Biological Conservation 233 (2019) 61–72

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

No safe haven: Protection levels show imperilled South African reptiles not sufficiently safe-guarded despite low average extinction risk

Krystal A. Tolley[a,b,*], Joshua Weeber[a], Bryan Maritz[c], Luke Verburgt[d], Michael F. Bates[e,f], Werner Conradie[g,h], Margaretha D. Hofmeyr[c], Andrew A. Turner[c,i], Jessica M. da Silva[a,j], Graham J. Alexander[k]

[a] South African National Biodiversity Institute, Kirstenbosch Research Centre, Private Bag X7, Newlands, Cape Town 7945, South Africa
[b] Centre for Ecological Genomics and Wildlife Conservation, University of Johannesburg, Auckland Park, 2006 Johannesburg, South Africa
[c] Department of Biodiversity and Conservation Biology, University of the Western Cape, Private Bag X17, Bellville 7535, South Africa
[d] Department of Zoology & Entomology, University of Pretoria, Pretoria 0001, South Africa
[e] Department of Herpetology, National Museum, P.O. Box 266, Bloemfontein 9300, South Africa
[f] Department of Zoology & Entomology, University of the Free State, P.O. Box 339, Bloemfontein 9300, South Africa
[g] Port Elizabeth Museum, P.O. Box 13147, Humewood 6013, South Africa
[h] School of Natural Resource Management, George Campus, Nelson Mandela University, George 6530, South Africa
[i] CapeNature, Scientific Services, Private Bag X5014, Stellenbosch 7599, South Africa
[j] Department of Botany and Zoology, Stellenbosch University, Private Bag X1, Matieland, 7602. Stellenbosch, South Africa
[k] School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, P.O. Wits, 2050 Johannesburg, South Africa

ARTICLE INFO

Keywords:
Africa
Biodiversity
Conservation
Global Reptile Assessment
Habitat loss
Reptilia

ABSTRACT

Compared to the global average, extinction risk for mainland African reptiles, particularly for South Africa, appears to be relatively low. Despite this, African reptiles are under threat primarily due to habitat loss as a result of agriculture, resource extraction, and urbanisation, and these pressures are expected to increase into the future. South Africa's reptile fauna is relatively well-studied, allowing an investigation of whether threat status assessment limitations are driving the comparably low threat status for the country, a large component of Africa's reptile fauna (ca. 25% of mainland African reptiles are found in South Africa). Extinction risk of South African reptiles was assessed as of 2018 using IUCN criteria and we 'backcast' these assessments to infer extinction risk circa 1990. A Red List Index (RLI: a measure of the extinction risk for a group of species) for 1990 and 2018 was estimated, and the protection level afforded to South African reptiles was investigated by intersecting reptile distributions with the network of protected areas. Finally, a coarse estimate of extinction rate was made. Level of extinction risk for South African reptiles (ca. 5.4%) is lower than the global average, and most currently threatened species would have already been at risk by 1990. The RLI was slightly lower for 2018 than for 1990, and the decrease was more prominent for endemic reptiles than for all reptiles combined. Most South African reptiles fall into the Well Protected category, implying that the protected area network has substantial conservation impact. However, many threatened reptile species are Poorly Protected or Not Protected. The current extent of the protected area network therefore, does not adequately mitigate extinction risk for reptiles. Furthermore, the protected area expansion plan for South Africa would not capture any additional threatened species within its boundaries. Despite the lower level of extinction risk indicated by IUCN assessments, it would be premature to assume that South African reptiles are faring better than reptiles globally based only on this one measure. Notably, two South African reptiles are Critically Endangered and theses are not found in protected areas, two others are already classified as Extinct, and rough estimates of extinction rates are similar to values estimated for other vertebrates. By considering additional metrics that are directly guided by our in-depth knowledge of the species, their distributions and the threats, we demonstrate that South African reptiles are under pressure and that risk of extinction is tangible for several species.

* Corresponding author at: South African National Biodiversity Institute, Kirstenbosch Research Centre, Private Bag X7, Newlands, Cape Town 7945, South Africa.
E-mail address: k.tolley@sanbi.org.za (K.A. Tolley).

https://doi.org/10.1016/j.biocon.2019.02.006
Received 22 November 2018; Received in revised form 30 January 2019; Accepted 5 February 2019
Available online 25 February 2019

1. Introduction

With > 2000 reptile species, continental Africa and associated islands are home to ca. 20% of the world's reptile species. Given the sustained high rate of species discovery and a general lack of knowledge of African reptiles (Tolley et al., 2016), current evaluations of species richness are most likely underestimates. For example, the rate of species descriptions for mainland African reptiles is climbing steadily (Tolley et al., 2016) with new discoveries being made, especially in regions that have historically received little survey attention (e.g. Conradie et al., 2016; Marques et al., 2018). Remarkably, the proportion of mainland African reptile species assessed to date that are at risk of extinction (Critically Endangered, Endangered, Vulnerable), appears to be slightly lower (ca. 13%; Tolley et al., 2016) compared to the global average (ca. 15%; Böhm et al., 2013). Further, South African reptiles appear to be even less threatened (ca. 10%; Bates et al., 2014). Does this discrepancy suggest that Africa's reptiles are not under substantial current and future threat of extinction, as compared to the global norm? Alternatively, could a lack of knowledge regarding threats (and taxonomy) be biasing the estimates of extinction risk downward for Africa? It is thought that habitat transformation, particularly due to agriculture, resource extraction and urbanisation, is the primary threat to those species that have been assessed to date (Jenkins et al., 2014; Tolley et al., 2016), and robust information on these threats for Africa is lacking. Regardless of the reason for the current discrepancy, it is likely that extinction risk will intensify given that these impacts on the landscape are linked to human population growth, as Africa's human population is projected to quadruple to over four billion by the end of the century (African Economic Outlook, 2014; Gerland et al., 2014). Africa's reptiles are therefore likely to become more threatened over time as the human footprint increases (e.g. Venter et al., 2016).

A major challenge to interpreting the seemingly low threat levels of African reptiles is that fewer than half (48%) of all mainland African species have been assessed for extinction risk. Moreover, the subset of those species that have been assessed is not a random sample of all species, but rather is biased to specific regions and taxonomic groups (Tolley et al., 2016). This could have led to a bias in perceived patterns of threat and it is likely that the current estimate of threat for African reptiles is inadequate. An alternative explanation for the seemingly low threat levels is that habitat transformation and the impacts of high human population growth are relatively recent phenomena, with most of the population growth occurring during the second half of the 20th century and the beginning of the 21st century (Gerland et al., 2014). This relatively recent population growth and concomitant habitat transformation might mean that African reptiles are characterised by an extinction debt whereby there is a time lag in the loss of populations or species (Halley et al., 2016; Hanski and Ovaskainen, 2002; Kuussaari et al., 2009; Tilman et al., 1994) and/or detection of losses. Essentially, our ability to assess the plausibility of this scenario is hindered by a lack of rigorous, repeated, conservation assessments for comprehensive reptile faunas.

