



Late Quaternary reptile extinctions: size matters, insularity dominates

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ABSTRACT

Aim A major Late Quaternary vertebrate extinction event affected mostly large-bodied 'megafauna'. This is well documented in both mammals and birds, but evidence of a similar trend in reptiles is scant. We assess the relationship between body size and Late Quaternary extinction in reptiles at the global level.

Location Global.

Methods We compile a body size database for all 82 reptile species that are known to have gone extinct during the last 50,000 years and compare them with the sizes of 10,090 extant reptile species (97% of known extant diversity). We assess the body size distributions in the major reptile groups: crocodiles, lizards, snakes and turtles, while testing and correcting for a size bias in the fossil record. We examine geographical biases in extinction by contrasting mainland and insular reptile assemblages, and testing for biases within regions and then globally by using geographically weighted models.

Results Extinct reptiles were larger than extant ones, but there was considerable variation in extinction size biases among groups. Extinct lizards and turtles were large, extinct crocodiles were small and there was no trend in snakes. Lizard lineages vary in the way their extinction is related to size. Extinctions were particularly prevalent on islands, with 73 of the 82 extinct species being island endemics. Four others occurred in Australia. The fossil record is biased towards large-bodied reptiles, but extinct lizards were larger than extant ones even after we account for this.

Main conclusions Body size played a complex role in the extinction of Late Quaternary reptiles. Larger lizard and turtle species were clearly more affected by extinction mechanisms such as over exploitation and invasive species, resulting in a prevalence of large-bodied species among extinct taxa. Insularity was by far the strongest correlate of recent reptile extinctions, suggesting that size-biased extinction mechanisms are amplified in insular environments.

Keywords

Body size, conservation, global, Holocene extinction, megafaunal extinctions, Quaternary, reptiles.

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INTRODUCTION

Body size represents one of the most identifiable traits of an organism and is closely tied to its functional ecology, life history, morphology and physiology (Peters, 1983). Size has also been strongly implicated in the risk of species extinction

(Diamond, 1984; Case *et al.*, 1998; Dirzo *et al.*, 2014). As evidence is accumulating that the planet is experiencing a mass extinction event rivalling those of the geological past (Barnosky *et al.*, 2011; Maclean & Wilson, 2011; Barnosky *et al.*, 2012; Ceballos *et al.*, 2015), increasing attention is

being paid to the factors responsible for this decline in biodiversity (e.g. Purvis *et al.*, 2000; Cardillo *et al.*, 2005; Brook *et al.*, 2008). Traits associated with increased vulnerability to extinction include habitat specialization, small geographical range, insularity and those associated with slow life histories such as low reproduction rates, late maturity, low population densities and large body size (Owens & Bennett, 2000; Cardillo *et al.*, 2006; Tingley *et al.*, 2013). During the last 50,000 years anthropogenic pressure is purported to have elevated vertebrate extinction rates far beyond the normal background level (Ceballos *et al.*, 2015).

Evidence from the Late Quaternary fossil record has revealed the extinction of a considerable array of vertebrates across the globe, particularly among large-bodied species (Martin & Klein, 1984; Brook & Bowman, 2002; Sandom *et al.*, 2014). During this period Eurasia and North America lost about 36% and 72%, respectively, of their large-bodied mammalian genera (Barnosky *et al.*, 2004). Twenty-three mammalian species > 10 kg, distributed across 15 genera, also vanished from the Australian fauna during the same time (Sandom *et al.*, 2014). This period further coincides with the extinction of the world's largest birds, the Madagascan elephant birds and New Zealand moas (about seven and ten species, respectively; Mitchell *et al.*, 2014). While the extinction wave was not exclusively restricted to megafauna (Owens & Bennett, 2000), and taphonomic size biases in the fossil record may be partially obscuring the exact trend (Damuth, 1982), most extinct species were indeed large. Large body size is correlated with slow life-history traits, and is strongly implicated in current species extinction risk (Cardillo *et al.*, 2005; Fritz *et al.*, 2009). The fossil record of Late Quaternary reptiles is poorly known compared with that of birds and mammals, perhaps because there are few palaeontologists studying late Cenozoic reptiles, especially in tropical countries where reptiles tend to occur in high numbers. Yet, several of the extinct reptile species, such as the Australian *Wonambi naracoortensis* (a snake), *Meiolania* sp. (a tortoise) and *Varanus priscus* (a lizard) were huge by current standards (Wroe, 2002; Conrad *et al.*, 2012; Rhodin *et al.*, 2015).

The loss of a considerable portion of the planet's megafauna during the Late Quaternary has sparked intense debate over the possible extinction mechanisms (Martin & Klein, 1984; Flannery, 1999; Johnson, 2006; Koch & Barnosky, 2006; Wroe, 2006; Johnson *et al.*, 2016). Many studies have focused on contrasting the biological traits between extinct and extant species (e.g. Johnson, 2002; Lorenzen *et al.*, 2011), and body size has often emerged as a key factor. Size-biased extinction has predominantly been identified in mammals, with a global loss of over 150 large mammalian species (≥ 44 kg in body size) since the last interglacial (Sandom *et al.*, 2014). The bird fossil record is not as well known, but nonetheless over a thousand mostly large-bodied species are estimated to have gone extinct during this time, many of them flightless, insular endemics (Duncan *et al.*, 2013). The proximate causes of extinction among birds and mammals have been attributed to direct and indirect anthropogenic pressure

and climate change (Ceballos *et al.*, 2015; Johnson *et al.*, 2016). Few studies have investigated size-bias trends and extinction mechanisms in Quaternary reptiles (but see Pregill, 1986; Kemp & Hadly, 2015). As current trends suggest that the reptile extinction rate is much higher than expected (Alroy, 2015), studies focusing on their extinction mechanisms are both timely and important.

