

Tracking Global Population Trends: Population Time-Series Data and a Living Planet Index for Reptiles

ANWESHA SAHA,^{1,2} LOUISE McRAE,¹ C. KENNETH DODD JR.,³ HECTOR GADSDEN,⁴ KELLY M. HARE,⁵ VIMOKSALEHI LUKOSCHEK,⁶ AND MONIKA BÖHM^{1,7}

¹Institute of Zoology, Zoological Society of London, Regent's Park, London NW1 4RY, United Kingdom

²Department of Genetics, Evolution and Environment, University College London, London WC1E 6BT, United Kingdom

³Department of Wildlife Ecology and Conservation, University of Florida, Gainesville, Florida 32611 USA

⁴Instituto de Ecología, A.C., Av. Lázaro Cárdenas No. 253, A.P. 386, C.P. 61600 Pátzcuaro, Michoacán, México

⁵School of Graduate Research, University of Waikato, Private Bag 3105, Hamilton 3240, New Zealand

⁶ARC Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, QLD, 4811, Australia

ABSTRACT.—Effective conservation action relies on access to the best-available species data. Reptiles have often been overlooked in conservation prioritization, especially because of a paucity of population data. Using data for 549 reptile populations representing 194 species from the Living Planet database, we provide the first detailed analysis of this database for a specific taxonomic group. We estimated an average global decline in reptile populations of 54–55% between 1970 and 2012. Disaggregated indices at taxonomic, system, and biogeographical levels showed trends of decline, often with wide confidence intervals because of a prevalence of short time series. We assessed gaps in our reptile time-series data and examined what types of publication they primarily originated from to provide an overview of the range of data sources captured in the Living Planet database. Data were biased toward crocodilians and chelonians, with only 1% and 2% of known lizard and snake species represented, respectively. Population time-series data stemmed primarily from published ecological research (squamates) and data collected for conservation management (chelonians and crocodilians). We recommend exploration of novel survey and analytical techniques to increase monitoring of reptiles, especially squamates, over time. Open access publication and sharing of data sets are vital to improve knowledge of reptile status and trends, aided by the provision of properly curated databases and data-sharing agreements. Such collaborative efforts are vital to effectively address global reptile declines.

RESUMEN.—La acción efectiva de conservación depende del acceso a los mejores datos disponibles de las especies. Los reptiles a menudo han sido pasados por alto en la priorización de la conservación, especialmente debido a la escasez de datos poblacionales. Utilizando datos para 549 poblaciones de reptiles que representan 194 especies de la base de datos de Living Planet, proporcionamos el primer análisis detallado de esta base de datos para un grupo taxonómico específico. Estimamos una disminución global promedio en las poblaciones de reptiles del 54–55% entre 1970 y 2012. Los índices desagregados a nivel taxonómico, de sistema y biogeográfico mostraron tendencias de disminución, a menudo con intervalos de confianza amplios debido a la prevalencia de series-temporales cortas. Evaluamos la disparidad en nuestros datos de series de tiempo de reptiles y examinamos de qué tipos de publicaciones se originaron, principalmente para proporcionar una visión general de la clase de fuentes de datos capturados en la base de datos de Living Planet. Los datos fueron sesgados hacia los cocodrilos y los quelonios, con solo la representación del 1% y 2% de las especies conocidas de lagartos y serpientes respectivamente. Los datos de las series de tiempo de las poblaciones se derivaron principalmente de la investigación ecológica publicada (escumatos) y de los datos recopilados para el manejo de la conservación (quelonios y cocodrilos). Recomendamos la exploración de estudios novedosos y técnicas analíticas para aumentar el monitoreo de los reptiles, especialmente de los escumatos, a lo largo del tiempo. Las publicaciones de acceso abierto y el intercambio de bases de datos son vitales para mejorar el conocimiento del estado y las tendencias de los reptiles, con la ayuda del suministro de bases de datos y acuerdos de intercambio de datos debidamente seleccionados. Tales esfuerzos de colaboración son vitales para abordar de manera efectiva la declinación mundial de los reptiles.

Reptiles inhabit a wide range of habitats in terrestrial, freshwater, and marine environments, represent essential components of food webs and ecosystems, and serve as bioindicators for environmental health (e.g., Read, 1998). Anthropogenic threat processes, such as habitat loss, climate change, pollution, and impacts from invasive species, are the principle drivers of worldwide declines in reptiles (e.g., Gibbons et al., 2000; Böhm et al., 2013). Globally, one fifth of reptile species are estimated to be at risk of extinction (Böhm et al., 2013), although this varies among regions (e.g., one fifth in Europe, Cox and Temple, 2009; one tenth in Southern Africa, Bates et al., 2014) and among different taxonomic groups (e.g., chelonians have the highest extinction risk and snakes have the lowest; Böhm et al., 2013). Global threat estimates may be underestimated, however, because many unassessed and Data Deficient species are likely to be small-ranged species with

inherently higher risk of extinction (Meiri, 2016). Overall, reptiles have been neglected in global conservation prioritization, predominantly because of the relative paucity of data on their status (Meiri and Chapple, 2016; Turtle Taxonomy Working Group, 2017).

Assessment of reptiles for conservation has been primarily through the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (<http://www.iucnredlist.org/>), using predominantly range-based criteria (e.g., 82% of squamates were assessed under IUCN Red List Criterion B [restricted geographic range] and 13% under Criterion D2 [very restricted population/range] in Böhm et al. [2013]), because few data are available on reptile population trends (needed for Criterion A and C). Range-based assessments may be too coarse to detect population declines, however, especially if these do not contribute to a decline in a species overall range. While extinction risk assessments using the IUCN Red List highlight species under immediate extinction threat, population time-series data perform better at detecting declines

⁷Corresponding author. E-mail: monika.bohm@ioz.ac.uk
DOI: 10.1670/17-076

before species reach elevated extinction risk, at least in discrete populations or over small spatial scales (e.g., Conner et al. 2016). Reading et al. (2010) documented population declines in a number of snake populations worldwide; however, many studies have focused on only a small number of species and populations, or on populations at specific localities, so that deriving a global picture of reptile population trends is difficult.

The Living Planet Index (LPI) is a global biodiversity indicator, built from aggregated abundance trends of vertebrate species populations, and is used to communicate biodiversity trends (World Wildlife Fund, 2016) and monitor progress toward the Aichi Biodiversity Targets set by the Convention on Biological Diversity (Butchart et al., 2010; Tittensor et al., 2014). The index aggregates individual time series of vertebrate population sizes or proxies from around the world to track average changes in abundance through time; it does this by averaging the change in abundance of species over time and conventionally begins in 1970 (Loh et al., 2005; Collen et al., 2009). This method has also been applied to produce LPIs by biogeographic realm (Collen et al., 2009) and at regional and national scales (e.g., Mediterranean wetland species [Galewski et al., 2011]; Arctic vertebrates [McRae et al., 2012]). Furthermore, the LPI has been used to investigate the effectiveness of conservation management by measuring species abundance trends in protected areas across Africa (Craigie et al., 2010) and to test policy scenarios (Nicholson et al., 2012).

Underlying the LPI is a database (Living Planet database, LPD; Zoological Society of London and World Wildlife Fund, 2017) containing over 18,000 population time series from more than 3,600 species. Reptiles are represented by 194 species and 549 population time series within the database: this equates to 1.85% of all described reptile species as of August 2016 (Uetz, 2016) and 6% of described vertebrates (Baillie et al., 2010). Taxonomic coverage in the database is a consequence of the approach to data collection. Because the database is populated using data available in the public domain, the content is neither completely random, as it is subject to biases inherent in ecological and conservation literature (Troudet et al. 2017), nor is it targeted, as the aim is to collect all of the available data on any vertebrate species from as broad a geographic coverage as possible. Coupled with this is the temporal disparity among the monitored populations in the database—population time series cover a large range of time periods, from 2–70 yr. Any indicators produced from this database require an understanding of the taxonomic, geographic, and temporal representation of the underlying data (Jones et al., 2011). Bias is inherent in global biodiversity databases (Boakes et al., 2010) but can be dealt with if impacts of biases on biodiversity indicators such as the LPI are recognized (Collen et al., 2009) and corrected where possible (McRae et al., 2017).