Unfortunately, habitat transformation is not the sole threat facing African reptiles. Several threats are less obvious and more difficult to quantify, especially when those species are poorly known, or when trends of habitat transformation mask population-level threats. For example, direct exploitation for the pet trade and traditional medicine is largely unmeasured but potentially of high impact in some situations and for certain species (Parusnath et al., 2017; Williams et al., 2016). Selective hunting (for direct consumption and/or the bushmeat trade) of large-bodied species such as crocodiles, tortoises and terrapins can have profound negative effects on populations and increases the likelihood of localized extinctions for targeted species (e.g. Petrozzi et al., 2016; Taylor et al., 2015). Domestic cats are a major predator of reptiles in Australia (Woinarski et al., 2018) and this is likely to hold true across some parts of Africa. This source of mortality is concerning as cat predation on reptiles is under-reported (Loyd et al., 2013), fortunately, a bias that can be corrected with on-cat cameras (Loyd et al., 2013; Morling, 2014). Roads have direct effects on reptiles and although there are few studies from South Africa (but see Collinson et al., 2015), the effects are likely to be similarly negative as for studies conducted elsewhere. Electrified fences are another lethal obstacle for several South African reptile species (Beck, 2010; Macray, 2017). Additionally, habitat fragmentation, inappropriate fire management, and the removal of apex predators and large herbivores profoundly impact ecosystem functioning. These impacts could be having unappreciated effects on population demographics, fecundity, survival and genetic diversity, causing 'enigmatic' declines (e.g. Cressey et al., 2014; Whitfield et al., 2007) due to disruption of natural demographic and ecological processes. Some effects may be subtle or difficult to discern without long-term monitoring. For example, some species that are listed as Least Concern due to their large geographic ranges (Criterion B) might occur at very low densities and therefore susceptible to Allee effects, particularly as a result of ongoing habitat fragmentation and degradation (e.g. Gibbons et al., 2000), and thus may decline more rapidly than expected. Consequently, the lack of regular, rigorous, conservation assessments throughout Africa might significantly underestimate threats.

South Africa's reptile fauna is diverse, with 407 species (264 lizards, 117 snakes, 24 chelonians, one crocodile) and over 50% endemism (Bates et al., 2014; Supplementary information: Table S1). This places South Africa's reptile fauna within the top 10% of diverse reptile faunas globally, despite the country's relatively small land area (1.22 million km^2). This also means that South Africa accounts for nearly a quarter of mainland African reptile diversity (as it is currently understood). South Africa's entire reptile fauna has been comprehensively assessed for threat status (see Bates et al., 2014) and ca. 10% of reptiles were considered to be at risk of extinction. As with continental patterns, the principal threats facing South African reptiles are habitat loss and alteration due to agriculture and urbanisation (Bates et al., 2014; Tolley et al., 2016).

Here, we take advantage of the fact that South Africa's reptile fauna is comparatively well-studied to investigate whether threat status assessment limitations are driving the comparably low threat status for the country, which represents a large component of Africa's reptile fauna. We re-assess the extinction risk of South African reptiles using IUCN criteria and assign threat categories to each species. We use standard protocols to assign each species to recognised categories for the present (2018) and 'backcast' assessments to infer the level of extinction risk for each species in 1990. Backcasting was necessary as most South African reptile species were not assessed in 1990 and for those that were, different categories and criteria were applied (Branch, 1988). Our backcasting allows for an estimate of the Red List Index (RLI), a measure of the extinction risk for a group of species (i.e. reptiles) over time (e.g. Böhm et al., 2013), revealing changes in potential causes of reptile decline. We also assess the level of protection currently afforded to South African reptiles by intersecting interpreted distributions of all reptiles with the network of nationally recognised protected areas. We made a coarse estimate of extinction rate and compared this to estimated rates for other major vertebrate groups. This information was then used to forecast extinction rates given the IUCN extinction risk categories that we assigned to South African reptiles.

2. Methods

2.1. Threat status, trends and protection level

Of the 407 species of reptiles currently known from South Africa (Supplementary information: Table S1), 15 peripheral species (i.e. ≤1% of their distribution in South Africa, including marine reptile species) and one introduced/established species (*Indotyphlops braminus*) were not evaluated (NE). Of the remaining 391 species, 209 are endemic or near-endemic (i.e. ≥90% of distribution within South Africa) and 182 are non-endemic. Two endemic species are classified as

Extinct. Some of these values differ from the previous (2014) assessments (see Bates et al., 2014) due to taxonomic changes, new species descriptions and because subspecies were included in Bates et al. (2014). The current species list also differs in the number of peripheral species due to the collection of new distribution information and because of our exclusion of marine reptiles.

South African reptiles were assessed following the IUCN process for extinction risk as of 2018 (as per IUCN Standards and Petitions Subcommittee, 2017; Mace et al., 2008). Global assessments were carried out for endemic/near-endemic species, whereas regional (i.e. national) assessments were carried out for non-endemics (Supplementary information: Table S1). Based on IUCN Red List Categories and Criteria V3.1 (IUCN, 2012), the following threat categories were assigned: Critically Endangered (CR), Endangered (EN), Vulnerable (VU), Near Threatened (NT), Least Concern (LC) and Data Deficient (DD). Most species were assessed on the "B" set of criteria, which relates to the quality, extent and fragmentation of remaining suitable habitat. These criteria were used due to the general absence of long-term population data that are required under other criteria. Interpreted distributions were drawn for each species guided by an assembled set of data from Bates et al. (2014), iNaturalist (https://www.inaturalist.org/), and major active collections in South Africa (Port Elizabeth Museum; National Museum, Bloemfontein), superimposed onto satellite imagery (courtesy Google Corporation), the most recent (from 2013) national land cover dataset (GeoTerraImage, 2015) as well as the regional vegetation map of South Africa (Mucina and Rutherford, 2006). The area of each distribution was defined as the area of the interpreted distribution measured in km^2 using the Africa Albers Equal Area Conic projection (EPSG: 102022). The Extent of Occurrence (EOO) was estimated by measuring the area of the minimum convex hull around the interpreted distribution. Area of Occupancy (AOO) for well-known species with small distributions was estimated using the new IUCN guidelines where the sum of occupied $2 \times 2\,km^2$ grid cells is given for species (IUCN Standards and Petitions Subcommittee, 2017). The EOO and AOO both have defined area thresholds, which were used to assign the appropriate threat category.

Using the process described above, each species was also evaluated for its threat status as of the year 1990 ('backcast'). The interpreted distributions were intersected with a vector layer denoting all natural areas in 1990 derived from the South African National land cover layer 1990 (NLC-1990) to examine the EOO or AOO for that time period in relation to available suitable habitat. We then postulated the severity of threats for 1990 and assigned a threat category based on the backcast EOO or AOO. Using the IUCN categories, we then generated a Red List Index (RLI) that equates to the proportion of species expected to remain extant in the near future (i.e. approximately 50 years, see Butchart et al., 2007). An RLI of 1 indicates that all species are Least Concern and none are at risk of extinction, whereas a score of 0 indicates that all species are extinct. The RLI was estimated for the two time-points, 1990 and 2018, by applying the RLI formula following Butchart et al. (2007). DD and NE species were excluded, and the same set of species was subjected to the assessment for both time points (as per Butchart et al., 2007). Therefore, RLI at each time point (t) was estimated as 1 minus the summed relative weights of the threat status for all species (ranging from 0 to 5, LC to EX), divided by the number of species included (i.e. 379, which excludes DD and NE species), multiplied by the extinction weight (i.e. 5):

$$RLI_t = 1 - \frac{\sum_s W_{c(t,s)}}{W_{EX} \times N} \tag{1}$$

where $W_{c(t,s)}$ is the relative weight for each species, W_{EX} is the relative weight assigned to extinct species (i.e. 5), and N is the total number of species assessed (excluding DD and species considered extinct at the first time point). Following this, we calculated a weighted RLI, whereby threat status values were weighted according to the proportion of a species' geographic distribution falling within South Africa. Proportions (P) were estimated based on the interpreted distribution maps and rounded off to a limited number of categories (0.10, 0.25, 0.50, 0.75, 0.90 or 1.0).

$$wRLI_t = 1 - \frac{\sum_s W_{c(t,s)} \times P}{W_{EX} \times N} \tag{2}$$

Although this distribution proportion rounding could reduce the precision of our weighted RLI estimate for the non-endemic species, we considered this approach appropriate as some of the non-endemic species distributions are not well-known outside of South Africa, and estimates on a finer resolution could not be made. The wRLI was estimated for all species combined, but also estimated separately for the subset of 207 extant endemic/near-endemic species.