Reptiles are one of the most species-rich land vertebrate groups (c. 10,400 species; Uetz & Hošek, 2016), and are the most poorly represented in conservation prioritization (Böhm *et al.*, 2016). Reptile traits associated with increased extinction risk include restricted geographical range, habitat specificity and large body size (Tingley *et al.*, 2013; Kemp & Hadly, 2015). Although extant large-bodied reptiles are purportedly more prone to extinction, this may have arisen due to a size bias in reptile assessments (Meiri, 2008). The sheer paucity of data on reptile distributions, population trends, life history and fossil record has thus far precluded a comprehensive taxon-wide assessment of their extinction risk correlates (Böhm *et al.*, 2016).

To better understand the threats faced by current extant reptiles, it is of crucial importance to elucidate the past trends and processes responsible for recent extinction events (Barnosky *et al.*, 2004). Palaeontological and archaeological records of Holocene reptile extinctions, although incomplete, provide an invaluable resource for identifying these factors (Pregill & Dye, 1989). Fossil evidence has revealed recent extinctions among several reptile lineages across the globe, and their disappearance is invariably attributed to human impacts (e.g. Pregill *et al.*, 1991; Hedges & Conn, 2012; Rhodin *et al.*, 2015). Estimations of body size also indicate that many of these reptiles, particularly from insular assemblages, were unusually large compared with their extant kin (Pregill, 1986; Kemp & Hadly, 2015).

To determine whether reptiles exhibit size-biased extinction, we assess body size distributions among extinct and extant assemblages across the globe. Reptile body size (and indeed that of all animals) is shaped by many factors including phylogeny, geography and different adaptive regimes. Where feasible, we therefore assess the size-bias trend across multiple taxonomic levels and geographical regions.

METHODS

Data collection

We collected data on the maximum body size of all 82 reptile species that have gone extinct since humans colonized their range (Table S1 in Supporting Information). These include 4 crocodile, 45 lizard, 9 snake and 24 turtle ('turtles' here refers to all members of the order Testudines) species. We scoured published sources including books, assessments by the International Union for the Conservation of Nature (IUCN) and the primary literature to determine the identities and body sizes of extinct reptile species. We considered species to be extinct if they are known only from fossils, or were declared extinct by the IUCN or in the primary literature, and if their extinction happened following human occupation of their range (c. 50,000 years for Australia, c. 14,000 years

for the Americas, *c.* 3000 years for Oceania, and *c.* 2000 years for Madagascar; Barnosky *et al.*, 2004; Burney *et al.*, 2004; Anderson, 2009). We compare these with the body sizes of 10,090 extant species we collected from published accounts (189 amphisbaenians, 24 crocodiles, 6045 lizards, 3513 snakes, 318 turtles and the one species of tuatara; Table S2 in Supporting Information). We converted all length data to masses using family and clade-specific length-mass allometric equations (Table S1). This is crucial as length is an inadequate measure of body size to compare across taxa with highly variable body shapes (Feldman & Meiri, 2013). A list of all data sources is given in Appendix 1.

We also collected data on the distribution of all extant and extinct species in order to take into account geographical patterns in extinctions of reptiles. Data on extant species were obtained from GARD (Global Assessment of Reptile Distributions, 2015), whereas data on extinct species were collected from the same sources as the body size data (listed in Table S1).

We classified each species as either an insular endemic or not, and assigned each species to a biogeographical realm. We used ArcGIS 10.0 (ESRI) to project shapefiles of reptile species distributions onto a map of biogeographical realms (Wallace, 1876). A species was assigned to a realm if all or the largest part of its distribution area fell inside that realm. A species was designated insular endemic if no part of its range overlapped with a continental landmass (therefore, we considered islands as any landmass smaller than Australia, the largest island with reptiles being New Guinea).

We also collected data on occurrence of extant species of reptiles in the fossil record to test for size biases in the fossil record. We searched in FossilWorks (<http://www.fossilworks.org>) and Google Scholar using the keywords 'Holocene', 'Late Pleistocene', 'Squamata' and 'Reptilia', as well as in two books on the Pleistocene herpetofaunas of North America and Europe (Holman, 1995; 1998), and collected data on the occurrence of 261 extant species of reptiles in the fossil record (4 amphisbaenians, 9 crocodiles, 94 lizards, 105 snakes, 48 turtles and the one species of tuatara; Table S2).

Permutation tests

Reptile size distributions are strongly right skewed (Feldman *et al.*, 2016), breaking the assumption of normality required for parametric statistical tests. Thus, we conducted permutation tests to compare body sizes of extant and extinct species. This was done (for all reptiles and separately for lizards, snakes, turtles and crocodiles) by pooling all extant and extinct species of each group, randomly selecting n species from the pool without replacement (where n is the observed number of extinct species within the examined taxon, e.g. $n = 45$ for lizards), and computing the t -statistic for the random selection using the formula

$$t_i = \frac{\mu_{\text{extinct}} - \mu_{\text{extant}}}{SE_{\text{extinct}}}$$

where μ_{extinct} is the mean body size of the random selection (simulated extinct species), SE_{extinct} is the standard error of the random selection and μ_{extant} is the mean body size of the

remaining, non-selected species in the pool (simulated extant species). This process was repeated for 100,000 iterations. Using the same formula we computed a t -statistic for the observed extinct and extant groups, and computed two sided P -values as the fraction of iterations with t -statistics at least as extreme as the observed value (with $\alpha = 0.05$).

