



Northward Shifts of the Distributions of Spanish Reptiles in Association with Climate Change

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Abstract: *It is predicted that climate change will drive extinctions of some reptiles and that the number of these extinctions will depend on whether reptiles are able to change their distribution. Whether the latitudinal distribution of reptiles may change in response to increases in temperature is unknown. We used data on reptile distributions collected during the 20th century to analyze whether changes in the distributions of reptiles in Spain are associated with increases in temperature. We controlled for biases in sampling effort and found a mean, statistically significant, northward shift of the northern extent of reptile distributions of about 15.2 km from 1940–1975 to 1991–2005. The southern extent of the distributions did not change significantly. Thus, our results suggest that the latitudinal distributions of reptiles may be changing in response to climate change.*

Keywords: climate-change impact, distribution changes, Spain, spatial distribution

Cambios Hacia el Norte en las Distribuciones de Reptiles Españoles en Asociación con el Cambio Climático

Resumen: *Se ha pronosticado que el cambio climático influirá en la extinción de algunos reptiles y que el número de esas extinciones dependerá de la capacidad de los reptiles para cambiar su distribución. Se desconoce si cambiará la distribución latitudinal de reptiles como respuesta a los incrementos de temperatura. Utilizamos datos de distribución de reptiles recolectados durante el siglo 20 para analizar si los cambios en la distribución de reptiles en España están asociados con incrementos de la temperatura. Controlamos los sesgos en el esfuerzo de muestreo y encontramos un cambio significativo, de 15.2 km, hacia el norte de la extensión norteña de las distribuciones de reptiles de 1940–1975 a 1991–2005. La extensión sureña de las distribuciones no cambió significativamente. Por lo tanto, nuestros resultados sugieren que las distribuciones latitudinales de reptiles pueden estar cambiando en respuesta al cambio climático.*

Palabras Clave: cambios de distribución, distribución espacial, España, impacto del cambio climático

Introduction

Ectothermic animals, in which biological and ecological processes are more dependent on environmental temperature than in endothermic animals, are assumed to have a higher probability of extinction in response to climate change than endothermic animals (Huey et al. 2009; Aragón et al. 2010). In fact, climate change is associated with the extirpation of several reptile populations

(Whitfield et al. 2007; Reading et al. 2010; Sinervo et al. 2010).

Species are more likely to change their distributions in response to climate change than to adapt to climate change in situ because current climate change may be too fast for genetic adaptation to occur (Bradshaw & Holzapfel 2006). Therefore, the number of extinctions will depend strongly on species' capacities to change their distributions (Foden et al. 2008). Low dispersal ability of

species and geographic barriers to movement are likely to increase extinction risk for some species (Massot et al. 2008). For example, it is estimated that 59% and 98% of South African and European reptiles, respectively, will become extinct or will undergo range retraction if they cannot change their distributions, whereas if they can migrate, extinctions will be 0% and 35%, respectively (Thomas et al. 2004; Araújo et al. 2006). If one assumes Iberian herptiles cannot migrate, then the distributions of 92% of Iberian reptiles and amphibians are predicted to contract, and 3% of the species will become extinct. If one assumes an unlimited capacity to migrate, it is estimated that the distributions of 46% of species will contract, whereas the distributions of 28% could increase (Carvalho et al. 2010).

Potential changes in spatial distribution in response to increases in temperature have been examined many times for a number of taxonomic groups (reviews in Walther et al. 2002; Root et al. 2003; Parmesan 2006). However, the few studies on this topic for reptiles are limited primarily to the examination of elevational changes in restricted geographic areas (Pounds et al. 1999; Raxworthy et al. 2008). As far as we know, only Hickling et al. (2006) analyzed changes in latitudinal distributions. They found that the distribution limits of two reptiles (*Lacerta agilis* and *Natrix natrix*) in the United Kingdom are not changing as temperature increases.

Some models predict that the effects of climate change on reptiles will be particularly acute in the Mediterranean in general and in the Iberian Peninsula in particular (Sala et al. 2000; Araújo et al. 2006; Thuiller et al. 2011; but see Deutsch et al. 2008). The temperature increased (approximately 0.3 °C) in the Iberian Peninsula during the 20th century, especially during the last 20 years of the century (Hulme & Sheard 1999; Jones et al. 1999). We used data on the distributions of reptiles in Spain during the 20th century to analyze whether the distributions of these reptiles have changed as climate has changed. We compared the distributions of reptile species before 1975 (year when the current period of warming began [IPCC 2007]) with distributions during 1991–2005.

