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Osmoregulatory ability predicts geographical range size in marine amniotes

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Species that are distributed over wide geographical ranges are likely to encounter a greater diversity of environmental conditions than do narrowly distributed taxa, and thus we expect a correlation between size of geographical range and breadth of physiological tolerances to abiotic challenges. That correlation could arise either because higher physiological capacity enables range expansion, or because widely distributed taxa experience more intense (but spatially variable) selection on physiological tolerances. The invasion of oceanic habitats by amniotic vertebrates provides an ideal system with which to test the predicted correlation between range size and physiological tolerances, because all three lineages that have secondarily moved into marine habitats (mammals, birds, reptiles) exhibit morphological and physiological adaptations to excrete excess salt. Our analyses of data on 62 species (19 mammals, 18 birds, 24 reptiles) confirm that more-widely distributed taxa encounter habitats with a wider range of salinities, and that they have higher osmoregulatory ability as determined by sodium concentrations in fluids expelled from salt-excreting organs. This result remains highly significant even in models that incorporate additional explanatory variables such as metabolic mode, body size and dietary habits. Physiological data thus may help to predict potential range size and perhaps a species' vulnerability to anthropogenic disturbance.

1. Introduction

Most major lineages of organisms contain species that vary in the geographical spread of their distribution; often, some taxa occur very widely whereas others are restricted to small areas (e.g. [1,2]). An extensive body of scientific literature has attempted to explain the causal factors underlying that diversity (e.g. level of spatial heterogeneity in abiotic or biotic factors; body size; behavioural flexibility [3–5]). Importantly, analyses of conservation threats identify the size of a species' range as a primary predictor of its vulnerability to decline and extinction (e.g. [6]). Thus, information on correlates of range size may facilitate our ability to predict conservation problems before declines occur (e.g. [7]).

One intriguing possibility is that we might find correlations between physiological traits and range size, for two reasons. First, a wide-ranging species is likely to encounter more extreme values for abiotic conditions (e.g. temperature, precipitation, salinity) simply because those conditions vary spatially; and hence, a larger distribution will expose the organism to a wider range of abiotic challenges. As a result, a species will only be able to expand its range over a large area if it is physiologically capable of dealing with those challenges. A narrow-range endemic does not face the same breath of challenges, and hence may have more limited physiological tolerance. Second, a larger range may impose spatially variable selection on physiological tolerances, such that we expect widespread taxa to evolve an ability

to deal with a wide range of challenges. Although those two hypotheses differ in the direction of causation (tolerance allows a large range versus a large range selects for tolerance), they make the same prediction. We expect that the extent of a species' geographical range should be positively correlated with its physiological capacity to deal with challenging abiotic conditions.

Secondarily marine tetrapods offer an ideal model system with which to test this idea. Three lineages (mammals, birds and non-avian reptiles) have evolved to exploit oceanic habitats, from an ancestral condition of terrestrial life. The ocean poses many novel challenges [8], but one of the most general and significant is the high salt concentration. Sodium chloride is inevitably taken into the body across permeable surfaces [9] and during feeding and incidental drinking [10–13], and marine tetrapods must be able to concentrate and expel excess salt if they are to survive [9]. Reflecting that strong selective force, all three oceanic radiations have been accompanied by the evolution of specialized salt-excreting structures (kidneys in mammals, salt glands in birds and reptiles, [14,15]). Nonetheless, excreting excess salt can entail significant energetic costs [9,14,16–18], and previous studies suggest that environmental and ecological factors affect the osmoregulatory ability of marine birds [19] and snakes [16]. For example, the efficiency of salt glands in marine snakes correlates with the size of the snakes' oceanic distributions and salinity levels within those distributions [20,21]. Previous studies have focused on a relatively limited number of taxa (i.e. snakes and birds), raising the issue of whether on a global level, oceanic salinity imposes significant energetic and hydric costs to air-breathing vertebrates. If so, salinity may influence habitat selection (i.e. selection of less saline areas) and thus geographical distribution across a broader phylogenetic diversity of marine vertebrates.