We evaluated the effectiveness of South Africa's protected area network toward ensuring that minimum viable populations of reptiles are protected (full protocol in Supplementary material: Appendix A1). We set a conservation target for protection of at least 10 fragments of habitat, each with areas of at least $10\,km^2$ (1000 ha) for a total of $100\,km^2$ for each species. The fragment size was considered to be the minimum area that would support viable populations, with the total area considered to be the total area needed to ensure the species survival into the future. The interpreted distributions for each species were then intersected with South Africa's protected area network (Government of South Africa, 2010). Protected areas recognised in terms of the South African National Environmental Management: Protected Areas Act (Act 57 of 2003) and considered secure into the future were included (Island Nature Reserves, Forest Wilderness Areas, Forest Nature Reserves, World Heritage Sites, Wilderness Areas, Provincial Nature Reserves and National Parks). Species that showed no intersect with protected areas were considered Not Protected, whereas those with at least ten $10\,km^2$ intersects with protected areas were considered Well Protected. Species with fewer than ten $10\,km^2$ intersects were then identified and protected areas within their distributions were tabulated. The efficacy of each protected area was assigned as good, fair or poor based on apparent vegetation intactness as represented by remotely sensed imagery, and/or on our own expert knowledge of the protected areas. This rating was used to weight the total area (km^2) for that protected area (1.0, 0.5, and 0.1, respectively). These weighted areas were summed to produce an estimate of the total area of the protected geographic range. The protection level for each species was then classified based on the proportion of the conservation target ($100\,km^2$ of total habitat) that was met (Not Protected: < 5% of target; Poorly Protected: 5–49% of target; Moderately Protected: 50–99% of target; Well Protected: 100% of target). Targets were down-weighted for non-endemic species according to the proportion of their overall distribution within South Africa (Supplementary information: Tables S1–S3). Four endemic species that fall within protected areas have distributions that are smaller than the minimum conservation target of $100\,km^2$ total (*Bradypodion caeruleogula*: $44\,km^2$, *B. nemorale*: $39\,km^2$, *B. ngomeense*: $26\,km^2$, *Hemicordylus nebulosus*, $10\,km^2$). Thus, even if their distributions are contained 100% within protected areas, they cannot meet the minimum conservation target. They were therefore excluded from the above process.

We created a species richness map on a $10 \times 10\,km$ grid by overlaying the interpreted distributions of all reptiles and extracting the number of species found in each grid (Fig. 1). Species richness was then intersected with the South African protected area network, as well as the proposed protected areas expansion network (Government of South Africa, 2010). We evaluated the level of species richness encapsulated by the current protected areas, as well as whether the planned protected areas expansion network would capture higher richness, and/or additional threatened species. The species richness layer was also intersected with the spatial layer of South African threatened ecosystems (DEA, 2011) in order to compare reptile richness within and outside of

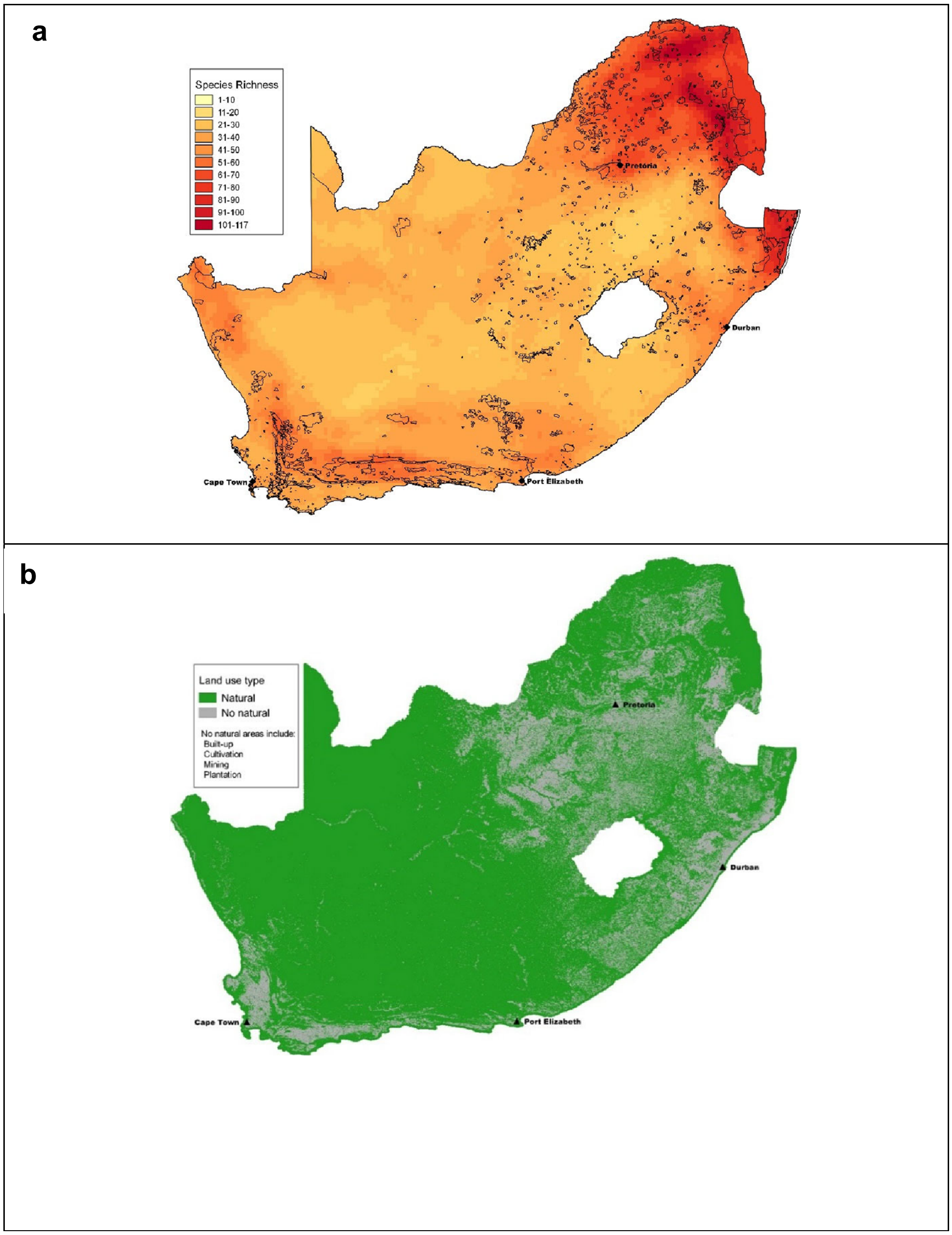

Fig. 1. a. Reptile species richness in South Africa (darker shading indicates higher richness) overlaid with the protected area network (polygons); b. land cover in South Africa (light grey shading indicates no natural land cover remaining).

threatened ecosystems. All 10 × 10 km grids that were only partially covered by these intersects were treated as follows: if the area of overlap was ≥50% the grid was included in the protected area, while grids with an overlap of < 50% were considered to be outside the protected area or threatened ecosystem. Boxplots were used to quantify species richness values under each scenario, comparing richness inside and outside protected areas or threatened ecosystems. A non-parametric two-sample Mann-Whitney *U* test was used to compare species richness within and outside each of the three networks (South African protected areas network, protected areas expansion network and the threatened ecosystems network, respectively). All spatial and statistical analyses were conducted with SAGA V6.3.0, QGIS V2.18.12 and/or R V.3.3.1 (Conrad et al., 2015; QGIS Development Team, 2018; R Development Core Team, 2017).