Here, we investigate global population trends and data gaps for reptiles using the LPI method (McRae et al., 2017). This represents the first time the LPI has been used to analyze in detail the global trends for a particular taxon. We analyze trends in reptile populations over time globally and in taxonomic and spatial subsets of the data. We identify data gaps by examining the taxonomic and geographic representativeness of the data set and test for bias toward threatened species. Finally, we assess the sources and quality (completeness and length) of reptile population time series to provide suggestions for reptile monitoring and conservation and establish priorities for expanding the current reptile data set.

MATERIALS AND METHODS

Calculation of Index Values.—Reptile population time-series data in the LPD were gathered from published and unpublished scientific studies. Apart from two time series for the Nile Crocodile, *Crocodylus niloticus*, which were shared confidentially, all the data sources are referenced and open access (www.livingplanetindex.org). Population time-series data are included in the LPD if they contain at least two data points, the monitoring method used is the same throughout the time series, the method used is reputable and appropriate for the species, and the units represent the size or abundance of the population being monitored (Collen et al., 2009). For each species, taxonomic information at the species level was verified against the taxonomy used by the IUCN Red List of Threatened Species (IUCN, 2016) and The Reptile Database (Uetz, 2016).

We followed previously published methods (Loh et al., 2005; Collen et al., 2009; McRae et al., 2017) to calculate an overall reptile population trend index over time. We used a general additive modeling (GAM) framework because of its ability to produce nonlinear forms of long-term trend analysis (Fewster et al., 2000). Annual trend values were computed using two methods: 1) a chain method for time series with less than six data points, and 2) GAM for time series with six or more data points (Collen et al., 2009). To calculate an index, we aggregated the data hierarchically by first taking the mean annual trend values for multiple population time series of each species:

$$\bar{d}_i = \frac{1}{n_i} \sum_{i=1}^{n_i} d_{ii} \quad (1)$$

where n_i is the number of population time series, and d_i is the annual rate of change for a population time series in a given year, given by

$$d_t = \log_{10}\left(\frac{N_t}{N_{t-1}}\right) \quad (2)$$

where N is the population measure and t is the year. We then aggregated the mean annual trend values for each species into a mean of all species to create the overall global index for reptiles:

$$I_t = I_{t-1} * 10^{\bar{d}_t}, I_0 = 1 \quad (3)$$

In addition to the overall global index, we calculated indices for the following disaggregated data sets (Table S1): taxonomic indices for squamates, crocodylians, and chelonians; system-level indices for terrestrial, freshwater, and marine reptiles; and biogeographical realm indices for Afrotropical, Australasian, Indomalayan, Nearctic, Neotropical, and Palearctic realms (Oceania was excluded because of too few data). The starting index value was set to 1 in 1970 with subsequent index values calculated by multiplying the mean annual trend for that year. The indices finished in 2012 because of the unavailability of data beyond that point for most of the species. For a few cases, because of insufficient time-series data for some years, the base year or end year were modified (e.g., the base year for analyses of Palearctic realm data was set to 1980). We used bootstrap resampling (bootstrap value = 10,000) (Collen et al., 2009) to create 95% confidence intervals (CIs) around each index value. These CIs were defined for each particular year using the bounds of the central 9,500 values for that year; they demonstrate the uncertainty in the index values inherited from the baseline in 1970 and propagated through the time series, although they do not reflect uncertainty in the annual

population estimates for each population time series or the average of multiple population time series for each species.

Following a recent approach to diversity-weighting the LPI method (McRae et al., 2017), we calculated a diversity-weighted reptile LPI. The difference between the global reptile index and a diversity-weighted one is that the former is an average of all species whereas the latter is a weighted average of species within each biogeographic realm subset. Using the World Wildlife Fund (WWF) Wildfinder database (WWF, 2006) for terrestrial and freshwater species and the Ocean Biogeographic Information System (OBIS, 2016) for marine species, we calculated total estimates of reptile species present in each of the biogeographic realms. Together, WWF Wildfinder and OBIS contained information for a total of 5,500 species of reptiles, which is around half the number of currently described reptile species. However, when we compared the proportions of reptile species by realm with those from a sampled species list broadly representative of global reptile diversity (Böhm et al., 2013), we found the values were comparable (Table S2) and therefore usable proxies for weighting by realm. The reptile data set was divided into five biogeographic realms (Australasia, Indo-Malaya, and Oceania were combined into an Indo-Pacific realm following McRae et al., 2017), and the weight applied to each was equal to the proportion of reptile species estimated to occur in that realm (Table S2).

Gap Analysis and Data Representativeness.—In addition to population time-series data, ancillary information was collected on taxonomic, geographical, and ecological aspects of each population. Taxonomically, we divided our data set into Crocodylia (or crocodilians; crocodiles, alligators, and gharials), Testudines (or chelonians; turtles, terrapins, and tortoises), Squamata (consisting of Sauria [lizards], Serpentes [snakes], and Amphisbaenia [worm lizards]), and the Rhynchocephalia (the tuatara). We investigated representativeness of our data set by using the estimates of reptile species present in each of the six biogeographic realms (as used for the weighted index described above) to assess the biogeographic representativeness of the reptile data by comparing this to the number of species per realm in the LPD. For this, we assigned each population to a biogeographic realm by taking geographic coordinates for each population from the data source or, if not reported, calculating a midpoint (i.e., a geographical mean of the range) as the location for that particular population. We also recorded the system (terrestrial, freshwater, and marine) where each population occurs (defined as the system where the population breeds and spends the majority of its lifetime).

To test whether our data set over- or underrepresented threatened species in each taxonomic group, system, and biogeographic realm, the number of species in each IUCN threat category (retrieved from the latest version of the IUCN Red List, with Critically Endangered, Endangered, and Vulnerable categories making up the three threatened categories; IUCN, 2016) in our data set was compared to the proportion in each threat category for reptiles as a whole, as estimated by a recent representative sampled assessment of 1,500 reptiles (Böhm et al., 2013). Recent analysis of this sampled assessment of reptiles showed that the majority of Data Deficient species lack data on population status and trends (Bland and Böhm, 2016). We excluded Data Deficient species from our gap analyses, as we would expect to have comparatively few data available for these species. For all gap analyses, we carried out individual binomial equality of proportions tests. To allow multiple comparisons based on taxonomy, system, and bioge-

graphical realm within binomial tests for each Red List category, we applied Bonferroni adjustments to our *P*-values. All statistical analyses were carried out in R v3.2.1 (R Core Team, 2015). To depict spatial representation of population time series, we overlaid locality points of populations onto maps of reptile species richness taken from Roll et al. (2017).

We assessed data quality as the fullness (number of data points) and mean length of population time series. We then compared these measures by system, biogeographic realm, and taxonomic group.