Based on the arguments we have developed above, we would therefore predict that more wide-ranging marine species (a) would encounter a wider range of salinity levels across their distributions; and (b) would exhibit a greater physiological capacity to excrete salt from the body. Previous analyses have suggested that additional factors such as body size, diet (herbivory–carnivory) and metabolic mode (ectothermy–endothermy) might also affect range size and/or physiological tolerances (e.g. [22,23]), so we included these traits in our analyses.

2. Material and methods

(a) Geographical range size

For 19 species of marine mammals and 24 species of reptiles (five turtles, seven crocodiles, 12 squamates) for which we had information on osmoregulatory abilities (see below), we used the IUCN Red List spatial dataset [24]. According to this dataset, a distribution range for a given species was defined by the combination of these IUCN codes:

- PRESENCE = 1 (Extant);
- ORIGIN 1 or 2 (Native or Reintroduced);
- SEASONAL less than 5 (excluding irregular presence).

For 18 species of birds for which we had information on osmoregulatory abilities (see below), we used the dataset from BirdLife International and Handbook of the Birds of the World [25]. A distribution range for a given species was defined by the combination of these IUCN codes:

- PRESENCE = 1 (Extant) OR PRESENCE = 5 (Extinct post 1500, no records in the last 30 years);

- ORIGIN 1 or 2 (Native or Reintroduced);
- SEASONAL less than 5 (excluding irregular presence).

Then, from this distribution range, we removed the inland areas corresponding to continents (obtained from the CIA World Data Bank II [26], implemented in the R package 'maps' [27]). Thus, we considered only marine areas (including coastal areas) of the geographical range of a given species.

(b) Oceanic salinity

Environmental data at the surface of the ocean (climatological annual and monthly mean salinity) were obtained from the World Ocean Atlas 2013 [28] at a resolution of 0.25 decimal degrees (downloaded at <https://www.nodc.noaa.gov/OC5/SELECT/woaselect/woaselect.html>). For each species, we extracted the annual mean, minimum and maximum value as well as the range (calculated as maximum minus minimum values) of salinity over its geographical range. We used the Practical Salinity Scale (pss) to quantify salinity levels.

All datasets were aggregated on rasters with a cell size of 0.25×0.25 decimal degrees, and area calculation was corrected by the real cell area according to latitude.

(c) Metabolic mode

We scored mammals and birds as endotherms, and reptiles as ectotherms. We note that some marine reptiles may be large enough, and have high-enough metabolic rates, to maintain relatively high body temperatures (e.g. [29]); however, the metabolic costs (and thus, rates of food intake) of ectotherms will always be far lower than those of comparable endotherms [30,31].

(d) Body size

We used body mass as an index of body size because of the highly variable morphology of the species under focus. Data on body size were extracted from published reports and the authors' unpublished data [32–36].

(e) Dietary habits

Diet was classified as carnivorous for species feeding mainly on animal prey (i.e. invertebrates, fish, squids, birds or mammals) or herbivorous for species feeding mainly on plants and/or algae (following [37]).

(f) Osmoregulatory ability

We used the concentration of sodium excreted as a proxy to quantify osmoregulatory ability. The ability of an animal to excrete excess salt depends on the rate of excretion, which in turn is the product of the concentration and the flow rate of excreted fluid. However, robust information on both of these variables was available only for a limited subset of species (electronic supplementary material, appendix S1). Importantly, comparisons using data from those species showed high correlations between the critical parameters (i.e. both rate of salt excretion and flow rate of excreted fluid were highly correlated with sodium concentration of the excreted fluids: electronic supplementary material, appendix S1). In consequence, we used measures of the concentration of sodium in excreted fluids to represent an organism's ability to excrete excess salt from the body.

For marine mammals that excrete excess sodium mostly via urine produced in the kidneys, we used data on sodium concentration in the urine as an index of osmoregulatory ability. For all marine mammalian species (including species that enter the ocean only occasionally), we extracted data from the review of Ortiz [14] as well as more recent studies [38,39]. We obtained

data on sodium concentration in the urine of 19 species of mammals (electronic supplementary material, appendix S2).