Fossil record biases

Due to the incompleteness of the fossil record, the results of our analyses might be biased if the sample size of extinct species is too low. This is of special concern as large-bodied taxa are more likely to be preserved (Damuth, 1982). To account for this, we performed rarefaction analyses. We randomly sampled 80%, 60%, 30% and 10% of the total extinct species (in each taxon) and ran the permutation tests (with only 10,000 iterations to reduce computational time) on these subsets. This sampling process was repeated 1000 times to generate rarefaction curves. We then examined for each curve the sampling effort at which the results of the permutation tests become non-significant, i.e. the minimum sampling required to achieve significance. This test informed us of the robustness of our analyses to low sample sizes due to missing data in the fossil record.

The fossil record itself may also be size-biased due to taphonomic issues, because larger bones have a higher chance of being preserved due to their low surface area to volume ratio (Damuth, 1982). We tested for this size bias by comparing the body sizes of extant reptile species that occur in the fossil record with all extant species. We performed permutation tests as described above for all reptiles, and separately for lizards, snakes, crocodiles and turtles. Furthermore, we repeated our analyses of size bias in extinct lizards after excluding all extinct species that are only known from fossils or subfossils (e.g. *Varanus priscus*). As this analysis only included a subset of species that went extinct after living specimens had been collected and scientifically described (28 species; e.g. *Ameiva cineracea*), rather than preserved remains, it should not be affected by a size bias in the fossil record.

Geographical biases

Late Quaternary reptile extinctions are heavily biased towards islands (Fig. 1). If insular species differ in body size from mainland species, observed size biases in extinct taxa may simply reflect insular size biases (i.e. if island reptiles are unusually large, then extinct reptiles would be larger than extant ones simply because insular species went extinct more often). To test whether extinction rates are indeed higher on islands, we performed Fisher exact tests with a null hypothesis of identical extinction frequencies for both mainland species and insular endemics. Using permutation tests as described above (with n representing the number of insular species) we then tested exclusively among extant species whether insular endemics are larger than mainland species. Furthermore, we examined whether an extinction size bias existed among insular endemic species only. This could not be performed for mainland species due to the extreme