Methods

Our data set included records of reptiles in Spain compiled by members of the Spanish Herpetological Society from 1940 to 2005. Sixty-five experts on specific species removed possible duplicates and erroneous records while they were compiling the Spanish herpetological atlas of amphibian and reptiles. They contacted authors of particular records when necessary (Pleguezuelos et al. 2002). We revised records for 2002–2005. With 97,494 final records, we believe this is one of the most complete national data sets of reptile distributions. Each record includes the geographic coordinates and the date

of observation. Nevertheless, records were collected opportunistically. For this reason, we controlled for variation in sampling effort (e.g., Tryjanowski & Sparks 2001).

In our analyses, we included only species that were found in at least 20 of the 5070 10×10 km cells that are fully within Spain, defined on the basis of Universal Transverse Mercator Units (UTMs) (ETRS89 UTM 30N), before 1975. We omitted 15 species that occur in Spain but did not meet this criterion, which reduced the sample to 30 species (Supporting Information). We estimated the latitudinal distribution of each species in Spain before 1940–1975 as the mean of the latitude of the centroid of the 10 northernmost and southernmost cells occupied by the species (Thomas & Lennon 1999; Brommer 2004; Hickling et al. 2006). When we estimated the latitudinal distribution on the basis of the 20 northernmost and the 20 southernmost grid cells, the estimated shift of the northern extent of the distribution was quantitatively similar (data not shown). We used the same method to calculate latitudinal distributions from records for 1991–2005. We calculated the change in the mean latitude of the northern cells and the change in the mean latitude of the southern cells of each species' distribution between the two periods. We used a single-sample *t* test to determine whether such variation was significantly >0 km.

A significant northward shift of the northern extent of a distribution may be indicative of a response to climate change, but also may be a consequence of an expansion unrelated to climate change or an increase in sampling effort (e.g., Tryjanowski et al. 2005). To control for a range expansion unrelated to climate change, we regressed the change in latitudinal distribution in kilometers against the change in the number of occupied cells (Thomas & Lennon 1999; Brommer 2004; Zuckerberg et al. 2009). The intercept of the regression line with the y-axis indicates the effective shift in the range, controlled for changes in the area occupied by the species, and the *t* test indicates whether such a shift differs significantly from zero (Zuckerberg et al. 2009).

This method has been widely used to examine changes in the distribution of birds. However, it may be ineffective with species for which the precise distribution is difficult to determine because the species is cryptic, as in the case of reptiles. If distributional data include many false negatives, an increase in the number of cells occupied does not necessarily indicate range expansion because the new cells may be in the center of the distribution. In our data set, the relation between the increase in number of occupied cells and the shift of the northern extent of the distribution was not statistically significant ($r = 0.01$, $p = 0.97$).

In contrast, the increase in number of records was significantly correlated with the shifts in the northern extent of the distribution (see the Results section). Therefore, to control for the change in sampling effort between the two study periods, we regressed the shift in the northern

extent of the distribution against the change in the number of records (each species was a replicate). Linear regression provided the best fit to the data; logarithmic and polynomial regressions yielded poorer fits. In the northern hemisphere when one controls for sampling effort, a response to climate change is suggested if there is a significant increase in the northern extent of the distribution, without significant changes in the southern extent of the distribution. If the northern and southern extents of a species distribution show a significant change (northward and southward, respectively), the most parsimonious explanation is an expansion of range that is independent of climate change. Therefore, we included a test of alternative explanations for a change in distribution (Sparks & Tryjanowski 2005).