Marine reptiles *sensu lato* (i.e. including birds) rely on specialized extrarenal salt glands to excrete concentrated solutions of salt. We collated data on sodium concentration of the fluids excreted by salt glands from marine reptilian species with salt glands (including species that enter the ocean only occasionally) from various sources [15,40–53]. We obtained data on sodium concentration in the salt gland fluids of 18 species of birds, 12 species of sea snakes, five species of turtles and seven species of crocodiles (electronic supplementary material, appendix S2).

Sodium concentration in the fluids excreted by the salt glands of the only species of marine lizard (the marine iguana *Amblyrhynchus cristatus*) was very high (1434 mM, [54]) and was qualified as ‘subject to contamination in nasal passages’ by the author [54]. As a consequence, we discarded this species from our analyses.

In order to reduce the variability of data on sodium concentrations collected through various methodologies and settings (e.g. wild versus captivity), we selected the maximum values available in published literature.

(g) Statistical analyses

In order to account for phylogenetic correlation in explaining variations in concentration of sodium excreted across species, we performed phylogenetic linear regressions using the R package ‘*phylolm*’ v. 2.6 [55] and the R package ‘*phylopath*’ v. 1.1.2 [56]. Phylogenetic path analysis was used to quantitatively compare competing causal evolutionary hypotheses. This method analyses the relative importance of alternative causal models, including direct and indirect paths of influence among variables [57]. Electronic supplementary material, appendix S3 shows the different path models that were tested.

The phylogenetic tree used in our analyses was built using tools available from the TimeTree website ([58], electronic supplementary material, appendix S2).

As the mean concentration of sodium excreted differed between species that osmoregulate via kidneys versus salt glands (see results), we standardized sodium concentration within each mode of osmoregulation (kidney for mammals, salt glands for reptiles *sensu lato*, i.e. including birds). Data on body mass and geographical range size (marine areas only) were log-transformed for the analysis [22].

We used Pagel’s lambda model of evolution, assuming Brownian motion [59]. Best models were selected according to the C-statistic information criterion corrected for small sample sizes (CICc), with a difference ≥ 2 in CICc identifying the top model (Δ CICc) [60]. In the case of top-ranking models being equivalent (i.e. Δ CICc less than 2), we performed model-averaging and weighted models by their likelihood to estimate the final path coefficients. The full averaging method was used, whereby path coefficients that do not occur in all models shrink toward zero.

Two different sets of analyses were performed. First, we ran a global analysis including all species in our dataset. Second, we split our dataset according to the mode of osmoregulation (renal versus salt gland) and metabolic mode (endothermy versus ectothermy) resulting in three separate analyses: mammals (renal osmoregulation), birds (salt glands in endothermic species) and reptiles (salt glands in ectothermic species). In these cases, the phylogenetic tree was trimmed in order to fit with each subset of species.

Analyses were done using R v. 3.6.1 [61].

3. Results

(a) Geographical range size

Marine range sizes varied from 3939 to 345 975 965 km² among species. Within groups, mean range size was 104 498 046 km²

(min–max: 3939–345 975 965 km²) for mammals, 13 407 032 km² (7090–122 115 395 km²) for birds and 32 199 232 km² (6128–266 813 370 km²) for reptiles (145 913 449 km² (193 829–266 813 370 km²) for turtles, 26 044 (6128–104 833 km²) for crocodiles and 3 586 001 km² (6800–13 357 218 km²) for squamates).

(b) Oceanic salinity

Salinity at the ocean surface ranged from 4.9 to 42.1 pss among species. Within groups, mean salinity was 33.3 pss (min–max: 4.97–41.9 pss) for mammals, 30.3 pss (4.97–42.10 pss) for birds and 33.6 pss (5.0–41.9 pss) for reptiles (34.3 pss (5.0–41.9 pss) for turtles, 32.8 pss (13.2–37.4 pss) for crocodiles and 33.7 (13.36–41.8 pss) for squamates).