2.2. Extinction rates

Two endemic South African reptiles are classified as extinct (*Tetradactylus eastwoodae* Hewitt & Methuen, 1913 and *Scelotes guentheri* Boulenger, 1887) and both extinctions are attributed to habitat transformation. These two species have been the target of intense searches and neither species has been recorded for many decades (90 and 131 years respectively; Bates et al., 2014). As an exploratory exercise, we estimated the rate of extinction for endemic reptiles per million species years (E/MSY) following Pimm et al. (2014) and Ceballos et al. (2015) using:

$$\frac{E}{MSY} = \left(\frac{\#extinctions}{\#species \times time - frame}\right) \times 1{,}000{,}000\ years \quad (3)$$

Extinction rate was estimated for three time-frames (historical, present, future). We made the assumption that modern habitat transformation was initiated during the early 1700s, and at that time there were no anthropogenic related extinctions (time zero). The rates were then estimated: 1) a time-frame of 300 years (ca. 1700–2000) was used to estimate 'historical' (i.e. past) extinction rate. Over that time period, there were two extinctions, and; 2) for the 'current' extinction rate, we assumed that without conservation interventions, the two presently Critically Endangered species would go extinct within the next century, resulting in a time period of 400 years over which we have a total of four extinctions, and; 3) the 'future' extinction rate was estimated by assuming that without conservation intervention all threatened species (CR, EN, VU species) are destined for extinction within a total time-frame of 1000 years (ca. 1700–2700). We acknowledge that these rates are based on a number of assumptions, particularly that the IUCN categories are good indicators of extinction risk at present and into the future. The actual risk and associated time-frames over which potential extinctions could occur in the future are certainly tenuous. These estimates are simply an interesting line of investigation for a comparison with global estimates.

3. Results

3.1. Threat status, trends and protection level

Of the 391 reptiles assessed, 12 species are classified as Data Deficient (DD) and two as Extinct, leaving 377 that were assigned a threat category. Five percent of these are considered at risk of extinction (CR, EN or VU), with another ca. 3% considered Near Threatened (Tables 1, S2). This differs from the previous assessments, where ca. 10% of species were considered threatened with extinction, and another 8% Near Threatened (Bates et al., 2014). Importantly, these differences are not due to effects of amelioration of threat status but are considered 'non-genuine' changes in the 2018 assessments due to our more rigorous application of the criteria as well as improved information on distribution and tangible threats.

Half of South Africa's threatened reptiles are at risk due to a reduction in extent and quality of habitat (Criterion B), and this figure rises to 64% if Near Threatened species are included (Supplementary information: Table S1). These species are distributed in areas with the highest land transformation, particularly in the south-western and north-eastern areas of South Africa (Fig. S1). Nine species are classified as threatened based on observed population declines (Category A) that may or may not relate directly to habitat loss. Most of these are chelonians, with only one lizard (*Smaug giganteus*) classified under Category A. There is a taxonomic bias in threat status, with 42% of all chelonians (in two families), 40% of Chamaeleonidae and 31% of Viperidae (all in the genus *Bitis*) being threatened (including the Near Threatened category). Although a notable number of species under threat are Scincidae (with one extinct species), skinks are an exceptionally species-rich group in South Africa (63 species) so the proportion of threatened species is not high within this family. It is noteworthy however that all skinks under threat (or extinct) are fossorial species.

Table 1
Extinction risk categories for South African reptiles as of 2018 and backcast to 1990 for a) all species and b) endemic species only. The numbers of species with a change for each category over the time period is given in the last row. Subtotal[1] refers to species with a threat status assigned, whereas subtotal[2] refers to the total number of species evaluated (i.e. including DD species). EX: Extinct, CR: Critically Endangered, EN: Endangered, VU: Vulnerable, NT: Near Threatened, LC: Least Concern, DD: Data Deficient.

	EX	CR	EN	VU	NT	LC	DD	subtotal[1]	subtotal[2]
a. All species									
2018									
sum	2	2	6	11	13	345	12	379	391
%	0.5	0.5	1.5	2.7	3.2	84.8	2.9	93.1	
1990									
sum	2	0	5	6	14	352	12	379	391
%	0.5	0.0	1.3	1.5	3.6	90.0	3.1	96.9	
Change	0	2	1	5	−1	−7	0		
b. Endemic species									
2018									
sum	2	2	6	7	168	12	12	197	209
%	1.0	1.0	2.9	3.3	80.4	5.7	5.7	94.3	
1990									
sum	2	0	5	6	171	13	12	197	209
%	1.0	0.0	2.4	2.9	81.8	6.2	5.7	94.3	
Change	0	2	1	1	−3	−1	0		

The backcasting exercise showed an increase in threatened species, from 3.3% in 1990 to 5.4% in 2018, which represents a 38% increase in the number of threatened species. In particular, 14 species have become more threatened (Table 2), with five of these moving from Least Concern to a threatened category. Six species increased by more than one step in threat category (*Chersobius boulengeri*, *C. signatus*, *Crocodylus niloticus*, *Dendroaspis angusticeps*, *Pelusios castanoides*, *Pelusios rhodesianus*). Also notable is that a fossorial skink (*Scelotes inornatus*) increased in threat status from EN to CR. Conversely, there was a positive change in threat status for one gecko (*Cryptactites peringueyi*) from VU to NT due to its recent discovery at several new localities (increase in EOO from 531 km^2 to 785 km^2). Although some newly-discovered localities are undoubtedly the result of improved survey effort (i.e., non-genuine change), others could indicate true range expansion as individuals are now regularly recorded on the walls of suburban houses that border historically known localities (Bates et al., 2018).

The weighted Red List Index showed a slight decrease between 1990 and 2018 (Fig. 2). This marginally lower RLI indicates a minor decreasing trend in the proportion of species expected to remain extant into the near future (i.e. approx. 50 years, see Butchart et al., 2007). When considering only endemic species, the decreasing trend is slightly more pronounced over the two time points (Fig. 2). Because there are only two time points, we cannot conclude whether the decrease in RLI points to a genuine negative trend over the longer term. While the change in RLI over this time is relatively minor, the proportion of species moving into a threat category is notable at 38%. This could indicate that the RLI is not particularly sensitive to pick up certain subtle changes, and that additional metrics should be used together with the RLI as a balanced, precautionary approach.

Of the 377 reptile species assessed for their protection level, all non-endemics are classified as Well Protected, whereas only 78% of endemics are Well Protected (Table 3, Fig. 3). Notably, both Critically Endangered reptiles are classified as Not Protected, and most Endangered species are not Well Protected (Table 4). Overall, only 2% of snakes (*Bitis albanica* and *Bitis inornata*) and 5% of chelonians (*Psammobates geometricus*) are not Well Protected, whereas ca. 17% of lizards (primarily geckos) are not Well Protected (Table 3, Supplementary information: Appendix S1).

Of the four species with range sizes smaller than the conservation target, one (*Hemicordylus nebulosus*) is distributed entirely within a provincial protected area; we consider this species Well Protected. The remaining species have large portions of their ranges in protected areas (*Bradypodion caeruleogula*: 71%, *B. nemorale*: 85%, *B. ngomeense*: 66%). We compared these proportions post hoc to other species with small ranges (e.g. 200–1000 km^2). For species in the Well Protected category, the proportion of their distribution that is protected ranged from 15 to 82%. Yet, for species in the Poorly Protected category, the proportion was < 1%. Given that all the four species have comparatively high proportions of their ranges in protected areas (66%–100%; similar to or higher than most Well Protected species), we consider them Well Protected.

Table 2
South African reptile species that showed a change in threat status between 1990 (backcast) and 2018. The protection level is given, as is the type of assessment (G: Global, N: National), the threat categories (1990 and 2018) and criteria. Details on the pressures causing the threat status change are summarised.