Sources of Reptile Population Time-Series Data.—We categorized the sources of reptile data according to the primary objective of data collection and publication. This classification has been used in the LPD based on the broad subject matters of the papers collated. We classified the sources into six groups described as follows:

- (1) Baseline monitoring: General monitoring such as annual census for a national park or an assessment to get basic status information for a population; e.g., a systematic assessment of marine turtles in the Dominican Republic to determine key nesting sites, population status, and current threats (Revuelta et al., 2012).
- (2) Conservation management: For monitoring management effectiveness or advising on management plan implementation, such as species action or recovery plans, effectiveness of reintroductions, or conservation assessments; e.g., continued monitoring of a species of special concern (*Graptemys geographica*) in Canada to identify demographic trends and establish some estimates of population size (Roche, 2002).
- (3) Natural resource management: Monitoring to assess the status of a population as a resource for human use or to assess accidental impact on species as a result of these activities; e.g., providing data on incidental catch of sea turtles *Dermochelys coriacea* and *Caretta caretta* in fishing gear near Tangier, Morocco (Benhardouze et al., 2012).
- (4) Population dynamics: Looking to answer ecological or demographical questions, i.e., cyclical patterns, mortality rates, density dependence, effects of perturbations, or habitat preference; e.g., a study identifying variables that drive population dynamics of reptiles in a sand dune landscape provided time-series data for the Flat-Tailed Horned Lizard *Phrynosoma mcallii*, Common Desert Iguana *Dipsosaurus dorsalis*, Zebra-Tailed Lizard *Callisaurus draconoides*, Sidewinder *Crotalus cerastes*, and Western Shovel-Nosed Snake *Chionactis occipitalis* (Barrows and Allen, 2010).
- (5) Tracking declining species: Monitoring of a declining or threatened species; e.g., declines were monitored in two Least Concern species of freshwater turtles in relation to urbanization in Texas (Brown et al., 2012).
- (6) Unspecified: Reason for study is not given in the data source.

We summarized the number of time series by taxon group that originated from each of these categories.

RESULTS

Living Planet Index for Reptiles.—On average, reptile populations have declined by 54% between 1970 and 2012, based on an unweighted LPI, and by 55% based on a weighted LPI approach

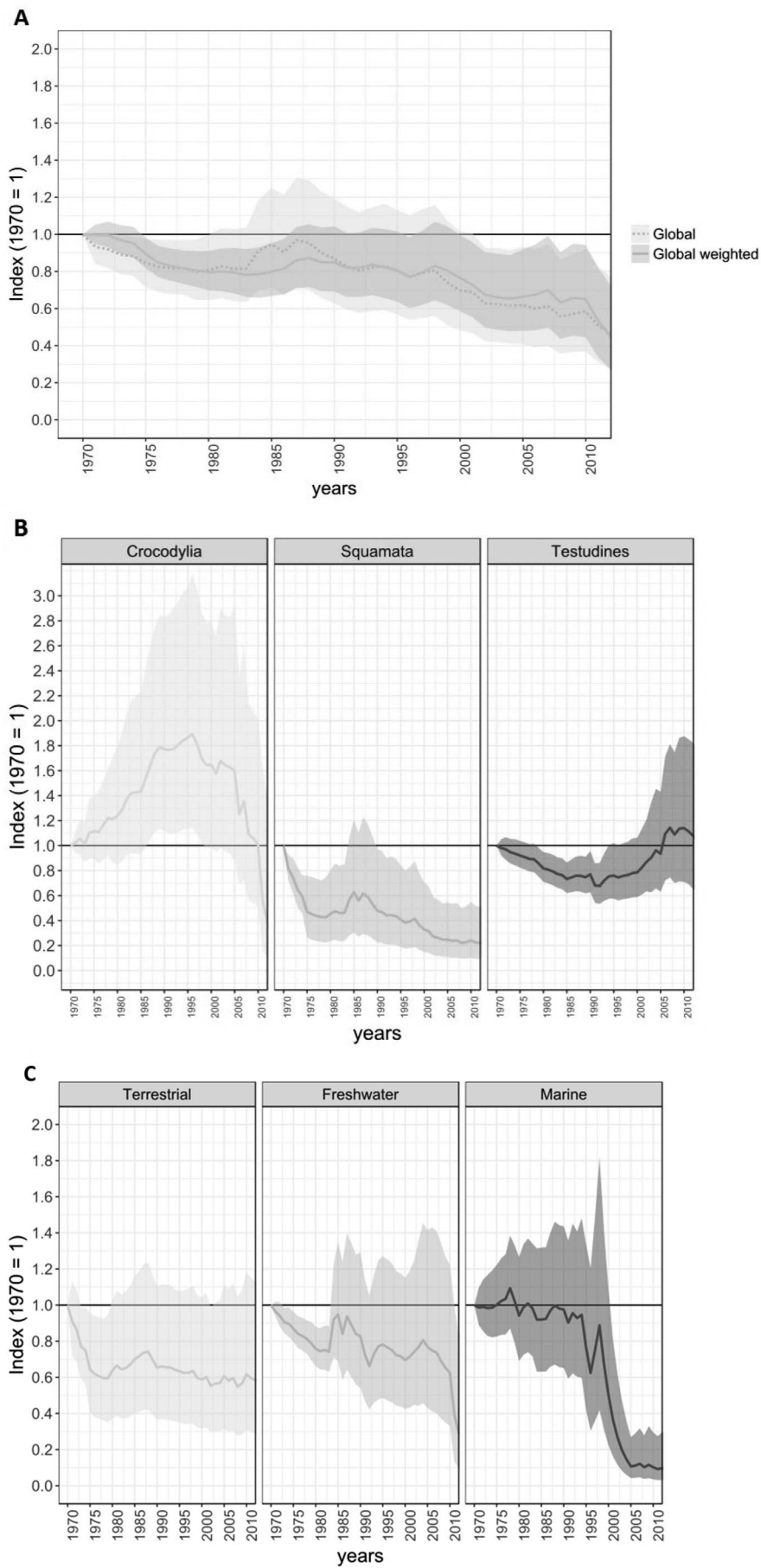


TABLE 1. Representation of threatened reptile species listed in the LPD across A. taxonomic groups, B. systems, and C. realms. Proportions observed (in our data set) and proportions expected (estimated from Böhm et al., 2013) are proportion of threatened species; P adj = Bonferroni adjusted P -value for multiple comparisons; ns = nonsignificant.

	Proportion observed	Proportion expected	χ^2	P	P adj	Over-/underrepresented
A. Taxonomic group						
Crocodylians	0.38	0.75	0.62	0.432	1	ns
Chelonians	0.60	0.51	0.29	0.589	1	ns
Squamates	0.17	0.18	<0.001	1	1	ns
Snakes	0.10	0.12	0.06	0.809	1	ns
Lizards	0.26	0.21	0.47	0.493	1	ns
All	0.36	0.19	24.23	<0.001	<0.001	+
B. System						
Terrestrial	0.21	0.19	0.27	0.602	1	ns
Freshwater/marine	0.46	0.29	3.54	0.060	0.600	ns
C. Realm						
Afrotropical	0.58	0.25	7.68	0.006	0.061	+
Australasian	0.26	0.16	1.82	0.178	1	ns
Indomalayan	0.92	0.14	43.78	<0.001	<0.001	+
Nearctic	0.21	0.14	0.91	0.341	1	ns
Neotropical	0.43	0.20	10.31	0.001	0.016	+
Palearctic	0.24	0.12	1.76	0.184	1	ns

(Fig. 1A). Prior to 1987, our data suggest an initial decline followed by an increasing population trajectory back almost to the baseline value (1987 unweighted index = 0.97, 95% CI = 0.71–1.31) (Fig. 1A), after which the index declines almost continuously until 2012 (2012 unweighted index = 0.46, 95% CI = 0.27–0.77).

Population abundance changes disaggregated by taxonomic group showed that squamate trends since 1970 most closely followed the overall trend in reptiles, though with an initial sharper decline (Fig. 1B). Chelonians showed a shallower decline with some recent increases since the early 1990s, and wider CIs, while crocodylians have shown overall increases between 1970 and 1995 although with wide CIs. The sudden drop in the latter graph is likely because of a data effect from a lack of time-series data after 2010.