A significant expansion of the northern extent of the distribution could also reflect a latitudinal bias in sampling effort, for example, if sampling effort was greater in the northern half of Spain during 1991–2005 than before 1975 or was greater in the south before 1975 than 1991–2005. We examined whether the geographic distribution of records differed in the two study periods with respect to the latitudinal center of Spain (44°69'695" N) with a single-sample *t* test. We also examined possible bias due to phylogeny, given that 19 out of 30 species were the families Colubridae and Lacertidae. If these families are prone to shift their distributions in response to changes in climate, this might bias results. We used analysis of variance to examine whether the distance the northern extent of the distribution shifted northward varied among families. Moreover, we tested whether the range of distribution of species reflected spatial autocorrelation at distances from 10 to 1000 km. We estimated Moran's *I* for the changes in the northern extent of the distribution with SAM 4.0 program (Rangel et al. 2010). We also tested whether mean elevation of the records varied between the two periods by comparing mean elevation with a *t* test.

We examined whether the shift in latitudinal distribution varied as a function of occupied latitude because it may be that southern species are more likely to move northward than northern species. In Spain northward movement of northern species is constrained by the Cantabrian Sea and the Pyrenees Mountains. We regressed the change in the northern extent of distributions against the latitudinal extent of species in 1940–1975 and included change in sampling effort as a covariate. We also examined whether the distance the northern latitudinal range of species changed was associated with biological variables. Larger species or those with higher breeding rates may have greater capacity to shift their ranges in response to environmental changes. We regressed the change in latitudinal extent against body size and breeding rate (data in Supporting Information) while controlling for the change in sampling effort. Data on body size and breeding rate were taken from Salvador and Pleguezuelos (2002).

In each statistical model, we used a Shapiro-Wilk test to examine whether the residuals were normally distributed (Quinn & Keough 2002). All tests were 2-tailed, and α was 0.05.

Results

Between 1940–1975 and 1991–2005, without controlling for sampling effort, the northern extent of the distribution of reptiles in Spain shifted significantly ($t_{29} = 7.6, p < 0.001$) northward (mean [SE] = 47.7 km [6.3]) (Fig. 1). The northern extent of the distribution of all species, except for *Lacerta bilineata*, shifted northwards ($z = 4.93, p < 0.001$). The number of records was positively correlated with the distance by which the northern extent of the distribution expanded ($r = 0.75, p < 0.001$). After controlling for sampling effort, the change in the

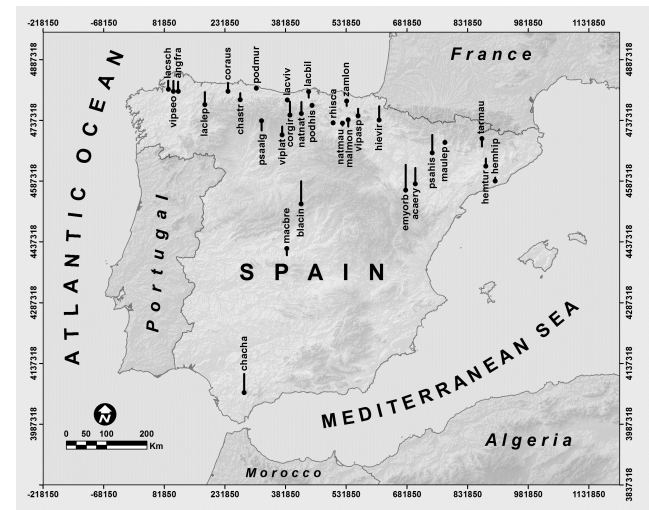


Figure 1. Linear changes in the northern extent of the distribution of 30 reptile species in Spain after controlling for sampling effort (dots, latitudinal centroids of the northern range 1940–1975; *acaery*, *Acanthodactylus erythrurus*; *angfra*, *Anguis fragilis*; *blacin*, *Blanus cinereus*; *chastri*, *Chalcides striatus*; *chacha*, *Chamaeleo chamaeleon*; *coraus*, *Coronella austriaca*; *corgir*, *Coronella girondica*; *emyorb*, *Emys orbicularis*; *bemtur*, *Hemidactylus turcicus*; *bembip*, *Hemorrhois hippocrepis*; *bievir*, *Hierophis viridiflavus*; *lacbil*, *Lacerta bilineata*; *lacsch*, *Lacerta schreiberi*; *macbre*, *Macroprotodon brevis*; *malmon*, *Malpolon monspessulanus*; *maulep*, *Mauremys leprosa*; *natmau*, *Natrix maura*; *natnat*, *Natrix natrix*; *podbis*, *Podarcis hispanica*; *podmur*, *Podarcis muralis*; *psaalg*, *Psammmodromus algirus*; *psabis*, *Psammmodromus hispanicus*; *rbisca*, *Rhinechis scalaris*; *tarmau*, *Tarentola mauritanica*; *timlep*, *Timon lepidus*; *vipasasp*, *Vipera aspis*; *viplat*, *Vipera latastei*; *vipseo*, *Vipera seoanei*; *zamlon*, *Zamenis longissimus*; *zooviv*, *Zootoca vivipara*).