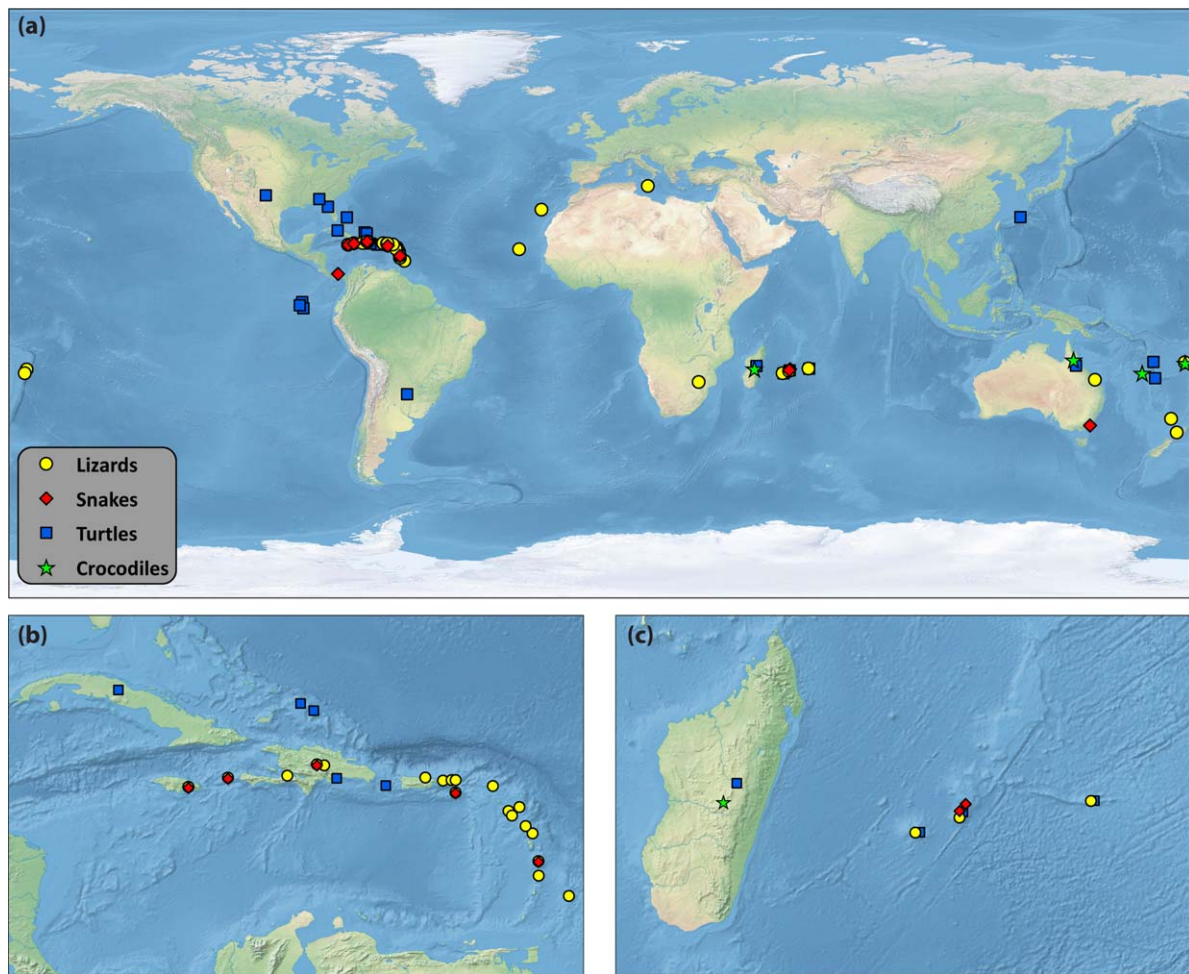


Figure 1 (a) Map showing the distribution of extinct reptile species, where (yellow) circles represent lizards, (red) diamonds represent snakes, (blue) squares represent turtles and (green) stars represent crocodiles (colour in online version only). Also presented are close-ups of the map in (b) the Caribbean and (c) the Mascarenes and Madagascar.

scarcity of extinct mainland reptiles for which we have data (see Results).

Reptile extinctions are also clearly geographically biased (Fig. 1). We used two approaches to account for different geographical patterns in reptile extinctions. First, we performed geographically weighted permutation analyses. This was carried out using permutation analyses as described above, but with a species selection probability from the pool dependent upon its biogeographical realm (i.e. the probability of selecting a species was proportional to the number of extinct species in its realm divided by the global number of extinct species). This ensured that each simulated extinct selection had the same distribution of realms as the observed distribution of extinct species. We conducted these analyses for all reptiles and for lizards, snakes and turtles separately. Crocodiles were omitted, because of the three realms in which there were extinct crocodiles, Oceania and Madagascar have no extant species.

Second, we ran permutation tests on three regional assemblages to determine whether the global patterns are

comparable across varying spatial scales. As only a few regions contained a sufficient number of extinct reptiles we only ran three such analyses: Caribbean lizards (31 extinct and 377 extant species), Mascarene lizards (five extinct and 19 extant species) and Galapagos tortoises (*Chelonoidis* spp., three extinct and seven extant species).

Phylogenetic biases

Finally, we examined whether the size biases in extinct reptilian taxa were phylogenetically skewed. We ran permutation tests on all reptile families (Dipsadidae, Gekkonidae, Iguanidae, Lacertidae, Leiocephalidae, Scincidae, Teiidae and Testudinidae) and genera (*Alinea*, *Ameiva*, *Chelonoidis*, *Hypsirhynchus*, *Leiocephalus*, *Leiopisma*, *Mabuya*, *Phelsuma*, *Spondylurus*) that include more than one extinct and one extant species.

All statistical analyses were performed in R v.3.2.0 (R Development Core Team, 2015).

RESULTS

Most of the extinct reptile species were insular endemics (Fig. 1), with a remarkably large concentration of extinct species in the Caribbean. Notable extinctions also occurred on the Mascarene, Galapagos, Melanesian and Polynesian islands. Relatively few reptiles (mostly turtles) went extinct in mainland regions, mostly in Australia. Eurasia is the only continental landmass from which no extinct reptiles are known from the Late Pleistocene to Holocene, while Africa and South America had a single extinction each.

Results of the permutation analyses are presented in Table 1. Across all reptiles there was a significant extinction size bias. The vast majority of extant reptiles are small, whereas extinct species were disproportionately large (Fig. 2). A similar pattern is also evident in the most species-rich reptilian taxon (coincidentally the one suffering most extinctions), namely lizards. Extinct lizards were nine times larger than extant lizards (Fig. 3a). This was also true for the Caribbean lizard assemblage, but it was not significant in the Mascarene lizard assemblage, despite extinct species being twice as large as extant ones (Table 1). Extinct turtles were 16 times larger than extant turtles (Fig. 3c). Interestingly, this was not true for the Galapagos tortoise assemblage. Surprisingly, extinct Galapagos tortoises were similar in size to extant ones. Unlike lizards and turtles, extinct crocodiles were significantly smaller than extant crocodiles (Fig. 3d). Finally, while extinct snakes were twice as large as extant snakes (Fig. 3b), this difference is not statistically significant (Table 1). All the observed differences between extinct and extant species held when our analyses were geographically weighted (Table 1).

The reptile fossil record is size biased (Fig. 2). Size biases are evident in the fossil records of lizards and snakes, with the species present in the fossil record representing a large-bodied subset of extant species. No such bias was detected in the fossil records of either turtles or crocodiles (Table 1). When we omitted from our analysis extinct species known only from the fossil record, we still detected a size bias: extinct lizards were four times larger than extant ones (Table 1).

The results of the rarefaction analyses on lizards and turtles (snakes and crocodiles were not analysed because their small sample size prohibited reduced sampling) indicate that our permutation analyses are robust despite the incompleteness of the fossil record. In both lizards and turtles, the median minimum sampling effort required to achieve significance, out of 1000 repetitions, was 60%. This means that we would get an equivalent pattern with little more than half the sampling effort we actually achieved.