The trajectories for disaggregation by system and realm show different patterns and varying CIs. While most trends are declining, freshwater and marine reptiles show the most-dramatic declines in both weighted (Fig. 1C) and unweighted indices (Fig. S1). Nearctic, Neotropical, and Afrotropical population trends showed irregular increase and decrease, with wide CIs, while trajectories for Australasian and Palearctic reptiles showed declines after an initial period of increase or stability (Fig. S2). Indomalayan population trends showed a continuous declining pattern and narrow CIs compared to the other realms.

Gap Analysis and Data Representativeness.—The LPD contains 549 time series from 194 reptile species representing 64% of crocodylians, 12% of chelonians, and only 2% of snake and 1% of lizard species (Fig. 2). Although amphisbaenians are not represented in the LPD, the database contains time series for the Tuatara (*Sphenodon punctatus*), the only extant species of the order Rhynchocephalia (Fig. 2). Threatened species were significantly overrepresented within our full data set, though this was

not found within taxonomic subgroups (Table 1); this is likely explained by the high proportion of highly threatened crocodylians and chelonians in the data set, so that the pattern of threatened species overrepresentation disappears within taxonomic groups. Likewise, threatened tropical species (Neotropical, Afrotropical, Indomalayan realms) also were significantly overrepresented. Least Concern and Data Deficient reptiles were significantly underrepresented (Table S3).

Spatial Distribution of Data.—Most data in the LPD originate from North America, with relatively sparse data from Africa and Southeast Asia (Fig. 3). This is particularly true for squamate reptiles (Fig. S3). Areas of estimated high species richness of reptiles were underrepresented within our time-series data, especially the Amazon region of South America, Central and Southern Africa, and Southeast and South Asia (Fig. 3). This result was supported by the assessment of representation by biogeographic realm (Table S4). This suggests that species from the Afrotropics, Indo-Malaya, and the Neotropics are significantly underrepresented in the LPD while species from the Nearctic and Australasia are significantly overrepresented.

Data Sources and Quality.—Most time-series data came from studies of ecological research (38% of time-series data) followed by data collected for conservation management (34%), tracking declining species (13%), and long-term monitoring programs (12%; Fig. 4). Conservation management and baseline monitoring were particularly important for data collection in chelonians and crocodylians whereas ecological studies of community or population dynamics were the main contributors to time-series data for squamate reptiles (Fig. 4).

The mean $\pm$ standard deviation (SD) time-series duration was 12.5 ± 8.7 yr, with a mean fullness (number of data points or years) of 9.0 ± 7.6 . Both measures of data quality varied amongst taxonomic groups, with crocodylians, chelonians, and snakes having the longest mean time series (14.2, 13.2, and 13.1

FIG. 1. Living Planet Indices (LPI) for reptiles from 1970 to 2012, based on 549 time series held in the Living Planet database (LPD). (A) All reptiles (194 species), unweighted (light grey, following Collen et al., 2009) and weighted (dark grey, following McRae et al., 2017); (B) by taxonomic group (crocodylians: 85 time series from 16 species; squamates [lizards and snakes]: 199 time series from 134 species; chelonians: 262 time series from 43 species; there were no population time series for amphisbaenians in the LPD); (C) by system (terrestrial: 211 time series from 132 species; freshwater: 154 time series from 52 species; marine: 183 time series from 15 species). The 95% confidence intervals were created around the mean index values with 10,000 bootstrap replicates.

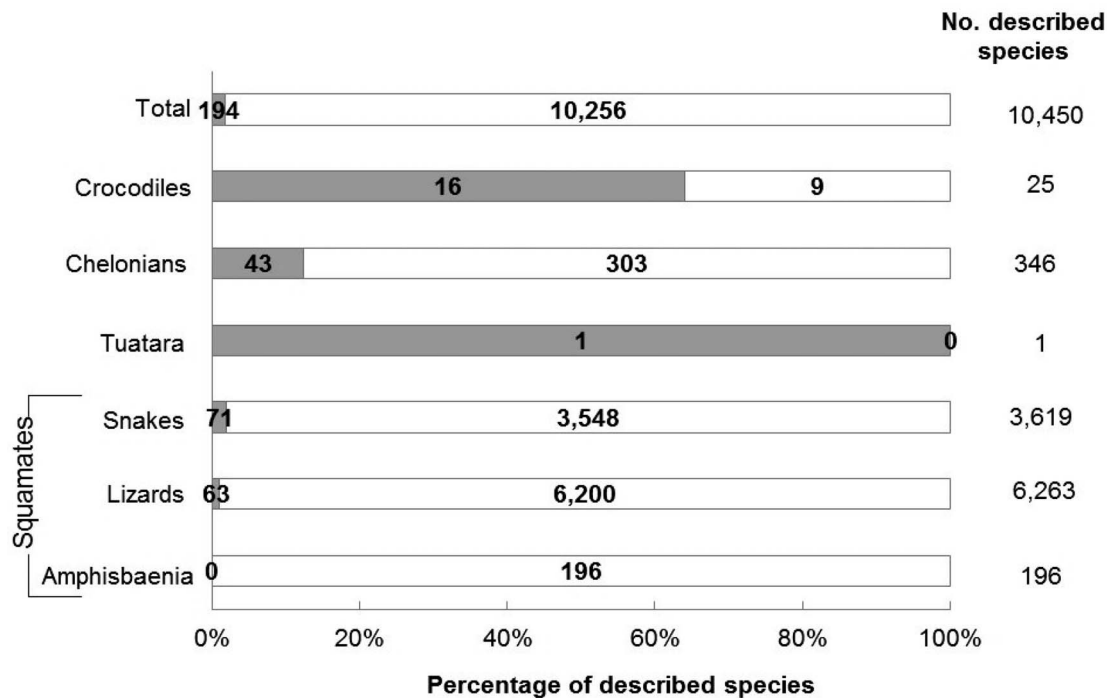


FIG. 2. Availability of reptile population time-series data in the LPD by major reptile taxonomic group. Overall numbers of species described are shown based on Uetz (2016).

yr, respectively) and lizards and the Tuatara having the shortest mean time series (8.2 and 5.0 yr, respectively; Fig. 5). Similarly, crocodilians, chelonians, and snakes had the most data points per time series (8.8, 10.1, and 9.2, respectively) compared to lizards and the Tuatara.

DISCUSSION

Over the last four decades, information collated in the LPD suggests an average decline of 54–55% within reptile populations, depending on the method used to calculate the index (Fig. 1A). These data corroborate prior suggestions that reptiles present a global conservation concern (Alroy, 2015). Previous studies estimated one in five species to be threatened with extinction (Böhm et al., 2013) and certain reptile groups, such as snakes, are suspected to be in widespread decline (Reading et al., 2010). To our knowledge, our study represents the first detailed analysis using the LPI method for a specific taxonomic group and shows that aggregated population time-series data are valuable for tracking changes in multiple species over time.

Our reptile index closely reflects population declines highlighted in the global LPI for vertebrates, which shows a 58% decline in vertebrate populations between 1970 and 2012 (WWF, 2016). Disaggregated by system, reptile population declines were most pronounced for freshwater and marine systems in reptiles, likely driven by the large number of chelonian and crocodilian time series in the data set; in the global LPI, declines are particularly high for freshwater vertebrates (81%) while terrestrial and marine vertebrates have seen declines of 38% and 36% each (WWF, 2016).