(c) Body size

Mean adult body mass ranged from 0.045 to 48 000 kg among species. Within groups, mean body mass was 7252.1 kg (min–max: 8.0–48 000 kg) for mammals, 2.3 kg (0.045–9.0 kg) for birds and 76.7 kg (0.1–600.0 kg) for reptiles (192.1 kg (0.6–600.0 kg) for turtles, 125.0 kg (17.0–272.0 kg) for crocodiles and 0.44 kg (0.1–1.06 kg) for squamates).

(d) Dietary habits

Overall, 13.2% of species were classified as herbivorous and the remaining 86.8% as carnivorous. Within groups, the proportion of herbivorous species was 5.5% (one species) for mammals, 26.3% (five species) for birds and 4.1% (one species) for reptiles (20% turtles, 0% crocodiles, 0% squamates).

(e) Osmoregulatory ability

The concentration of sodium excreted ranged from 28.2 to 1100 mmol l⁻¹ among species. Within groups, mean concentration of sodium excreted was 266.9 mmol l⁻¹ (min–max: 28.2–523.0 mmol l⁻¹) for mammals, 667.7 mmol l⁻¹ (263.0–1100.0 mmol l⁻¹) for birds and 635.7 mmol l⁻¹ (186.0–878.0 mmol l⁻¹) for reptiles (831.6 mmol l⁻¹ (760.0–878.0 mmol l⁻¹) for turtles, 527.8 mmol l⁻¹ (186.0–740.0 mmol l⁻¹) for crocodiles and 616.9 mmol l⁻¹ (414.0–798.0 mmol l⁻¹) for squamates).

(f) Tests of predictions

(i) More widespread species will encounter a greater range of salinities

Geographical marine range size was positively correlated with maximum salinity ($F_{1,58} = 19.53$, $r^2 = 0.25$, $p < 0.0001$, figure 1) and negatively correlated with minimum salinity ($F_{1,58} = 14.11$, $r^2 = 0.19$, $p = 0.0004$, figure 1). Range size was also positively correlated with the annual range of salinity ($F_{1,58} = 17.30$, $r^2 = 0.23$, $p = 0.0001$, figure 1) and with mean salinity ($F_{1,58} = 11.04$, $r^2 = 0.16$, $p = 0.001$, figure 1).

(ii) More widespread species will have higher osmoregulatory ability

Using multifactorial phylogenetic models, our results confirmed that factors such as metabolic mode, diet and body size affect geographical range size (as reported by previous studies, [22,23]), but that the relationship between range size and osmoregulatory ability remained highly significant