Family	Species	Endemic status	Protection Level	Type	Category 1990	Category 2018	Criteria 2018	Threat change	Pressures
Pelomedusidae	*Pelusios castanoides*	Not endemic	Well	N	LC	VU	A4ac	Negative (2 steps)	Population declines estimated due to deterioration of wetlands from pollution and direct habitat conversion for forestry and agriculture.
Pelomedusidae	*Pelusios rhodesianus*	Not endemic	Well	N	LC	VU	A4ace	Negative (2 steps)	Population declines estimated due to deterioration of wetlands from pollution and direct habitat conversion for forestry and agriculture.
Testudinidae	*Chersobius boulengeri*	Endemic	Well	G	LC	EN	A4ace	Negative (3 steps)	Population decline observed due to loss in habitat from agriculture and ranching (small and large scale), and increased predation from Pied Crow (*Corvus albus*).
Testudinidae	*Chersobius signatus*	Endemic	Well	G	NT	EN	A4ace	Negative (2 steps)	Population decline observed due to habitat fragmentation from agriculture.
Testudinidae	*Kinixys lobatsiana*	Endemic	Well	G	NT	VU	A4cde	Negative (1 step)	Population decline inferred due to habitat destruction from urbanisation, mining and agriculture.
Testudinidae	*Kinixys natalensis*	Endemic	Well	G	NT	VU	A4c	Negative (1 step)	Population decline inferred due to habitat loss from agriculture, timber plantations and urban development.
Testudinidae	*Psammobates geometricus*	Endemic	Not	G	EN	CR	A4ace	Negative (1 step)	Known population reduction of > 90% due to land transformation from dense & unsuitable alien vegetation, cattle farming, introduced feral pigs and other subsidised predators.
Testudinidae	*Psammobates tentorius*	Endemic	Well	G	LC	NT	A4ce	Negative (1 step)	Population decline inferred due to increased predation from Pied Crow (*Corvus albus*) and habitat degradation due to agriculture and urbanisation.
Crocodylidae	*Crocodylus niloticus*	Not endemic	Well	N	LC	VU	A2ac	Negative (3 steps)	Population decline inferred due to deterioration of water quality from pollution and damming, alien invasive species, loss of prey base, and persecution.
Chamaeleonidae	*Bradypodion dracomontanum*	Endemic	Well	G	LC	NT	B1b(iii)	Negative (1 step)	Habitat loss due to increase in subsistence agriculture and reduction in habitat quality.
Chamaeleonidae	*Bradypodion thamnobates*	Endemic	Poorly	G	VU	EN	B1ab(iii,v)	Negative (1 step)	Habitat loss due to urban development, reduction in EOO and increase in fragmentation.
Gekkonidae	*Cryptactites peringueyi*	Endemic	Not	G	VU	NT	B1a	Positive (1 step)	New localities recorded, increase in EOO.
Scincidae	*Scelotes inornatus*	Endemic	Not	G	EN	CR	B1ab(i,ii,iii)	Negative (1 step)	Habitat loss due to urban development, reduction in EOO, local extinctions observed and increase in habitat fragmentation.
Elapidae	*Dendroaspis angusticeps*	Not endemic	Well	N	LC	VU	B2ab(ii,iii,iv,v)	Negative (2 steps)	Habitat loss due to urban development, reduction in EOO, local extinctions observed and increase in habitat fragmentation.
Viperidae	*Bitis armata*	Endemic	Well	G	NT	VU	B1ab(i,ii,iii,iv,v)	Negative (1 step)	Habitat loss due to urban development, reduction in EOO and local extinctions observed.

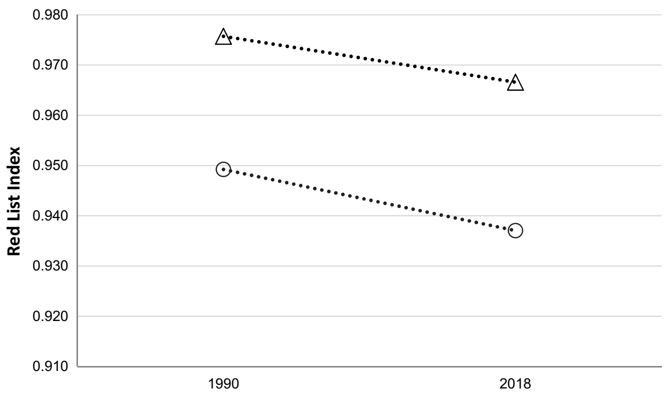

Fig. 2. The Red List Index (weighted) for South African reptiles estimated at 1990 and 2018 for all reptile species (triangles), and for endemics only (circles).

Species richness is significantly higher within the current protected area network than outside (U = 2,164,700, $p \leq 0.001$; Fig. 4), suggesting that the protected area network covers reptile richness better than expected by chance. Richness would also be higher in the planned expanded network than outside it (U = 4,326,400, $p \leq 0.001$). However, only four of the 18 species currently Not Protected occur within the planned extension of protected areas (Supplementary information: Appendix S1), and all of these are Least Concern (*Afroedura leoleonsis*, *Afroedura rupestris*, *Cordylus imkeae* and *Goggia matzikamaensis*). While the expanded protected area network would result in greater areas for overall protection for the majority of reptile species, it would fail to improve the protection level of the majority of inadequately protected or threatened species. Species richness values are significantly higher within threatened ecosystems than outside them (U = 1,456,100, $p \leq 0.01$; Fig. 4).

3.2. Extinction rates

Of the 209 endemic and near-endemic reptiles, two are considered extinct, two are Critically Endangered and 19 are in other threat categories. The historical extinction rate (over the last 300 years) was estimated at 32.4 E/MSY, the current rate (over a total of 400 years) as 48.5 E/MSY, and the future rate (over a total of 1000 years) as 97.1 E/MSY.

4. Discussion

Approximately 5.4% of South Africa's reptiles are at risk of extinction at present, which represents a 38% increase in risk since 1990. Similar to reptiles across the globe, the primary factor driving extinction risk is habitat loss (Böhm et al., 2013; Jenkins et al., 2014; Tolley et al., 2016). Comparatively, South African reptiles appear to be faring better than the global average, given that 15% of reptiles are threatened globally (Böhm et al., 2013). Even when considering the previous country-wide set of assessments (Bates et al., 2014) where 10% of reptile species were considered threatened (an additional 8% Near Threatened), South Africa appears to be doing better than the global average. However, many of these earlier assessments have been downgraded due to improved information and knowledge of criteria, raising questions regarding consistency and repeatability when carrying out IUCN assessments. Thus, differences between the global average and the new South African assessments may be due to the stricter application of the criteria. Additionally, the global study was based on a random sample of 1500 species (ca. 16% of all described reptiles at the time), which were assessed for extinction risk (Böhm et al., 2013). This random sample was assumed to provide a good cross-section of species representative of the global fauna's threat status. However, because there may be bias in the sample, the genuine state of global threat is unknown. Conversely, our study is based on an entire fauna which should be representative of the threat status for the country. Therefore, the two studies are not directly comparable.

4.1. Backcasting

There is a 38% increase in the proportion of threatened species since 1990, but the weighted Red List Index (wRLI) changed only marginally between 1990 and 2018. The RLI shows a slightly steeper decrease for endemic species than for all species combined, suggesting that endemic species are faring worse over time. Habitat loss was the primary factor driving risk, and an interrogation of the two comprehensive national land cover maps for South Africa (1990 and 2013) shows that most of the habitat degradation and fragmentation (18.2%) occurred prior to 1990 (GeoTerraImage, 2015, 2016). In fact, between 1990 and 2013 there was relatively little additional conversion of natural land cover (ca. 2.3% within the total of 18.2% since historical times). Given that habitat loss is the main pressure related to extinction risk, and that land cover change has been minimal in the last few decades, the lack of prominent change in RLI is not surprising.