Reptile extinction events were remarkably prevalent on islands. Seventy-three of the 82 extinct species (89%) were insular endemics ($P < 0.01$ for lizards, snakes and turtles; $P = 0.02$ for crocodiles; Fig. 4) while only 26% of extant species are insular. When mainland species are excluded from the analyses, removing the confounding effects of size differences between island and mainland species, all the observed

size biases still appear (Table 1). Even the inclusion of mainland species does not change the pattern. Furthermore, the differences in body size between insular endemics and mainland species do not reflect the size differences between extinct and extant species (Table 1). Extant insular endemic lizards and snakes are significantly smaller than mainland species. Insular crocodylians are similar in size to mainland ones. Only in turtles are insular species larger than mainland species (see also Itescu *et al.*, 2014), but the difference is not nearly as large as between extinct and extant species. Therefore, large lizards and turtles, and small crocodiles, went extinct regardless of whether they were on islands or on the mainland.

The global patterns were not always reflected at the family and genus levels. Extinct Dipsadid snakes, Leiocephalid and Scincid lizards and Testudinid turtles were larger than extant ones (Table 1, Fig. 5a). Four families (Gekkonidae, Iguanidae, Lacertidae and Teiidae) showed no significant trends. Of nine genera tested, only *Leiocephalus* (the sole genus in Leiocephalidae) showed a significant size bias (Fig. 5b), although in some genera and families there may be an issue of statistical power due to small sample sizes (Table 1).

DISCUSSION

The global extinction of the Late Quaternary vertebrate megafauna indicates that body size may have played a pivotal role in recent extinction events. We find that recently extinct reptiles were much larger than extant ones. Size biases, however, differ across the four major reptile groups. Extinctions were biased towards large lizards and turtles and small crocodiles, while there was no significant size bias in snakes. Our results also suggest that the observed size bias in extinct lizards is not general across clades but is phylogenetically skewed and driven by the largest members of only a few clades that have gone extinct (e.g. *Leiocephalus* spp., a large skink, *Chioninia coctei*, and the largest gecko, *Hoplodactylus delcourti*, and lizard, *Varanus priscus*, to have ever lived). Our analyses may have been conservative, as we used the maximum size reported for each species regardless of whether it was measured in extant populations or estimated from sizes of subfossil conspecifics. In many extant taxa (e.g. *Gallotia stehlini*, *Gallotia bravoana*, *Chioninia vaillantii*, *Diploglossus pleii*, *Anolis cuvieri*; see, e.g., Pregill, 1986) these maximum sizes were estimated for recently extinct populations, and living members are much smaller. Small sample sizes of extinct taxa may also mask their true size maxima, making them appear smaller than they really were (Meiri, 2007).

Comprehensive assessments of the reptile fossil record remain sparse, and worse; most reptiles are and were small-bodied (Feldman *et al.*, 2016). Hence, their bones are often badly preserved or missed altogether, making species-level identification impossible in many cases. This may cause a possible bias in favour of large-bodied species in the fossil record (Damuth, 1982). Indeed, we found evidence of such a bias – extant species that are represented in the fossil record are roughly seven times larger than the mean size of all

extant species. However, *extinct* is not the same as *fossil*, and many extinct species are known from intact, well-preserved museum specimens for which no taphonomic effect is imaginable. When we omitted extinct species only known from fossils or subfossils from our analyses, and only examined

species that were collected alive prior to their extinction (and therefore suffer from no taphonomic biases), we still managed to detect a size bias towards larger extinct lizard species. Furthermore, some of our uncovered patterns (e.g. small extinct crocodiles, similarly sized extinct snakes) cannot be

Table 1 Results of the permutation analyses.

	Extinct		Extant		P-value
	Mean	<i>n</i>	Mean	<i>n</i>	
Reptiles	867 g	82	22.5 g	10090	0
Lizards	88.9 g	45	9.5 g	6045	0
Lizards (no fossils)	38.6 g	29	9.5 g	6045	0.0002
Snakes	126.9 g	9	61.7 g	3513	0.51
Turtles	61.6 kg	24	3.8 kg	318	0
Crocodiles	68 kg	4	191.9 kg	24	0.04
Caribbean lizards	43.3 g	31	6.8 g	377	0
Mascarene lizards	15.2 g	5	7.3 g	19	0.19
Galapagos Tortoises	113.5 kg	3	134.9 kg	7	0.29

Size-bias in the fossil record of extant species

	Fossils		All		P-value
	Mean	<i>n</i>	Mean	<i>n</i>	
Reptiles	350.6 g	261	22.5 g	10090	0
Lizards	69.5 g	94	9.5 g	6045	0
Snakes	297.7 g	105	61.7 g	3513	0
Turtles	4.2 kg	48	3.8 kg	318	0.72
Crocodiles	228.3 kg	9	191.9 kg	24	0.6

Geographically weighted analyses

	Extinct		Extinct		P-value
	Mean	<i>n</i>	Mean	<i>n</i>	
Reptiles	867 g	82	22.5 g	10090	0
Lizards	88.9 g	45	9.5 g	6045	0
Lizards (no fossils)	38.6 g	29	9.5 g	6045	0.0006
Snakes	126.9 g	9	61.7 g	3513	0.54
Turtles	61.6 kg	24	3.8 kg	318	0

Insular endemics only

	Extinct		Extant		P-value
	Mean	<i>n</i>	Mean	<i>n</i>	
Reptiles	589.3 g	73	14.5 g	2627	0
Lizards	80.7 g	43	8.4 g	1832	0
Snakes	56.6 g	8	40.9 g	741	0.68
Turtles	68.7 kg	19	8.6 kg	34	0
Crocodiles	59 kg	3	166 kg	3	0.05