Although the overall reptile index is relatively robust with comparatively narrow CIs, disaggregation by system, realm, or taxonomic group introduces large amounts of uncertainty into our index calculations. For example, disaggregation by taxonomic group shows widening CIs and much more erratic (yet

declining) trends, especially for crocodilians and chelonians (Fig. 1B). This shows that even for these better-represented groups, there can still be a high level of uncertainty in the index values calculated because of contrasting signals in the underlying population trends. This can be exacerbated when the data set contains many short time series, but this is less likely to be the case for those groups that have a longer average length of time series compared to data from other reptile taxa. Chelonian trends show the shallowest declines; CIs become wider over time, likely because the interannual variability in nesting sea turtles means that peak and low counts may occur in different years according to species and location—something that can introduce high uncertainty around the index values for any given year. The implication from our results that some trends in chelonian species are more favorable might be true for marine turtles, as suggested by a recent assessment (Mazaris et al., 2017). The authors also noted that they found a greater significance in trends, both positive and negative, with increasing time-series length, emphasizing the importance of monitoring to be conducted long-term (Mazaris et al., 2017). This importance is reflected in our data set because, although turtles had some of the longest time series in the database on average, turtle lifespan may vastly exceed the length of time series represented in the LPI.

Although the highly species-rich squamates were the least-represented taxonomic group within the data set, the number of squamate species in the database still exceeded that for other taxonomic groups, so the trend in squamates most closely followed the overall reptile index trend. Recent studies suggested global declines in snakes (Reading et al., 2010), yet the quantification and verification of global snake declines likely requires further time-series data to allow meaningful disaggregation of the squamate data set. Freshwater reptiles showed more dramatic declines than did terrestrial reptiles, strongly following the trends shown for crocodilians and chelonians,

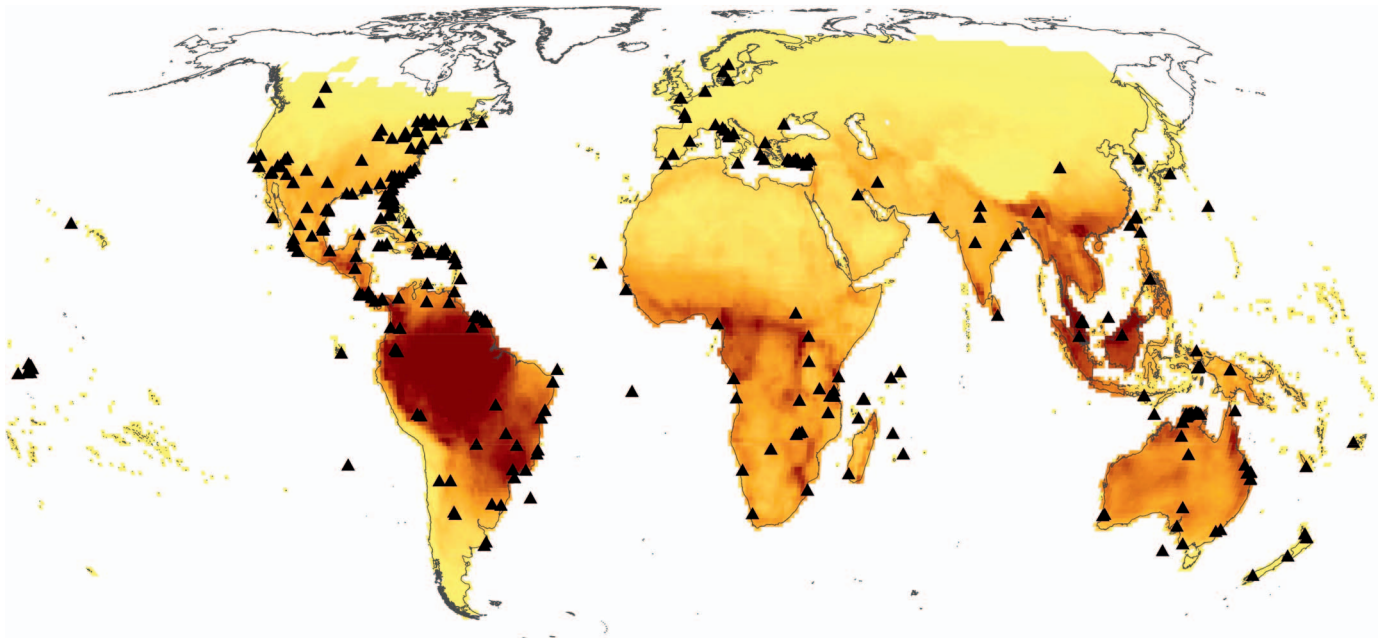


FIG. 3. Spatial distribution of population time-series data (triangles) for reptiles with data held in the LPD, superimposed on a global map of reptile species richness at 1-degree spatial resolution (Roll et al., 2017). Darker cells have higher species richness (maximum richness is 204 species per cell). Separate maps by taxon groups are presented in Figure S3.

most of which are freshwater species, but also reflecting the pattern observed for freshwater species in the global LPI for vertebrates (WWF, 2016). Similar dramatic declines appeared in the marine reptile index. All realm-based indices with the exception of the Palearctic index show a lack of recent time-series data while the index of Indomalayan reptiles has the tightest confidence intervals, suggesting that individual time series obtained for that region are likely to be undergoing similar declines.

Reptiles are the least-represented taxon in the LPD (McRae et al., 2017), especially the species-rich lizards and snakes, which have 6,263 and 3,548 described species, respectively (Uetz, 2016). Within available time-series data, quality varied amongst taxonomic groups, with some indication that time series were

longer and fuller in long-lived species. Our data suggest that crocodilians and chelonians are generally the focus of long-term monitoring studies, reflecting the longer time frames needed to determine population trends within these species compared to short-lived species. For example, Dorcas et al. (2007) collected 21 yr of mark-recapture data for the diamondback terrapin (*Malaclemys terrapin*) in South Carolina, USA, to assess whether observed declines in the population were caused by mortality from crab traps. Many intensive crocodile monitoring programs exist because of the potential economic value of these species in sustainable harvests (e.g., Nile Crocodile; Wallace et al., 2013) while many chelonians, especially sea turtles, have been the focus of conservation monitoring (e.g., Loggerhead Sea Turtle in Brazil; Marcovaldi and Chaloupka, 2007). On the other hand,

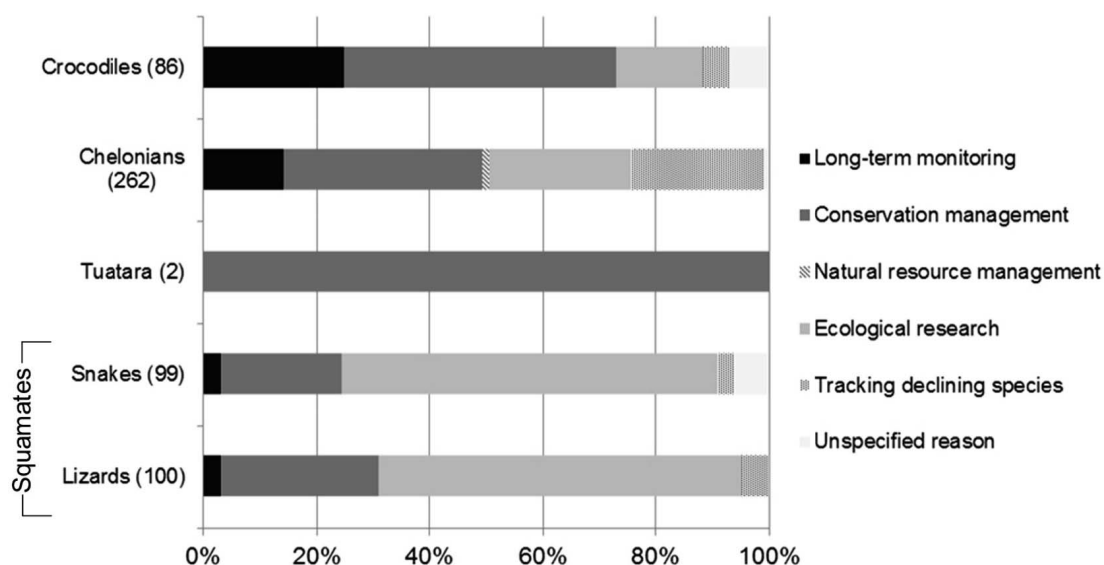


FIG. 4. Data sources publishing time-series data for reptiles, by major reptile group. There were no population time series for amphisbaenians in the LPD.