The somewhat negligible additional conversion of natural habitat over the last 25 years relative to the conversion prior to 1990, creates an expectation that the set of species at risk in the backcast and current assessments should be similar or identical. However, there is a 38% increase in the proportion of threatened species; 14 have moved to a higher risk category (half of which moved from LC into a threat category). Five of the species that showed an increased extinction risk were assessed on Criterion B, with habitat loss directly implicated. Three of these (*Bitis armata*, *Dendroaspis angusticeps* and *Scelotes inornatus*) are habitat specialists with small ranges (1566 km^2, 732 km^2, 2.9 km^2, respectively) near major coastal metropolitan centres (Cape Town and Durban). There have been local extirpations of populations of these species due to intense urbanisation, which has reduced their ranges (Alexander, 1990; Alexander, 2018; Alexander et al., 2018; Maritz and Turner, 2018). Against the national backdrop of ca. 2.3% land cover loss between 1990 and 2013, land cover loss within the ranges of these species is 5.1%, 6.9% and 14.0%, respectively. Therefore, habitat specialists with small ranges that are positioned near urban centres may be under additional pressure, despite what appears to be little overall land cover change in the last 25 years.

Backcasting revealed that nine species moved to a higher threat category under Criterion A (population size reduction) between 1990 and 2018, viz. eight tortoises/terrapins and the Nile Crocodile (*Crocodylus niloticus*). Direct and indirect impacts from water pollution have been implicated in population reductions of *C. niloticus* (Ashton, 2010; Botha et al., 2011). For tortoises, population declines and disruption of metapopulation dynamics are likely due to habitat degradation from agriculture and urban expansion, electric fencing and altered fire regimes. At least one of the tortoises (*Chersobius signatus*) also appears to be impacted by illegal collecting for the pet trade (Hofmeyr et al., 2018). Another major threat to tortoises and possibly other reptiles is Pied Crow predation, which can decimate populations (e.g. *C. signatus*; Loehr, 2017). Pied Crow numbers have been increasing over the past three decades, particularly in the south-western and southern regions of South Africa (Cunningham et al., 2015) and this increased pressure could be detrimental to not only tortoises but also other small reptiles. Clearly, species that have shifted to a higher threat category should be prioritised for monitoring of population trends into the future.

4.2. Protection level

Roll et al. (2017) highlight the fact that, globally, an average of only 3.5% of the area of reptile geographic ranges fall within protected areas. However, their measure does not necessarily relate directly to extinction threat because a widespread species may have only a small

Table 3
Protection level and threat category summaries for South African reptiles: a) all species, b) snakes, c) lizards, d) chelonians and e) crocodilians. Percentages are based on the number evaluated. Well: Well Protected, Moderate: Moderately Protected, Poor: Poorly Protected, Not: Not Protected. Species that where Not Evaluated1 for Protection Level are not included in the summaries. Threat categories as in Table 1.

a) All reptiles

Protection Level	All species	Endemic /Near endemic	Non-endemic
Well	347 (89.2%)	166 (80.2%)	181 (99.5%)
Moderate	11 (2.8%)	11 (5.3%)	0
Poor	11 (2.8%)	11 (5.3%)	0
Not	20 (5.1%)	19 (9.2%)	1 (0.5%)
Number evaluated	*389*	*207*	*182*
Extinct[a]	2	2	0
Peripheral/Introduced[a]	16	0	16
Total	407	209	198

b) Snakes

	Threat category						
Protection Level	CR	EN	VU	NT	LC	DD	Total
Well	0	0	2	1	105	1	109
Moderate	0	0	0	0	0	0	0
Poor	0	1	0	0	0	0	1
Not	0	0	0	0	0	1	1
Total	0	1	2	1	105	2	111
c) Lizards							
Well Protected	0	1	2	5	209	2	219
Moderately Protected	0	0	1	3	3	4	11
Poorly Protected	0	1	0	1	7	1	10
Not Protected	1	1	1	2	9	4	18
Total	1	3	4	11	228	11	258
d) Chelonians							
Well Protected	0	2	4	1	11	0	18
Moderately Protected	0	0	0	0	0	0	0
Poorly Protected	0	0	0	0	0	0	0
Not Protected	1	0	0	0	0	0	1
Total	1	2	4	1	11	0	19
e) Crocodiles							
Well Protected	0	0	1	0	0	0	1

[a] Not evaluated.

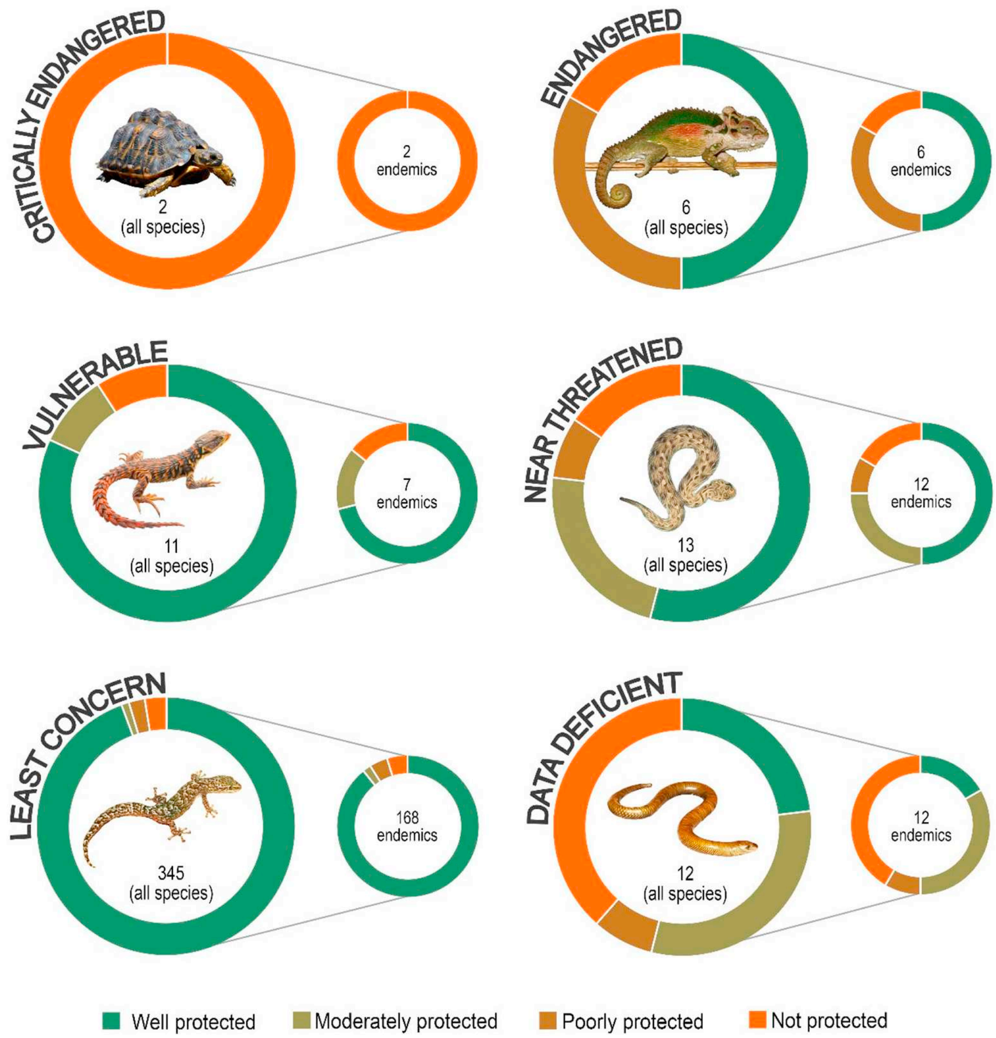

Fig. 3. The proportion of South African reptiles (all species, and endemics only) for each protection level, given each IUCN threat category. Absolute number of species in each threat category are indicated, and examples of species for each threat category are shown - Critically Endangered: *Psammobates geometricus*, Endangered: *Bradypodion thamnobates*, Vulnerable: *Smaug giganteus*, Near Threatened: *Bitis schneideri*, Least Concern: *Afrogecko porphyreus*, Data Deficient: *Acontias wakkerstroomensis*. For a colour version of this figure, refer to online version of the article.