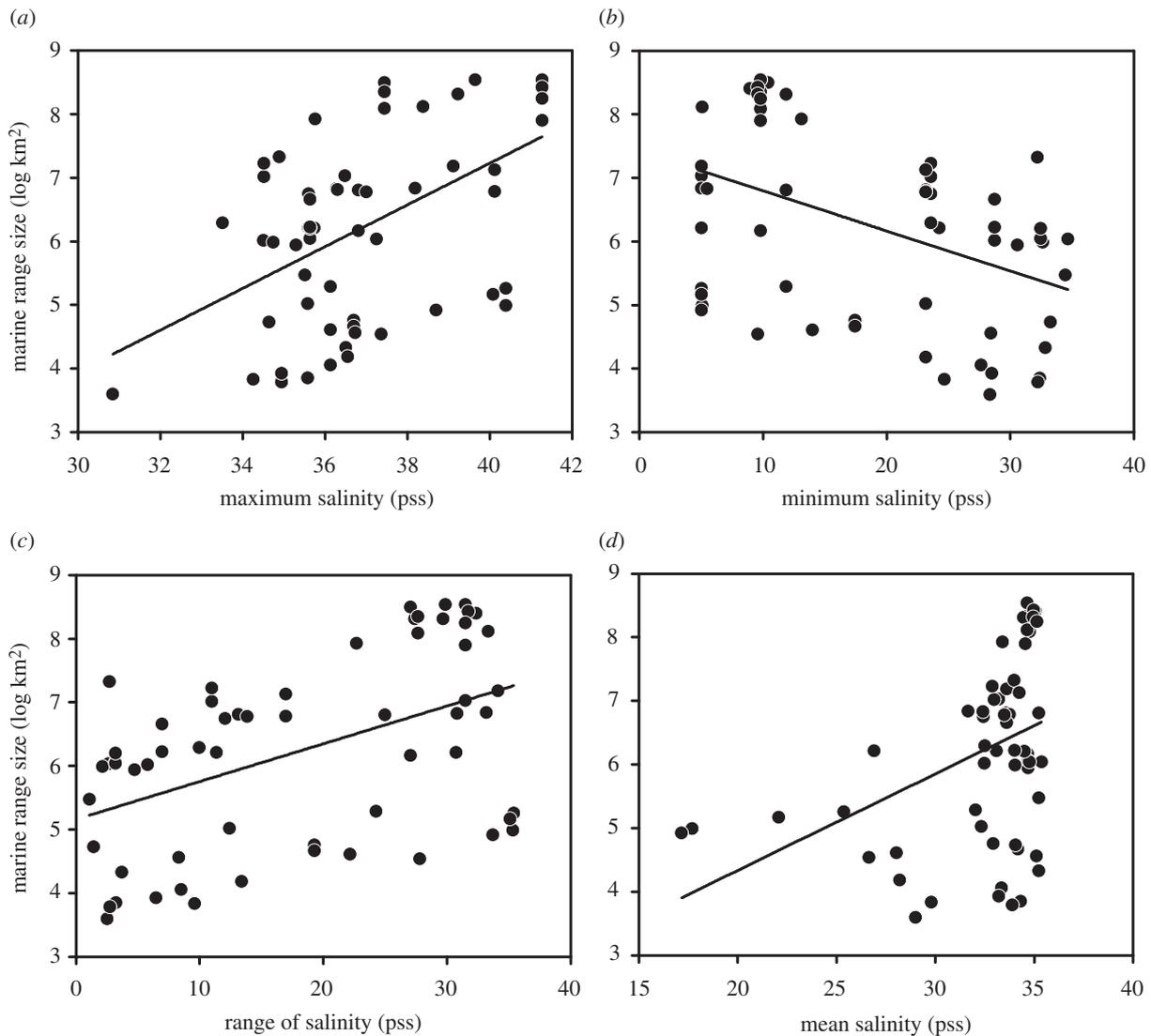


Figure 1. Relationships between maximum (a), minimum (b), range (c) and mean (d) salinity and geographical marine range size across the species included in our study. Each point represents data for a single species.

even after the effects of these additional factors were incorporated into our analyses.

(g) All species

According to model selection (table 1), a marine species' geographical marine range size was positively influenced by body mass (i.e. larger species had larger ranges, table 2), by metabolic mode (i.e. endothermic species had larger ranges, table 2), as well as by osmoregulatory ability (table 2). The area of a species' marine distribution was also affected by diet, either directly (herbivorous species had smaller ranges, table 2) or indirectly (through a negative effect of herbivory on the concentration of excreted sodium, table 2).

(h) Mammals (renal osmoregulation)

Both variables included in our model (body mass and sodium concentration in the urine) positively influenced the range sizes of marine mammals (tables 1 and 2, and figure 2).

(i) Birds (salt glands in endothermic species)

In birds, the size of marine distribution was positively influenced by osmoregulatory efficiency (tables 1 and 2, and

figure 2), negatively affected by body mass (table 2), and affected also by diet (i.e. herbivorous species had smaller ranges, table 2).

(j) Reptiles (salt glands in ectothermic species)

Both variables included in our model (body mass and sodium concentration excreted by the salt gland) positively influenced the range sizes of marine reptiles (tables 1 and 2, figure 2).