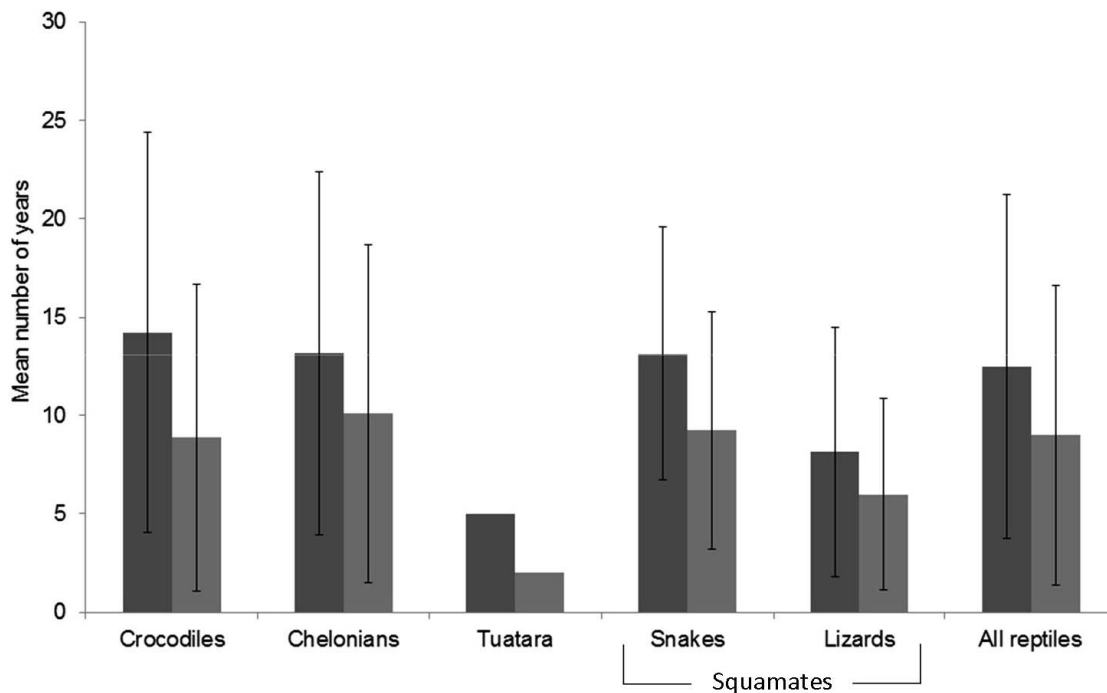


FIG. 5. Mean time-series length (dark grey) and mean fullness of time-series data (light grey) for reptiles in the LPD, both expressed as mean number of years, by major reptile group. Note: the reptile index covers a period of 42 yr, between 1970 and 2012. There were no population time series for amphisbaenians in the LPD.

squamates are widely studied in community and physiological ecology (Willson, 2016), and squamate time-series data mostly stemmed from ecological studies of population or community dynamics such as the 7 yr of data collected by Barrows and Allen (2010) on the population dynamics of six species of reptiles in a sand dune habitat. Ecological studies are often aimed at addressing specific questions and tied to limited funding sources and, as a consequence, often are comparatively short (Proença et al., 2017).

Our data set underrepresented species from tropical realms and overrepresented threatened species. Overall, 39% of reptile time-series data and 66% of the reptile species in the reptile index come from European and North American species whereas data from tropical populations are comparatively rare; this is a general trend within the LPD (Collen et al., 2009), although targeted data searches and weighting of the index (McRae et al., 2017) have helped to address this issue. Sampled IUCN Red List assessments showed that 21% of reptiles were Data Deficient: most of these were found in tropical regions (Böhm et al., 2013) and 52% lacked information on population trends and status (Bland and Böhm, 2016). Unsurprisingly, we found that Data Deficient species were significantly underrepresented in our data set. Similarly, regional work has emphasised that many Afrotropical reptile species are too inadequately sampled to allow status assessments (Tolley et al., 2016). Data biases may further arise because funding for monitoring is generally associated with threatened species (Martin-Lopez et al., 2011). In addition, research on threatened species may feature more prominently in international journals while ecological or baseline research from tropical regions may often be published in regional and national journals. Increasing data contributions from tropical countries is a high priority of the LPI and involves increasing outreach to researchers within underrepresented regions as well as overcoming language barriers to access research findings.

Filling gaps in taxonomic coverage in the LPD is especially difficult for the currently underrepresented squamates, which generally are more difficult to observe than are crocodilians and chelonians (Balestrin and Cappellari, 2011). Snakes are cryptic, secretive, often rare, and challenging to sample (Durso et al. 2011; Willson, 2016). Basic ecological and abundance information for fossorial and arboreal squamates is very limited (How and Shine, 1999; Böhm et al., 2013), because of the logistic difficulties of surveying these species (Henderson et al., 2016). As a result, our database is entirely lacking in time-series data for certain taxa such as the fossorial Amphisbaenia.

The relatively recent emergence of conservation assessments for reptiles has helped to expand knowledge of reptile status at global and regional scales (Cox and Temple, 2009; Böhm et al., 2013; Jenkins et al., 2014; Tolley et al., 2016). Whereas many of these assessments are based on criteria of restricted range, data on reptile time series held within the LPD can supplement assessments of species extinction risk using information on population reductions (e.g., IUCN Red List criterion A). This is especially true where multiple time series have been collated for a species, therefore allowing inferences of trends over time at the species level. Widely sharing best-practice techniques for sampling reptile abundances (e.g., Henderson et al. 2016; Lettink and Monk, 2016; Willson, 2016;) and the adaptation of available technology to reptile monitoring (e.g., camera trapping for reptiles, Welbourne et al. 2017) may enhance our ability to gather meaningful population data for reptiles and to address data biases.

Reptiles feature prominently in the study of ecological systems, despite an apparent past publishing bias toward endotherm organisms (Hecnar, 2009). Although improved data publication has occurred over recent years through open access publishing, along with a push toward reproducible science that results in the publication of raw data as supplementary materials, there is a need to increase data collection and/or

publication for reptile monitoring, especially to fill data gaps in the tropics. We recommend that researchers collect data using standardized and species-appropriate methods that allow repeatability in the future and increase both number and length of population time series. Widely sharing results for ecological research (Reichman et al., 2011) and for conservation purposes (e.g., LPI and other conservation assessments) is vital. This includes sharing population time-series data that may form the raw underlying data of more-advanced ecological analyses, and often may not be reported in the scientific literature, as well as past data which may be inaccessible in researcher notebooks or old formats of digital storage. To facilitate a process of fair data sharing, data need to be properly curated, data-sharing agreements need to be drawn up to remove concerns about data use without permission or attribution to the original author (e.g., Reichman et al., 2017), and there is a need to establish workflows to assist researchers with the extraction of old data stored in notebooks or outdated digital formats. The option to store data confidentially in the LPD is available so that data can contribute to large-scale analysis without compromising sensitive locations or species data. Lastly, there is a need to develop methods for monitoring underrepresented species using novel methods and approaches, especially within the vast group of squamate reptiles (Welbourne et al., 2017), a group that still remains underrepresented in conservation assessments as a result of persisting data gaps on population trends. Increasing availability of monitoring data for reptiles will help to improve the LPI for underrepresented species and allow data to be used in elaborate analyses on regional variation in trends, the impact of specific threats, and whether we are ultimately able to stop and reverse reptile declines in the future.