Extant only					
	Insular endemic		Mainland		P-value
	Mean	<i>n</i>	Mean	<i>n</i>	
Reptiles	14.5 g	2627	26.2 g	7463	0
Lizards	8.4 g	1832	10 g	4213	0
Snakes	40.9 g	741	68.8 g	2782	0.001
Turtles	8.6 kg	34	3.1 kg	284	0.01
Crocodiles	166 kg	3	195.9 kg	21	0.67
Families					
	Extinct		Extant		P-value
	Mean	<i>n</i>	Mean	<i>n</i>	
Dipsadidae	153.6 g	4	39 g	745	0.02
Gekkonidae	20.1 g	3	4.8 g	1034	0.37
Iguanidae	3 kg	3	1.6 kg	41	0.21
Lacertidae	3.8 kg	2	8.5 g	319	0.08
Leiocephalidae	61.3 g	9	18.3 g	20	0.05
Scincidae	32.6 g	20	6 g	1559	0.0003
Teiidae	160.2 g	2	44.2 g	148	0.22
Testudinidae	60 kg	20	7.9 kg	51	0
Genera					
	Extinct		Extant		P-value
	Mean	<i>n</i>	Mean	<i>n</i>	
<i>Alinea</i>	22.3 g	2	18.5 g	2	0.83
<i>Ameiva</i>	160.2 g	2	63.7 g	30	0.24
<i>Chelonoidis</i>	48.8 kg	10	98.6 kg	11	0.12
<i>Hypsirhynchus</i>	130.8 g	2	72 g	7	0.44
<i>Leiocephalus</i>	61.3 g	9	18.3 g	20	0.05
<i>Leiopisma</i>	383.2 g	2	25.5 g	2	0.33
<i>Mabuya</i>	23.4 g	5	20.9 g	3	0.63
<i>Phelsuma</i>	62.2 g	2	4.5 g	50	0.19
<i>Spondylurus</i>	11.9 g	4	13.3 g	13	0.79

For each examined group (e.g. turtles, Caribbean lizards, Dipsadidae, etc.) the means and sample sizes of the examined groups are listed together with the corresponding *P*-values. The larger of each two compared means and significant *P*-values (with $\alpha = 0.05$) are in bold. *P*-values of 0 mean that none of the 100,000 iterations had a *t*-statistic as extreme as the observed one.

explained by such a bias. Despite the apparent robustness of our results to taphonomic bias we advise caution whenever analyses of body sizes of extinct species are attempted, and a size bias in the fossil record must be tested and corrected for.

Both intrinsic life-history traits and extrinsic factors such as climate change and anthropogenic pressure are linked to species survival (Brook *et al.*, 2008). Cardillo *et al.* (2005) found that small mammals (< 3 kg) are threatened by environmental factors while larger mammals are threatened by a

combination of extrinsic environmental factors and intrinsic biological traits. These factors are purported to act in synergy, whereby the simultaneous action of separate processes has a stronger effect than the sum of individual effects (Brook *et al.*, 2008). In lizards we find evidence that larger species may indeed have been more susceptible to extinction, as 38 of the 45 extinct lizards were larger than the extant mean of 9.5 g, 19 of them being over an order of magnitude larger. Kemp & Hadly (2015) recently reported a size bias in

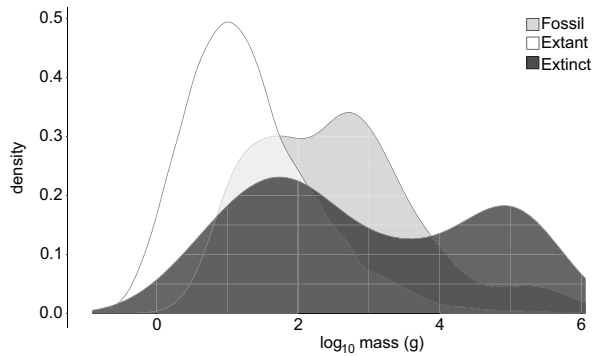


Figure 2 Density plot of reptile body sizes, with extant species in white, extant species represented in the fossil record in light grey and extinct species in dark grey. The two peaks in body size of extinct species correspond to the smaller-bodied squamates (lizards and snakes) and the larger-bodied turtles and crocodiles.

Caribbean lizard species, with extinction probability increasing with body size. They concluded that larger-sized lizards with ‘slower’ life histories were more prone to extinction due to environmental change and anthropogenic pressure, factors purported to increase in intensity on islands. Further research is required to elucidate whether a precise mass threshold exists, and, if present, identify the underlying extinction mechanisms. Such extinction mechanisms may offer particular insight considering that large lizards typically lay larger, rather than smaller, clutches (Bauwens & Diaz-Uriarte 1997; Meiri *et al.*, 2012) and thus low fecundities are unlikely to have triggered extinctions.