4. Discussion

In all three vertebrate lineages that we examined, larger geographical marine range sizes were associated with higher osmoregulatory ability. This result remained significant even after we added additional explanatory variables (such as metabolic mode, body size and diet) to our models. As predicted *a priori*, then, more widespread species encountered a wider range of oceanic salinities, and were physiologically better able to deal with excess salt loads.

The covariates we included in our analyses (metabolic mode, size, diet) all affect the size of area needed to provide enough resources to support an individual and are expected

Table 1. Results of model selection according to the groups (for all species, mammals (renal osmoregulation), birds (salt glands in endotherms) and reptiles (salt glands in ectotherms)). Number of conditional independencies (k), number of parameters estimated (q), C-statistic information (C), C-statistic information criterion with correction for small sample sizes (CICc), Δ CICc, likelihoods (l_i) and CICc weights (w_i) for each model tested. 'Na' stands for concentration of excess sodium excreted. Interactions are indicated by ''.

	models	k	q	C	p	CICc	Δ CICc	l_i	w_i
all species	Indirect.Diet	5	10	0.71	1	25.1	0	1	0.407321
	Direct	6	9	3.89	0.9853	25.4	0.312	0.85552	0.348471
	Full	4	11	0.13	1	27.5	2.408	0.30001	0.122201
	Indirect.Metabolism	5	10	3.12	0.9784	27.5	2.413	0.29926	0.121893
	Basic	7	8	22.7	0.0653	41.5	16.361	0.00028	0.000114
mammals	BodyMass.Na	1	5	0.68	0.7133	15.7	0	1	0.873
	BodyMass	2	4	8.45	0.0764	19.5	3.85	0.146	0.127
birds	BodyMass.Diet.Na	3	7	1.19	0.978	25.4	0	1	0.83
	BodyMass.Diet	4	6	10.41	0.237	29.4	4.05	0.1322	0.11
	Full	2	8	0.22	0.994	30.6	5.25	0.0723	0.06
reptiles	BodyMass.Na	1	5	0.16	0.923	13.5	0	1	0.767
	BodyMass	2	4	5.77	0.217	15.9	2.38	0.305	0.233

Table 2. Coefficients (values \pm s.e.) obtained by model averaging of the selected models for each group (for all species, mammals (renal osmoregulation), birds (salt glands in endotherms) and reptiles (salt glands in ectotherms)). 'Na' stands for concentration of excess sodium excreted and 'RSmar' stands for marine distribution range size.

group	effect	dependent variable	
		Na	log(RSmar)
all species	Metabolism	—	0.337 \pm 0.660
	log(BodyMass)	—	0.636 \pm 0.159
	Diet	-0.268 \pm 0.404	-0.441 \pm 0.344
	Na	—	0.364 \pm 0.086
mammals	log(BodyMass)	—	0.788 \pm 0.127
	Na	—	0.329 \pm 0.127
birds	Diet	—	-0.517 \pm 0.405
	log(BodyMass)	—	-0.175 \pm 0.184
	Na	—	0.556 \pm 0.188
reptiles	log(BodyMass)	—	0.630 \pm 0.238
	Na	—	0.255 \pm 0.129

to influence home range size, an effect that our results highlight at the species level. Body mass strongly influenced the area over which a species occurs, perhaps because individuals of larger species can move further [22]. In addition, body size positively influences diving ability (both the duration of apnoea and depth of dive: [31,62–65]), which in turn may broaden foraging habitat, and thus the oceanic areas available to these species. An exception to this relationship was observed in birds, where larger size was associated with smaller not wider distributions. Within this lineage, dispersal may be constrained in larger flightless species when compared with smaller flying seabirds.

Endothermic lineages (mammals and birds) that maintain elevated and relatively stable body temperatures can exploit both warm and cold water masses, and hence extend from polar to tropical areas [23]. Conversely, ectothermic species are unable to exploit water below their thermal optimum [23], and accordingly, most ectothermic marine tetrapods occur within tropical areas (e.g. [16,66], but see [29]). Similarly to metabolic mode, diet (i.e. herbivory versus carnivory) also influenced distribution range, both globally and when restricting the analysis to birds (low number of herbivorous species in mammals (West Indian manatee solely) and reptiles (green sea turtle solely) precluded these analyses in these lineages). Because the depth of light penetration restricts the availability of algae and seagrass to shallow waters [67], herbivorous species are constrained to specific habitats for foraging.