Acknowledgments.—MB is kindly supported by the Rufford Foundation; LM and the Living Planet Index (LPI) is supported by WWF. We kindly acknowledge the many individuals and organizations who have contributed data to the LPI and the dedicated volunteers, students, and staff, past and present, who have made the data collation and analysis possible.

LITERATURE CITED

- ALROY, J. 2015. Current extinction rates of reptiles and amphibians. *Proceedings of the National Academy of Science* 112:13003–13008.
- BAILLIE, J. E. M., J. GRIFFITHS, S. T. TURVEY, J. LOH, AND B. COLLEN. 2010. *Evolution Lost: Status and Trends of the World's Vertebrates*. Zoological Society of London, UK.
- BALESTRIN, R. L., AND L. H. CAPPELLARI. 2011. Reproduction and feeding ecology of *Amphisbaena munoai* and *Anops kingi* (Amphisbaenia, Amphisbaenidae) in the Escudo Sul-Rio-Grandense, southern Brazil. *Iheringia Serie Zoologia* 101:93–102.
- BARROWS, C. W., AND M. F. ALLEN. 2010. Patterns of occurrence of reptiles across a sand dune landscape. *Journal of Arid Environments* 74:186–192.
- BATES, M. F., W. R. BRANCH, A. M. BAUER, M. BURGER, J. MARAIS, G. J. ALEXANDER, AND M. S. VILLIERS. 2014. *Atlas and Red List of the Reptiles of South Africa, Lesotho and Swaziland*. South African National Biodiversity Institute, South Africa.
- BENHARDOUZE, W., M. AKSISSOU, AND M. TIWARI. 2012. Incidental captures of sea turtles in the driftnet and longline fisheries in northwestern Morocco. *Fisheries Research* 127–128:125–132.
- BLAND, L. M., AND M. BÖHM. 2016. Overcoming data deficiency in reptiles. *Biological Conservation* 204:16–22.
- BOAKES, E. H., P. J. K. MCGOWAN, R. A. FULLER, D. CHANG-QING, N. E. CLARK, K. O'CONNOR, AND G. M. MACE. 2010. Distorted views of biodiversity: spatial and temporal bias in species occurrence data. *PLoS Biology* 8:e1000385.
- BÖHM, M., B. COLLEN, J. E. M. BAILLIE, P. BOWLES, J. CHANSON, N. COX, G. HAMMERSON, M. HOFFMANN, S. R. LIVINGSTONE, AND M. RAM. 2013. The conservation status of the world's reptiles. *Biological Conservation* 157:372–385.
- BROWN, D. J., A. D. SCHULTZ, J. R. DIXON, B. E. DICKERSON, AND M. R. J. FORSTNER. 2012. Decline of red-eared sliders (*Trachemys scripta elegans*) and Texas spiny softshells (*Apalone spinifer emoryi*) in the Lower Rio Grande Valley of Texas. *Chelonian Conservation and Biology* 11:138–143.
- BUTCHART, S. H. M., M. WALPOLE, B. COLLEN, A. VAN STRIEN, J. P. W. SCHARLEMANN, R. E. A. ALMOND, J. E. M. BAILLIE, B. BOMHARD, C. BROWN, AND J. BRUNO. 2010. Global biodiversity: indicators of recent declines. *Science* 328:1164–1168.
- COLLEN, B., J. LOH, S. WHITMEE, L. MCRAE, R. AMIN, AND J. E. M. BAILLIE. 2009. Monitoring change in vertebrate abundance: the Living Planet Index. *Conservation Biology* 23:317–327.
- CONNER, M. M., J. J. KEANE, C. V. GALLAGHER, T. E. MUNTON, AND P. A. SHAKLEE. 2016. Comparing estimates of population change from occupancy and mark-recapture models for a territorial species. *Ecosphere* 7:e01538.
- COX, N. A., AND H. J. TEMPLE. 2009. *European Red List of Reptiles*. Office for Official Publications of the European Communities, Luxembourg.
- CRAIGIE, I. D., J. E. M. BAILLIE, A. BALMFORD, C. CARBONE, B. COLLEN, R. E. GREEN, AND J. M. HUTTON. 2010. Large mammal population declines in Africa's protected areas. *Biological Conservation* 143:2221–2228.
- DORCAS, M. A., J. D. WILLSON, AND J. W. GIBBONS. 2007. Crab trapping causes population decline and demographic changes in diamond-back terrapins over two decades. *Biological Conservation* 137:334–340.
- DURSO, A. M., J. D. WILLSON, AND C. T. WINNE. 2011. Needles in haystacks: estimating detection probability and occupancy of rare and cryptic snakes. *Biological Conservation* 144:1508–1515.
- FEWSTER, R. M., S. T. BUCKLAND, G. M. SIRIWARDENA, S. R. BAILLIE, AND J. D. WILSON. 2000. Analysis of population trends for farmland birds using generalized additive models. *Ecology* 81:1970–1984.
- GALEWSKI, T., B. COLLEN, L. MCRAE, J. LOH, P. GRILLAS, M. GAUTHIER-CLERC, AND V. DEVICOR. 2011. Long-term trends in the abundance of Mediterranean wetland vertebrates: from global recovery to localized declines. *Biological Conservation* 144:1392–1399.
- GIBBONS, J. W., D. E. SCOTT, T. J. RYAN, K. A. BUHLMANN, T. D. TUBERVILLE, B. S. METTS, J. L. GREENE, T. MILLS, Y. LEIDEN, S. POPPY, ET AL. 2000. The global decline of reptiles, déjà vu amphibians. *Bioscience* 50:653–666.
- HECNAR, S. J. 2009. Human bias and the biodiversity knowledge base: an examination of the published literature on vertebrates. *Biodiversity* 10:18–24.
- HENDERSON, R. W., R. POWELL, J. MARTIN, AND P. LOPEZ. 2016. Arboreal and fossorial reptiles. Pp. 139–153 in C. K. Dodd Jr.(ed.), *Reptile Ecology and Conservation: A Handbook of Techniques*. Oxford University Press, UK.
- HOW, R. A., AND R. SHINE. 1999. Ecological traits and conservation biology of five fossorial 'sand-swimming' snake species (*Simoselaps*: Elapidae) in south-western Australia. *Journal of Zoology* 249:269–282.
- IUCN (INTERNATIONAL UNION FOR CONSERVATION OF NATURE). 2016. The IUCN Red List of Threatened Species 2016.2. Available at <http://www.iucnredlist.org>.
- JENKINS, R. K. B., M. F. TOGNELLI, P. BOWLES, N. COX, J. L. BROWN, L. CHAN, F. ANDREONE, A. ANDRIAMAZAVA, R. R. ANDRIANTSIMANARILAFY, AND M. ANJERINIANINA. 2014. Extinction risks and the conservation of Madagascar's reptiles. *PLoS One* 9:e100173.
- JONES, J. P. G., B. COLLEN, G. ATKINSON, P. W. J. BAXTER, P. BUBB, J. B. ILLIAN, T. E. KATZNER, A. KEANE, J. LOH, E. McDONALD-MADDEN, ET AL. 2011. The why, what, and how of global biodiversity indicators beyond the 2010 target. *Conservation Biology* 25:450–457.
- LETTINK, M., AND J. M. MONK. 2016. Survey and monitoring methods for New Zealand lizards. *Journal of the Royal Society of New Zealand* 46:16–28.
- LOH, J., R. E. GREEN, T. RICKETTS, J. LAMOREUX, M. JENKINS, V. KAPO, AND J. RANDERS. 2005. The Living Planet Index: using species population time series to track trends in biodiversity. *Philosophical Transactions of the Royal Society B-Biological Sciences* 360:289–295.
- MARCOVALDI, M. A., AND M. CHALOUPKA. 2007. Conservation status of the loggerhead sea turtle in Brazil: an encouraging outlook. *Endangered Species Research* 3:133–143.
- MARTIN-LOPEZ, B., J. A. GONZALEZ, AND C. MONTES. 2011. The pitfall-trap of species conservation priority setting. *Biodiversity and Conservation* 20:663–682.

