R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.* **3**: 217–223.

Rhodin, A.G.J., van Dijk, P.P. & Parham, J. 2008. Conservation biology of freshwater turtles and tortoises. *Chel. Res. Mono.* **5**: 1–38.

Rödder, D., Lawing, A.M., Flecks, M., Ahmadzadeh, F., Dambach, J., Engler, J.O. *et al.* 2013. Evaluating the significance of paleophylogeographic species distribution models in reconstructing Quaternary range-shifts of Nearctic chelonians. *PLoS ONE* **8**: e72855.

Rostal, D.C., McCoy, E.D. & Mushinsky, H.R., eds. 2014. *Biology and Conservation of North American Tortoises*. John Hopkins University Press, Baltimore, MD.

Schauble, C.S. 2004. Variation in body size and sexual dimorphism across geographical and environmental space in the frogs *Limnodynastes tasmaniensis* and *L. peronii*. *Biol. J. Linn. Soc.* **82**: 39–56.

Smith, R.J. 1999. Statistics of sexual size dimorphism. *J. Hum. Evol.* **36**: 423–459.

Snover, M.L., Adams, M.J., Ashton, D.T., Bettaso, J.B. & Welsh, H.H. 2015. Evidence of counter-gradient growth in western pond turtles (Actinemys marmorata) across thermal gradients. *Freshwater Biol.* **60**: 1944–1963.

St. Clair, R.C.S. 1998. Patterns of growth and sexual size dimorphism in two species of box turtles with environmental sex determination. *Oecologia* **115**: 501–507.

Stamps, J.A. 1993. Sexual size dimorphism in species with asymptotic growth after maturity. *Biol. J. Linn. Soc.* **50**: 123–145.

Stephens, P.R. & Wiens, J.J. 2009. Evolution of sexual size dimorphisms in emydid turtles: ecological dimorphism, Rensch's rule, and sympatric divergence. *Evolution* **63**: 910–925.

Stillwell, R.C. & Fox, C.W. 2007. Environmental effects on sexual size dimorphism of a seed-feeding beetle. *Oecologia* **153**: 273–280.

Stillwell, R.C. & Fox, C.W. 2009. Geographic variation in body size, sexual size dimorphism and fitness components of a seed beetle: local adaptation versus phenotypic plasticity. *Oikos* **118**: 703–712.

Stillwell, R.C., Morse, G.E. & Fox, C.W. 2007. Geographic variation in body size and sexual size dimorphism of a seed-feeding beetle. *Am. Nat.* **170**: 358–369.

Tesche, M.R. & Hodges, K.E. 2015. Rethinking biogeographic patterns: high local variation in relation to latitudinal clines for a widely distributed species. *Oecologia* **179**: 139–149.

Van Dijk, P.P., Iverson, J.B., Shaffer, H.B., Bour, R. & Rhodin, A.G.J. 2014. Turtle Taxonomy Working Group: Turtles of the world, 2012 update: annotated checklist of taxonomy, synonymy, distribution, and conservation status. Conservation Biology of Freshwater Turtles and Tortoises: A Compilation Project of the IUCN/SSC Tortoise and Freshwater Turtle Specialist Group. Chelonian Research Monographs No, 5. http://www.iucn-tftsg.org/wp-content/uploads/file/Accounts/crm_5_000_checklist_v7_2014.pdf

Yu, B.-G., Zheng, R.-Q., Zhang, Y. & Liu, C.-T. 2010. Geographic variation in body size and sexual size dimorphism in the giant spiny frog *Paa spinosa* (David, 1875) (Anura: Ranoidae). *J. Nat. Hist.* **44**: 1729–1741.

Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A. & Smith, G.M. 2009. Mixed effects modelling for nested data. In: *Mixed Effects Models and Extensions in Ecology with R*, pp. 101–142. Springer, New York.

Supporting information

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

Table S1 AICc scores and weights from a 95% confidence set of linear mixed-effects models (LMM) that predict the direction of sexual size dimorphism in turtles.

Table S2 AICc scores and weights from a 95% confidence set of phylogenetic generalized least squares (PGLS) models that predict the direction of sexual size dimorphism in turtles.

Data deposited at Dryad: https://doi.org/10.5061/dryad.4hc42

Received 16 August 2017; accepted 6 December 2017