While it is evident that recent extinction events can rarely be attributed to a single cause (Didham *et al.*, 2005), emergent trends implicate the fundamental role of both direct and

indirect anthropogenic pressure (Davies *et al.*, 2006; Koch & Barnosky, 2006; Dirzo *et al.*, 2014; Johnson *et al.*, 2016). Direct evidence of human-mediated extinction among reptiles is documented in the over-harvesting of giant iguanas on south-west Pacific islands (Pregill & Steadman, 2004) and giant tortoises in the islands of the Caribbean, Indian Ocean and Pacific Ocean (Rhodin *et al.*, 2015). It is evident that humans targeted these large-bodied reptiles precisely because their size represented a substantial source of nutrition, whilst their lack of defence mechanisms reduced the risk taken during their capture. Interestingly, our study indicates that among the Galapagos giant tortoises, the extinct species were not the largest members of the assemblage, and in fact many larger species (*Chelonoidis becki*, mass 154 kg; *Chelonoidis vicina*, mass 249 kg; *Chelonoidis nigra*, mass 277 kg) still survive to this day. Similarly, the sole remaining extant giant tortoise in the western Indian Ocean (*Aldabrachelys gigantea*, mass 217 kg) is the second largest species within this assemblage following the extinct *Cylindraspis indica* (mass 222 kg). It may be that the smaller giant tortoise species may have been preferentially targeted by 18th-century sailors due to ease of transport, resulting in their eventual extinction (Hansen *et al.*, 2010), while the larger species proved to be more of a handful.

For crocodiles and snakes, the extinction mechanisms and role of body size are harder to pinpoint. Two of the four extinct crocodiles (*Mekosuchus inexpectatus* and *Volia athollandersoni*) were confined to Pacific islands (Molnar *et al.*, 2002). While this undoubtedly increased their vulnerability to extinction, evidence for direct hunting by humans, as in the case of the Pacific meiolaniid tortoises, is lacking (Molnar *et al.*, 2002). In the case of the Madagascan crocodile (*Voay robustus*, mass 97 kg) competitive displacement by the larger *Crocodilus niloticus* (mass 591 kg) and human colonization

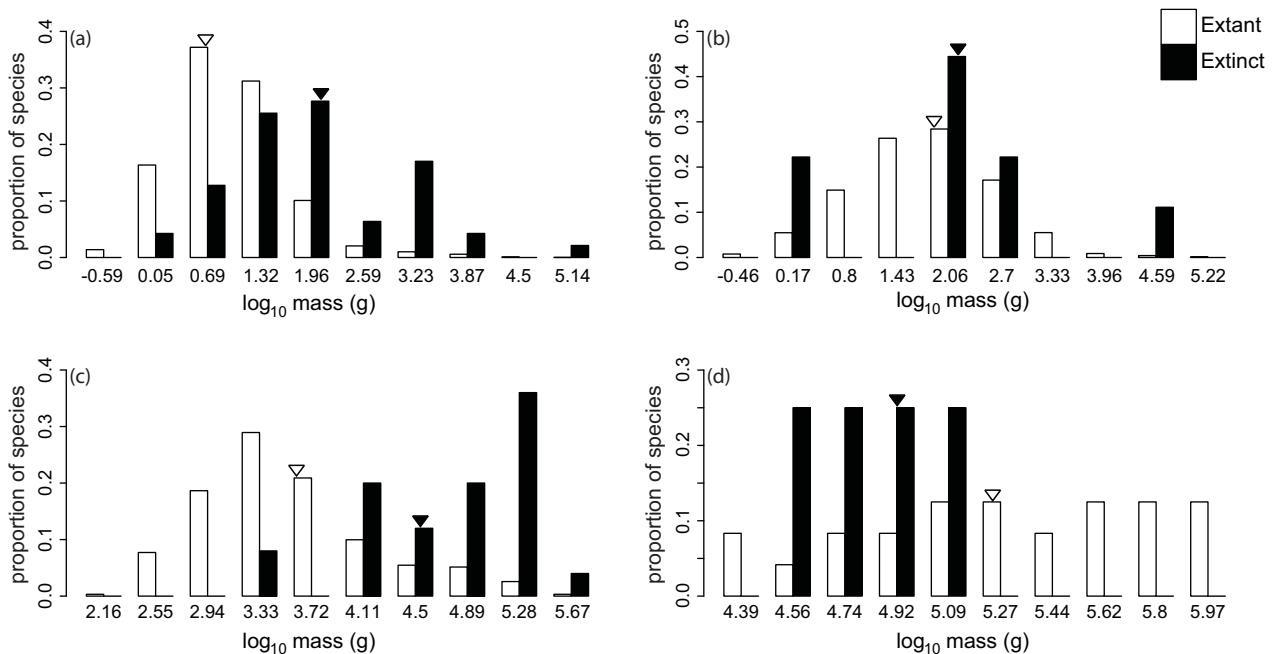
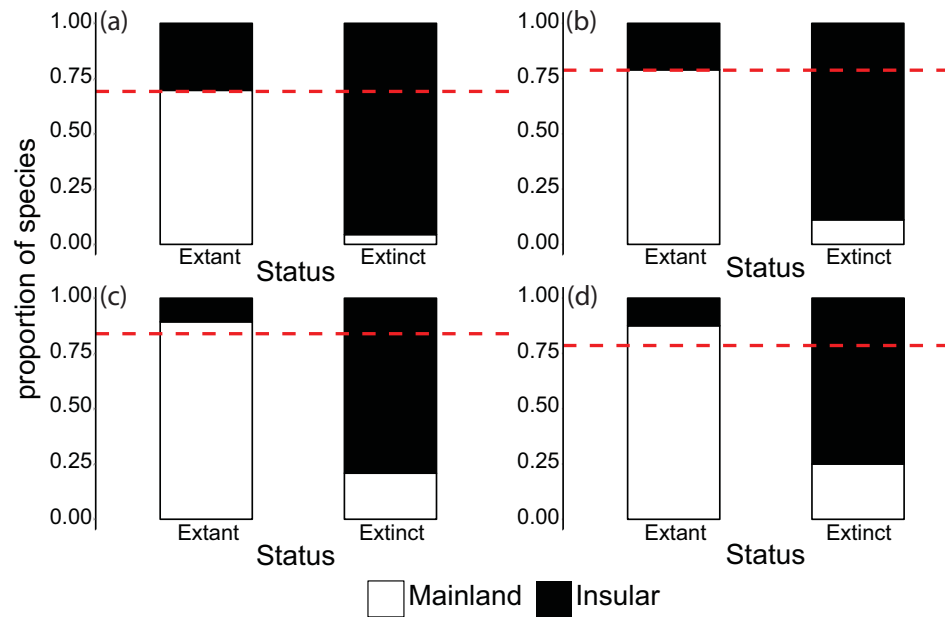