Table 4

Summary for protection level (PL) given each threat category for South African reptiles: a) endemic species, and b) all species. Protection Level categories as in Table 3. Threat categories as in Table 1.

	Threat category						
	CR	EN	VU	NT	LC	DD	Total
a) PL all species							
Well	0	3	9	7	326	2	347
Moderate	0	0	1	3	3	4	11
Poor	0	2	0	1	7	1	11
Not	2	1	1	2	9	5	20
Total	2	6	11	13	345	12	389
b) PL endemic species							
Well	0	3	5	6	150	2	166
Moderate	0	0	1	3	3	4	11
Poor	0	2	0	1	7	1	11
Not	2	1	1	2	8	5	19
Total	2	6	7	12	168	12	207

fraction of its range in protected areas, but this may still be an area that is extensive enough to mitigate against extinction. Rather, Roll et al.'s (2017) measure highlights general inadequacies of the global protected area networks for the conservation of reptiles. Reptiles fare worse in this regard than do birds and mammals, possibly because designation of protected areas is often prioritised for the conservation of these taxa, and this does not serve as a good surrogate for lizards and turtles (Roll et al., 2017). In comparison, our measure of protection is aimed at evaluating extinction risk – we assumed that a minimum of 100 km^2 of the protected range was enough to mitigate against extinction, and this minimum was met for 88% of all South African reptile species (78% of endemics). This was achieved with only 6.5% of South Africa's land area officially protected, as compared to 12.5% of land under protection globally (Watson et al., 2014).

Although most South African reptiles are considered Well Protected, both Critically Endangered South African reptiles are Not Protected and half of the Endangered reptile species are Poorly or Not Protected. That is, some of the species at greatest risk of extinction are not included in protected areas, suggesting that the current protected area network is not a safeguard to ensure the survival of threatened reptile species, despite adequate protection for Least Concern species. Furthermore, it may be naïve to assume that setting up a fragmented system of protected areas, even if considered ample in number and size, will be sufficient to maintain population connectivity and metapopulation dynamics over the long-term for any species (see Akçakaya et al., 2006), regardless of threat status. Indeed, some threatened and Near Threatened reptiles are Well Protected (Tables 2, S2), which is

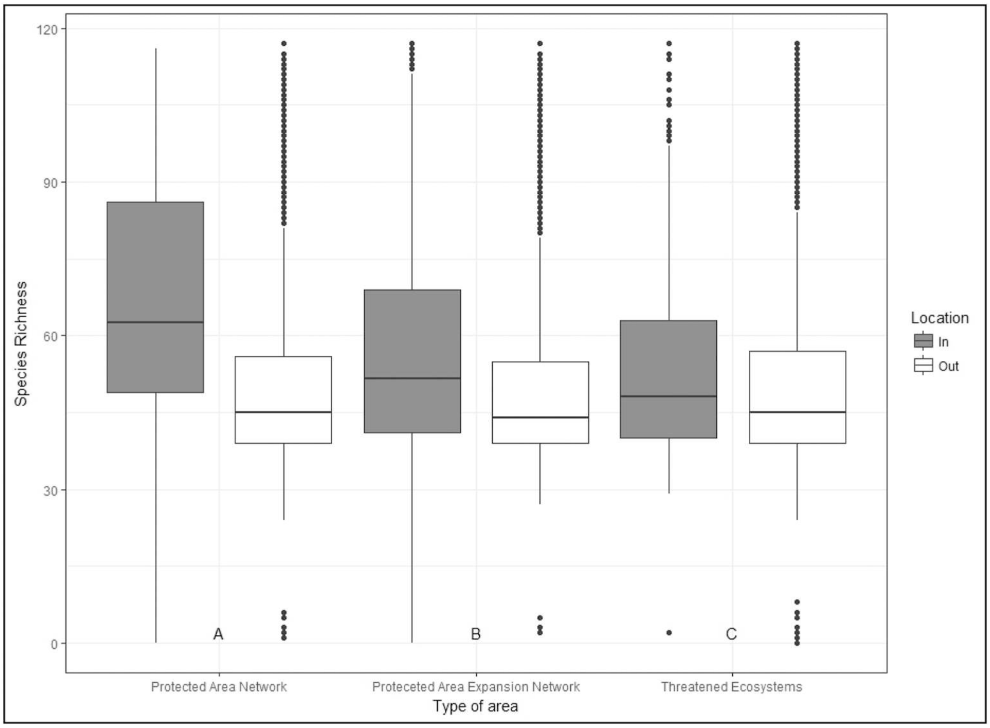

Fig. 4. Boxplots of species richness values for reptiles in South Africa, a. within and outside of protected areas, b. within and outside of the planned protected areas expansion network, and c. within and outside threatened ecosystems. Median values are shown inside each box (horizontal line), the upper (75th) and lower (25th) percentiles are represented by the box boundaries, and the whiskers show the upper (95%) and lower (5%) percentiles (dots represent values outside these percentiles).

surprising. If the protected area network were sufficient to ensure species survival, Well Protected species should be not threatened. This is not the case and could be a warning sign that the protected area network does not suffice to maintain metapopulation dynamics, and that the mere existence of a protected area network does not guarantee that species are not at risk.

Snakes have previously been considered 'well protected' in South Africa (Lombard et al., 1995). Superficially, this reflects our summary of protection levels with only one (of > 100) snake species falling outside the Well Protected category. However, our detailed analysis shows that this species is at risk of extinction and is Poorly Protected (*Bitis albanica*, EN). This species has been recognised as species of conservation concern in a global context (Maritz et al., 2016). Therefore, while landscape level analyses may be suitable on a coarse scale (Lombard et al., 1995), such analyses cannot account for risk to imperilled species. By concluding that snakes are well protected, Lombard et al. (1995) essentially refer to the > 100 Least Concern species, most of which have large distributions. Ostensibly, because their distributions are large, they are likely to fall within a protected area. Clearly, it is important to account for factors such as extinction risk, or distribution size (Böhm et al., 2016) to ensure early detection of population declines that could lead to species extinctions.

We found that reptile species richness is higher within protected areas than outside of them, suggesting that the current protected area network is reasonably well positioned for capturing overall reptile diversity. Indeed, there is a high density of protected areas where reptile richness is high (Supplementary information: Fig. S2). South Africa has a National Protected Areas Expansion Strategy (NPAES) with a target to expand the protected area network to 12% of land by 2028 and potential protected areas have been identified (Government of South Africa, 2010). These protected areas were chosen through systematic biodiversity planning, whereby all ecosystems were represented using biodiversity thresholds to retain predetermined percentages of the original extent of each ecosystem (Government of South Africa, 2010). Our analysis shows, however, that the total area captured in the expanded protected area network would have an overall lower average reptile richness than the current protected area network. This is because the spatial distribution of the potential protected areas (Supplementary information: Fig. S3) would be in areas of low reptile richness, which would decrease the overall average richness for protected areas. Indeed, the expansion network would add only four currently Not Protected but Least Concern reptile species to the list of those within protected areas (*Afroedura leoloensis*, *A. rupestris*, *Cordylus imkeae* and *Goggia matzikamaensis*). Therefore, the expansion network plan based on ecosystem thresholds would not improve protection for threatened reptile species, nor would it markedly improve protection in terms of reptile species richness. Our results highlight a potential drawback to the protected area expansion planning process that should be explored for other taxonomic groups, particularly as the implementation of the network expansion would be a costly endeavour and should be maximised to better protect both species and ecosystems. It would be useful to examine the distribution of Poorly and Not Protected species for other taxonomic groups to highlight important areas of overlap. Such information should assist to inform and possibly refine the current NPAES, particularly to encompass species of concern within the proposed expanded protected area network.