The most novel result of our analyses is that osmoregulatory ability is positively associated with the marine distribution ranges of tetrapods both globally and within each of the groups that we analysed (see also [20,21], for examples restricted to marine snakes). The mechanistic basis for this relationship probably involves the energetic costs of excreting excess salt [9,14,18], as described for two lineages of marine tetrapods (birds: [17,18,68]; snakes: [16]) and are likely to occur in other taxa also [9,14]. Because occupancy of a large oceanic area increases the range of salinity levels encountered, a larger marine distribution is likely to increase the costs of maintaining hydro-mineral balance.

Understanding the proximate mechanisms that link environmental variation to species responses can provide a strong (and general) basis for accurate predictions [69,70]. In our investigations, however, causation remains unclear: does geographical range drive physiological abilities, or does physiology drive geographical range? Further studies are required to tease apart these two competing hypotheses, exploiting the opportunity to identify causation via phylogenetic signals. For example, if high osmoregulatory ability typifies an entire phylogenetic lineage, then variation in range size within members of that group cannot be attributed to variation in

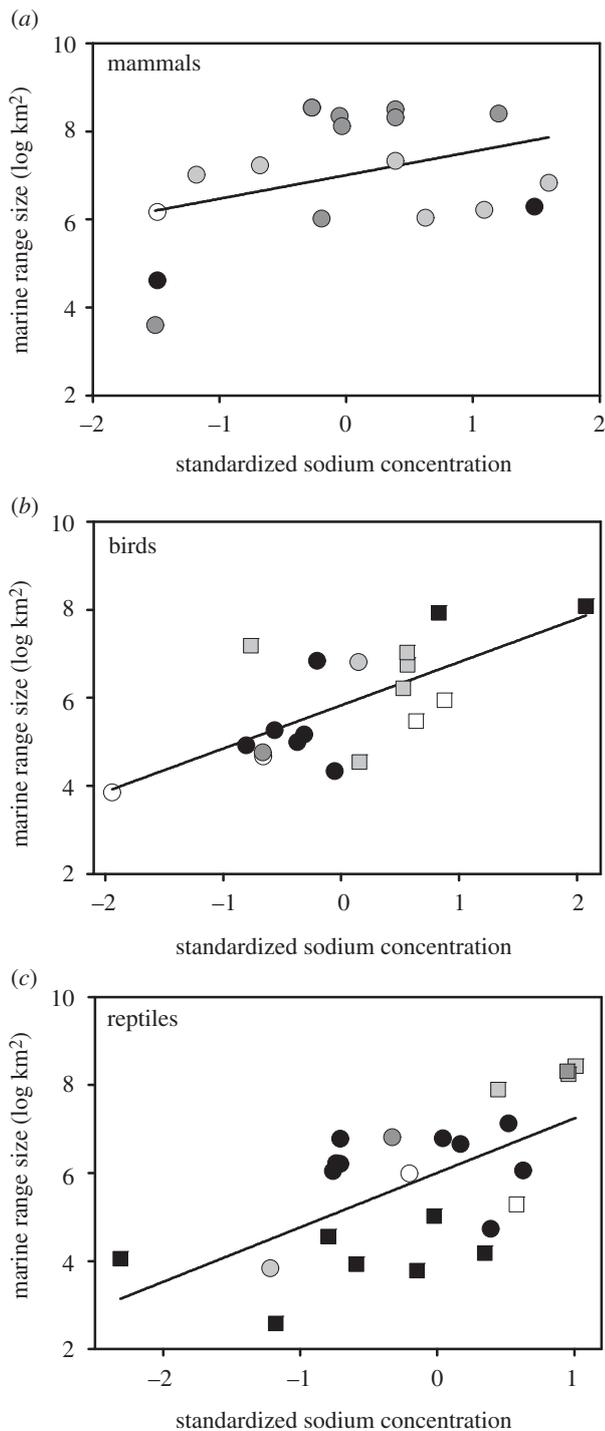


Figure 2. The relationship between osmoregulatory ability (standardized sodium concentration in the urine for mammals (a) or secreted by the salt gland for birds and reptiles (b,c)) and the size of the geographical marine range in tetrapods. For mammals (a), symbols as follows: black for Mustelids, light grey for Pinnipeds, dark grey for Cetaceans and white for Sirenia. For birds (b), symbols as follows: circles: black for Anseriforms, white for Gruiforms, light grey for Pelecaniforms, dark grey for Phalacrocoracidae; squares: black for Procellariiforms, white for Sphenisciforms, light grey for Charadriiforms. For reptiles (c), symbols as follows: circles: black for sea snakes, white for sea kraits, light grey for Homalopsid snakes, dark grey for Acrochordid snakes; squares: black for Crocodylians, white for Emydidae turtles, light grey for Cheloniidae sea turtles and dark grey for Dermochelyidae. Each point represents data for a single species.

physiological capacities. That is, a capacity to excrete excess salt might be necessary but not sufficient to promote geographical expansion. By contrast, a tight link between

salt-excreting traits and range sizes in comparisons among closely related species would suggest a strong functional relationship. Osmoregulatory ability has been predicted to constrain geographical range size in marine snakes [20,21], and this approach could be usefully extended to other marine taxa in order to unequivocally identify causation.