- MAZARIS, A. D., G. SCHOFIELD, C. GKAZINO, V. ALMPANIDOU, AND G. C. HAYS. 2017. Global sea turtle conservation successes. *Science Advances* 3:e1600730.
- MCRÆ, L., M. BÖHM, S. DEINET, M. GILL, AND B. COLLEN. 2012. The Arctic Species Trend Index: using vertebrate population trends to monitor the health of a rapidly changing ecosystem. *Biodiversity* 13:144–156.
- MCRÆ, L., S. DEINET, AND R. FREEMAN. 2017. The diversity-weighted Living Planet Index: controlling for taxonomic bias in a global biodiversity indicator. *PLoS One* 12:e0169156.
- MEIRI, S. 2016. Small, rare and trendy: traits and biogeography of lizards described in the 21st Century. *Journal of Zoology* 299:251–261.
- MEIRI, S., AND D. G. CHAPPLE. 2016. Biases in the current knowledge of threat status in lizards, and bridging the ‘assessment gap.’ *Biological Conservation* 204:6–15.
- NICHOLSON, E., B. COLLEN, A. BARAUSSE, J. L. BLANCHARD, B. T. COSTELLOE, K. M. E. SULLIVAN, F. M. UNDERWOOD, R. W. BURN, S. FRITZ, J. P. G. JONES, ET AL. 2012. Making robust policy decisions using global biodiversity indicators. *PLoS One* 7:e41128.
- OBIS (OCEAN BIOGEOGRAPHIC INFORMATION SYSTEM). 2016. Distribution records of marine vertebrate species (numerous data sets). Available at <http://www.iobis.org>. Archived by WebCite at <http://www.webcitation.org/6wCTRbTpf> on 3 January 2018.
- PROENÇA, V., L. J. MARTIN, H. M. PEREIRA, M. FERNANDEZ, L. MCRÆ, J. BELNAP, M. BÖHM, N. BRUMMITT, J. GARCÍA-MORENO, R. D. GREGORY, ET AL. 2017. Global biodiversity monitoring: from data sources to essential biodiversity variables. *Biological Conservation* 213:256–263.
- R CORE TEAM. 2015. R: a language and environment for statistical computing. R Foundation for Statistical Computing. Available from: <http://www.R-project.org>. Accessed 3 January 2018.
- READ, J. L. 1998. Are geckos useful bioindicators of air pollution? *Oecologia* 114:180–187.
- READING, C. J., L. M. LUISELLI, G. C. AKANI, X. BONNET, G. AMORI, J. M. BALLOUARD, E. FILIPPI, G. NAULLEAU, D. PEARSON, AND L. RUGIERO. 2010. Are snake populations in widespread decline? *Biology Letters* 6:777–780.
- REICHMAN, O. J., M. B. JONES, AND M. P. SCHILDHAUER. 2011. Challenges and opportunities of open data in ecology. *Science* 331:703–705.
- REVUELTA, O., Y. M. LEON, P. FELIZ, B. J. GODLEY, J. A. RAGA, AND J. TOMÁS. 2012. Protected areas host important remnants of marine turtle nesting stocks in the Dominican Republic. *Oryx* 46:348–358.
- ROCHE, B. 2002. COSEWIC status report on the northern map turtle *Graptemys geographica* in Canada. Committee on the Status of Endangered Wildlife in Canada. Canada.
- ROLL, U., A. FELDMAN, M. NOVOSOLOV, A. ALLISON, A. M. BAUER, R. BERNARD, M. BÖHM, F. CASTRO-HERRERA, L. CHIRIO, AND B. COLLEN. 2017. The global distribution of tetrapods reveals a need for targeted reptile conservation. *Nature Ecology & Evolution* 1:1677–1682.
- TITTENSOR, D. P., M. WALPOLE, S. L. L. HILL, D. G. BOYCE, G. L. BRITTEN, N. D. BURGESS, S. H. M. BUTCHART, P. W. LEADLEY, E. C. REGAN, AND R. ALKEMADE. 2014. A mid-term analysis of progress toward international biodiversity targets. *Science* 346:241–244.
- TOLLEY, K. A., G. J. ALEXANDER, W. R. BRANCH, P. BOWLES, AND B. MARITZ. 2016. Conservation status and threats for African reptiles. *Biological Conservation* 204:63–71.
- TROUDET, J., P. GRANDCOLAS, A. BLIN, R. VIGNES-LEBBE, AND F. LEGENDRE. 2017. Taxonomic bias in biodiversity data and societal preferences. *Scientific Reports* 7:9132.
- TURTLE TAXONOMY WORKING GROUP (Rhodin, A. G. J., J. B. Iverson, R. Bour, U. Fritz, A. Georges, H. B. Shaffer, and P. P. van Dijk). 2017. Turtles of the world: annotated checklist and atlas of taxonomy, synonymy, distribution, and conservation status. 8th ed. Pp. 1–292 in A. G. J. Rhodin, J. B. Iverson, P. P. van Dijk, R. A. Saumure, K. A. Buhlmann, P. C. H. Pritchard, and Mittermeier, R. A. (eds.), *Conservation Biology of Freshwater Turtles and Tortoises: A Compilation Project of the IUCN/SSC Tortoise and Freshwater Turtle Specialist Group*. Chelonian Research Monographs 7. Chelonian Research Foundation and Turtle Conservancy, USA.
- UETZ, P. 2016. The Reptile Database. Available at <http://www.reptile-database.org>. Archived by WebCite at <http://www.webcitation.org/6wCSxf3v5> on 3 January 2018.
- WALLACE, K. M., A. J. LESLIE, T. COULSON, AND A. S. WALLACE. 2013. Population size and structure of the Nile crocodile *Crocodylus niloticus* in the lower Zambezi valley. *Oryx* 47:457–465.
- WELBOURNE, D. J., D. J. PAULL, A. W. CLARIDGE, AND F. FORD. 2017. A frontier in the use of camera traps: surveying terrestrial squamate assemblages. *Remote Sensing in Ecology and Conservation* 3:133–145.
- WILLSON, J. D. 2016. Surface-dwelling reptiles. Pp. 125–138 in C. K. Dodd Jr.(ed.), *Reptile Ecology and Conservation: A Handbook of Techniques*. Oxford University Press, UK.
- WWF (WORLD WILDLIFE FUND). 2006. WildFinder: online database of species distributions, ver. Jan-06. Available at <http://www.worldwildlife.org/WildFinder>. Archived by WebCite at <http://www.webcitation.org/6wCSOHRva> on 3 January 2018.
- . 2016. Living Planet Report 2016. Risk and Resilience in a New Era. World Wildlife Fund International, Switzerland.
- ZOOLOGICAL SOCIETY OF LONDON AND WORLD WILDLIFE FUND. 2017. The Living Planet Database. Available at <http://www.livingplanetindex.org>. Archived by WebCite at <http://www.webcitation.org/6wCSqGb28> on 3 January 2018.

Accepted: 23 March 2018.

Published online: 14 June 2018.

SUPPLEMENTARY DATA

Supplementary data associated with this article can be found online at <http://dx.doi.org/10.1670/17-076.s1>.