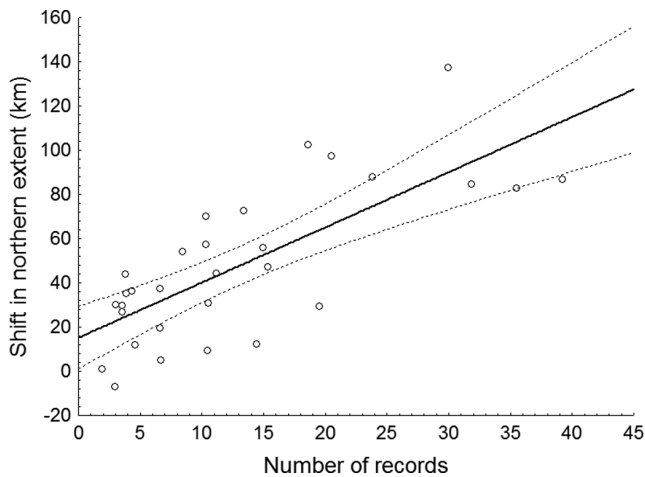


Figure 2. Results of a linear regression of the distance the northern extent of reptiles in Spain changed between 1940–1975 and 1991–2005 relative to sampling effort (number of records). The intercept with the y-axis indicates the magnitude of the northward shift between 1940–1975 and 1991–2005 when sampling effort is controlled. The dashed lines are the 95% CIs.

northward extent of the distribution was much smaller (15.2 km [6.9]) (Fig. 2), but remained significantly >0 ($t_{28} = 2.2$, $p = 0.04$). The southern extent of the distribution of reptiles also appeared to expand when we did not control for sampling effort ($t_{29} = 6.0$, $p < 0.001$), but not when we controlled for sampling effort ($t_{28} = 1.7$, $p = 0.11$). The shift in the southern extent of the distribution was also correlated positively with sampling effort ($r = 0.54$, $p < 0.01$). When we controlled for sampling effort, the northern extent of the distribution of 22 of 30 species increased significantly ($z = 2.37$, $p = 0.02$). Shifts both northward and southward of the northern and southern extents of the distributions, respectively, were significantly correlated ($r = 0.59$, $p = 0.001$). The shift northward of the northern extent of the distributions remained significant when controlling for the southward shift of the southern extent of the distributions ($t_{28} = 3.3$, $p < 0.01$). However, the shift of the southern extent of the distributions did not remain significant when we controlled for the shift northward of the northern extent of the distributions ($t_{28} = 1.1$, $p = 0.27$). Therefore, anything that caused the extension of the southern distributions did not completely account for the extension of the northern distributions.

From 1940–1975, sampling was biased toward northern Spain; average latitude of records was 4539842 N ($t_{29} = 2.2$, $p = 0.03$), but from 1991–2005, the average latitude of records (4480117 N) did not significantly differ from the average latitude of the study area (4469695 N) ($t_{29} = 0.3$, $p = 0.77$). Therefore, the northward shift

of the northern extent of the distribution was not an artifact of sampling bias. The distance by which the extent of the northern distribution shifted did not vary significantly among families of reptiles ($F_{9,20} = 1.57$, $p = 0.19$). Northern extents within Spain of the distributions of Colubridae and Lacertidae changed the least among families (mean [SE] = 8.34 km [6.68] and 10.92 km [7.04], respectively); these changes were below the average for all reptiles. This result suggests that the proportion of recorded species from these families did not bias the results. Moreover, the northern distributions were not spatially autocorrelated (Moran's $I < 0.2$; $p > 0.2$ for every distance). Mean elevation of the records did not vary between 1940–1975 and 1991–2005 (mean = -2.9 m [19.0]; $t_{29} = 0.1$, $p = 0.89$).