Figure 3 Body size distributions of extant (white) and extinct (black) species of (a) lizards, (b) snakes, (c) turtles, and (d) crocodiles. Mean body sizes of each group are represented by triangles.

Figure 4 Plots showing the ratio between insular endemics (black) and mainland species (white) for (a) lizards, (b) snakes, (c) turtles, and (d) crocodiles. The dashed line represents, in each taxon, the predicted ratio between insular endemics and mainland species under a null hypothesis of equal extinction frequencies on islands and mainlands.



have been proposed as possible extinction mechanisms (Brochu, 2007). In Australia, human impact is implicated in the extinction of a suite of vertebrates including a small crocodile (*Quinkana fortirostrum*), a giant snake (*Wonambi*

naracoortensis) and the huge Megalania (*Varanus priscus*; Prideaux *et al.*, 2010; Johnson *et al.*, 2016).

Almost all extinct reptiles were island endemics, with insularity highlighted as a key factor increasing a species' risk of extinction. Indirect human impact, such as the introduction of invasive carnivores (e.g. *Herpestes auropunctatus*, *Felis catus*) and rats (*Rattus* spp.) is directly linked to the extinction of a wide variety of insular reptile species (e.g. Hedges & Conn, 2012). The introduced Indian mongoose (*Herpestes auropunctatus*) had a devastating effect on the Caribbean fauna, being a factor in the extinction of 16 skink and three snake species (Henderson & Powell, 2009; Hedges & Conn 2012). Interestingly, the only extinct mainland lizard species, the South African *Tetradactylus eastwoodae*, is also the smallest extinct lizard (1.8 g).

In conclusion, although the current fossil record undoubtedly represents a subset of species that actually went extinct during the Late Quaternary, emergent trends reveal that the reptile extinction rate was much higher on islands, while a large body represents a further, less straightforward, cause for extinction (and only in some reptile groups, not all). It is clear that relatively recent historical threats were particularly pronounced in insular environments. Some exceptionally large-bodied reptiles were also particularly prone to extinction through human-mediated rapid and prolonged harmful conditions, combined with slow life histories inhibiting their ability to recover. Recent extinction processes have evidently varied across the reptile phylogeny, geographical area and time, yet body size has often played a role, whether direct or indirect, in the persistence or disappearance of species.

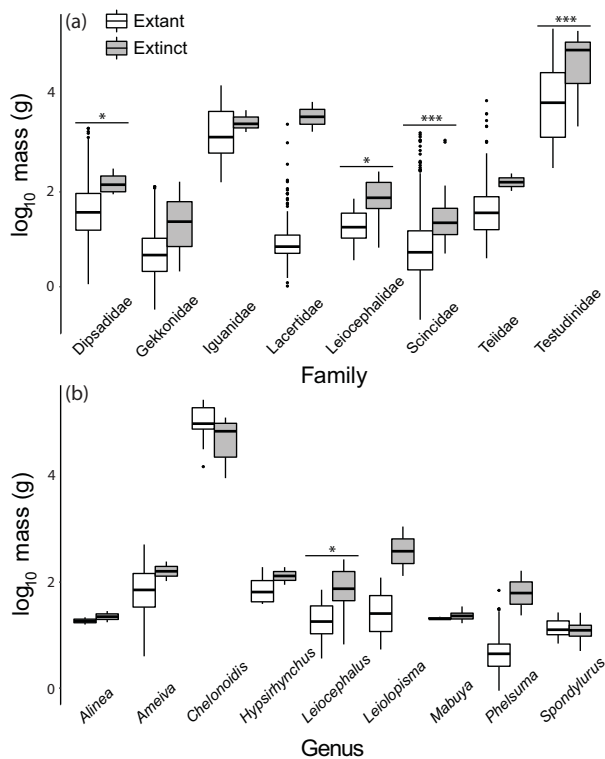


Figure 5 Body sizes of extant and extinct species of reptiles in each family (a) and genus (b) examined. Body sizes were compared using permutation tests: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's website:

Table S1. Body sizes of extinct reptiles, with references for length-mass conversion equations of lizards, snakes and turtles.

Table S2. Body sizes of extant reptiles.

Appendix S1. Body sizes and distributions of all late Quaternary extinct reptile species. Snout-vent length of lizards and snakes and carapace length of turtles were converted to mass using allometric equations developed by Meiri (2010), Itescu (2012), Feldman & Meiri (2013) and Novosolov *et al.* (2013).

Appendix S2. Body sizes of all extant reptiles included in the study. Crocodile masses were converted from length data using the equations in Table S1 (the general equation was used for Gavialidae).

APPENDIX 1 DATA SOURCES

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