Further investigations are required in order to assess how fine-scale variation in the ecology of marine tetrapods interacts with osmoregulatory abilities. For example, more detailed explorations of osmoregulatory costs associated with prey type (e.g. isosmotic invertebrate versus hyposmotic vertebrate prey) could clarify how dietary influences on osmoregulation affect range size. Similarly, osmoregulatory organs (and thus salinity tolerance) exhibit a high degree of phenotypic flexibility, notably as a function of access to freshwater sources and behavioural osmoregulation (freshwater drinking, [19]). Many secondarily marine tetrapods are amphibious and commute between the marine realm and terrestrial environments (where freshwater is available). Species that are better able to acquire freshwater on land, and thus tolerate dehydration, may display greater environmental tolerances, and hence geographical distributions [21]. In addition, other environmental characteristics may influence osmoregulatory processes. For example, high environmental temperatures increase evaporative water loss. Accordingly, temperature and salinity both influence osmoregulation in shorebirds [19] and environmental tolerances in marine snakes [21]. Given our results and current changes in climatic conditions (see below), interactive influences of salinity and temperature are expected to strongly affect geographical range size of marine tetrapods.

Finally, our results can be used to improve our ability to predict responses relevant to conservation, a critical issue at a time when current environmental conditions are changing [71]. Although most of the scientific research dealing with the consequences of climate change in marine areas has focused on variation in oceanic temperature [72], our study emphasizes a major role for salinity, a parameter whose biological effects have attracted far less attention [16,18,20,21]. The salinity of several marine areas has already been affected by climate change [73,74], suggesting that we need to understand how changes in oceanic salinity may affect the energy budgets of marine species—and hence, may imperil the persistence of populations and curtail the geographical distribution of marine tetrapods. Given the costs associated with osmoregulation in other marine taxa (e.g. fish, [13]), we need to consider this critical parameter if we are to accurately predict the consequences of climate change for marine biodiversity.

Data accessibility. The dataset supporting this article has been uploaded as part of the electronic supplementary material.

Authors' contributions. F.B. proposed the initial idea and together with H.B.L. and R.S. contributed to its development. F.B. and D.P. collated the data and performed the analyses with input from H.B.L. and R.S. All authors discussed the results, and substantially contributed to the writing. All authors gave final approval for publication and agree to be held accountable for the work performed therein.

Competing interests. We declare we have no competing interests.

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