The distance by which the northern extent of the distributional range shifted north was correlated with the location of the northern range in 1940–1975. The northern extents of the distributions of species with southernmost mean distributions shifted northward by greater distances, whereas the distance of the shift lessened as the mean latitude of the species distribution occurred farther north ($\beta = -0.32$, $F_{1,27} = 5.27$, $p = 0.03$; effect of sampling effort: $F_{1,27} = 17.37$, $p < 0.001$). The shift in the northernmost latitudinal extent was not related to body size ($F_{1,27} = 1.18$, $p = 0.29$) or breeding rate ($F_{1,27} = 0.23$, $p = 0.64$).

Discussion

After controlling for sampling effort, geographic bias in sampling, phylogeny, and spatial autocorrelation, the northern limits of the distribution of reptiles in Spain shifted northward between 1940–1975 and 1991–2005. Given that in general populations of the species we examined are declining (Pleguezuelos et al. 2002), this shift in distribution is unlikely to be associated with expansions in the area occupied by the species. Our results are consistent with this idea because there was no similar shift southward in the southern limits of species' ranges. Moreover, the magnitude of the change in northern range limits increased as the northern limit of species became more southerly, probably because the shifts in ranges of species in northern Spain were constrained by the Cantabrian Sea and Pyrenees Mountains.

The mean latitude of the ranges of the species we examined shifted northward by an equivalent of 0.5 km/year [SE 0.2], which is similar to the magnitude of range shifts in other taxonomic groups (Parmesan & Yohe 2003). Assuming that this rate of movement is consistent among years, such a shift is plausible because reptiles in Spain have a dispersal capacity >0.5 km/year (e.g., Galán 1999; Ayres & Cordero 2007; Martínez-Freiria et al. 2010; Supporting Information). Hickling et al. (2006) found

that the northern range limits of 16 taxonomic groups of vertebrates and invertebrates increased by a mean of between 1.3 and 2.6 km/year in the United Kingdom by the end of the 20th century. They found that the northern range limits of birds have changed the least, whereas those of groups that are less mobile, such as Diplopoda or Isopoda, have higher rates of distributional change. Results of other studies suggest that changes in the distribution of birds (0.6–5.4 km/year) are similar to or slightly greater than changes in the distribution of other taxonomic groups (e.g., Hitch & Leberg 2007; La Sorte & Thompson 2007; Devictor et al. 2008). These results suggest that the rate at which species move northward is not limited exclusively by their dispersal capacity but also by other factors, such as the distribution of habitat (Hill et al. 2001; Menéndez et al. 2006; Devictor et al. 2008). We found no relation between biological traits presumably related to dispersal capacity (body size, breeding rate) and the magnitude of range shift.

Results of previous studies show changes in reptiles' elevational distribution in mountains (Pounds et al. 1999; Raxworthy et al. 2008) and changes in phenology and fitness in response to increases in temperature (e.g., Bull & Burzacott 2002; Chamaillé-Jammes et al. 2006; Moreno-Rueda et al. 2009), but studies of changes in latitudinal distribution over large extents included a limited number of species and have had conflicting results (Hickling et al. 2006). We are the first to show there is a correlation between changes in latitudinal distribution and increases in temperature for a wide variety of species of reptiles in Spain. Studies for which results show a northward shift of species' ranges in a variety of taxonomic groups have been conducted primarily in North America and northern Europe (Sanz 2002), whereas studies in Spain have been limited to a few species (e.g., Carrillo et al. 2007). Species' responses to increases in temperature may vary latitudinally (Parmesan 2007; Deutsch et al. 2008). Our results suggest that species in Mediterranean environments may also shift their distributions in response to rising temperatures.

Our finding that reptiles are expanding their northern ranges, potentially in response to climate change, could mean the probability of extinction associated with increases in temperature may be lower than expected. However, the capacity of response among reptiles is not necessarily related to their dispersal capacity and it may be constrained by geographic barriers.

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Supporting Information

The list of the species used in this study and data on body size, breeding rate, and movement capacity (Appendix S1) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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