4.3. Are South Africa's reptiles faring well?

Our analyses show that compared to the global estimate, a low percentage of South Africa's reptiles are at risk of extinction. However, this does not mean that the country's reptiles are faring well from a conservation perspective: many threatened reptiles are not Well Protected and conversely, threatened species that are considered Well Protected are in decline. The most severely threatened species tend to occur in close proximity to major coastal metropolitan centres where there is disproportionately high pressure from land transformation, and there are two documented reptile extinctions, both apparently due to habitat loss. While the IUCN threat status statistics are an important guide to understand extinction risk, these additional indicators suggest that South African reptiles may not be faring as well as the IUCN threat status statistics indicate alone.

Notably, the two South African reptile extinctions make up half of all known IUCN-documented continental reptile extinctions, although poorly-known areas elsewhere in continental Africa (Tolley et al., 2016) could have experienced undocumented extinctions. Regardless, this lends weight to the notion that South African reptiles are at a critical point, despite the lower percentage of species classified as threatened. *Scelotes guentheri* from the eastern coast of South Africa has not been recorded since its original description in 1887. Originally, it might have had a very restricted distribution in the present-day city of Durban, which was settled by Europeans in the early 1800s ("Port Natal"). Subsequently, much of the land was converted for agriculture and later, urbanised. *Tetradactylus eastwoodae*, described in 1911, has not been recorded since 1928 (Bates et al., 2014). Much of the grassland habitat of this species was converted to alien tree plantations in the 1950s, and recent targeted searches in the remaining grassland fragments were unsuccessful (Bates et al., 2014). Therefore, it appears that land transformation, associated with human population expansion, has brought about the demise of these two species.

While pre-Anthropocene background extinction rates vary from 0.1 to 2 E/MSY, our rough estimates of current and projected extinction rates for South African reptiles of 32 to 97 E/MSY are indicative of a fauna that is in increasing jeopardy. We assert that our analyses realistically assess the conservation status of South Africa's reptiles and do not overinflate the proportion of species that are classified as threatened. Our results also reveal the importance of detailed analysis of datasets and we warn against over-generalisation – the fact that range-restricted species also tend to be poorly protected means that threatened species should be evaluated individually and at an appropriate spatial scale.

5. Conclusions and caveats

Through backcasting, we show that threat status for South African reptiles deteriorated between 1990 and 2018 and that most of the impacts on reptile species occurred prior to 1990 when the majority of habitat was modified. The overall threat status for South African reptiles (5%) appears to be relatively low compared to mainland Africa as a whole (13%) and to the global average (15%), with most species considered as Well Protected, and this could be an explanation for the lower threat status. South Africa's terrestrial protected areas (including inland waters), is well below the Convention on Biological Diversity target of 17% area coverage (www.cbd.int/sp/targets). Regardless, they are reasonably well managed to conserve natural habitat as required by the South African National Environmental Management: Protected Areas Act (Act 57 of 2003) regulations, which establishes a consistent set of legal requirements (including management effectiveness monitoring) for the management of formal protected areas. Compared to some other regions in Africa where protected areas are not always afforded funding, strong regulations, management or law enforcement (see Watson et al., 2014), South Africa's reptiles may indeed see benefit from its protected area network. Despite this, many threatened species are not Well Protected. If the strategy to expand South Africa's protected areas could be re-evaluated to consider the distributions of threatened species (reptiles and others), an expansion of this network could indeed be worthwhile in terms of biodiversity conservation.

During our evaluation, it was clear that there are several gaps and weaknesses in our data that need to be addressed to improve the accuracy and robustness of similar exercises conducted in the future. We need to have better species-specific measures of the protection levels afforded by the protected areas – we based the 'good, fair, poor' categorisations of protected areas largely on apparent vegetation intactness as represented by remotely sensed imagery, which is not necessarily a good proxy for protection. We are also sorely missing studies on population dynamics, especially those that give measures of numbers and density, effects of habitat fragmentation and roads, and the impacts of predation by domestic cats and other predators that now thrive in the Anthropocene. Finally, an evaluation of extinction debt is needed so that we are not unduly lulled into a false sense that good or fair levels of protection (i.e. with occurrence in protected areas) for reptiles is enough to ensure that extinction risk is low.

Conflict of interest

We declare no conflict of interest.

Acknowledgements

We would like to thank all the participants in the IUCN Red List review workshop, and experts consulted during the assessment process: Aaron Bauer, William Branch, Marius Burger, Michael Cunningham, Jean-Jacques Forgus, James Harvey, Adriaan Jordaan, Buyisile Makhubo, John Measey, Stuart Nielsen, Alex Rebelo, Anders Rhodin, Paula Strauss, Jody Taft, Nicolas Telford. Thanks to Bianca Fizzotti for assistance with figures and maps. The assessments were funded by the South African National Biodiversity Institute and facilitated by the IUCN Global Reptile Assessment, with assistance from Phil Bowles, Craig Hilton-Taylor and Domitilla Raimondo.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2019.02.006.

References

African Economic Outlook, 2014. African Economic Outlook 2014: Global Value Chains and Africa's Industrialisation. African Development Bank, Organisation for Economic Cooperation and Development, United Nations Development Programme.

Akçakaya, H.R., Mills, G., Doncaster, C.P., 2006. The role of metapopulations in conservation. In: Macdonald, D.W., Service, K (Eds.), Key Topics in Conservation Biology. Blackwell Publishing, pp. 64–84.

Alexander, G.J., 1990. Reptiles and amphibians of Durban. Durban Mus. Novit. 15, 1–41.

Alexander, G.J., 2018. Dendroaspis angusticeps. South African Red List of Threatened Specieshttp://speciesstatus.sanbi.org/.

Alexander, G.J., Tolley, K., Weeber, J., Conradie, W., Marais, J., Bauer, A.M., 2018. *Scelotes inornatus*. The IUCN Red List of Threatened Species 2018: e.T178207A115659621. (Downloaded on 19 November 2018).

Ashton, P.J., 2010. The demise of the Nile crocodile (*Crocodylus niloticus*) as a keystone species for aquatic ecosystem conservation in South Africa: the case of the Olifants River. Aquat. Conserv. Mar. Freshwat. Ecosyst. 20, 489–493. https://doi.org/10.1002/aqc.1132.

Bates, M.F., Branch, W.R., Bauer, A.M., Burger, M., Marais, J., Alexander, G.J., de Villiers, M.S., 2014. The Atlas and Red List of the Reptiles of South Africa, Lesotho and Swaziland. In: Suricata, vol. 1 South African National Biodiversity Institute, Pretoria. https://doi.org/10.1007/s13398-014-0173-7.2.

Bates, M.F., Branch, W.R., Conradie, W., 2018. *Cryptactites peringueyi*. The IUCN Red List of Threatened Species 2018: e.T41229A115654342. (Downloaded on 20 November 2018).

Beck, A., 2010. Electric Fence Induced Mortality in South Africa. University of the Witwatersrand, Johannesburg, South Africa (M.Sc. Thesis, 75 pp.).

Böhm, M., Collen, B., Baillie, J.E.M., Bowles, P., Chanson, J., Cox, N., Hammerson, G., Hoffmann, M., Livingstone, S.R., Ram, M., et al., 2013. The conservation status of the world's reptiles. Biol. Conserv. 157, 372–385. https://doi.org/10.1016/j.biocon.2012.07.015.

Böhm, M., Williams, R., Bramhall, H.R., Mcmillan, K.M., Davidson, A.D., Garcia, A., Bland, L.M., Bielby, J., Collen, B., 2016. Correlates of extinction risk in squamate reptiles: the relative importance of biology, geography, threat and range size. Glob. Ecol. Biogeogr. 25, 391–405. https://doi.org/10.1111/geb.12419.

Botha, H., Van Hoven, W., Guillette, L., 2011. The decline of the Nile crocodile population in Loskop Dam, Olifants River, South Africa. Water SA 37, 103–108.

Branch, W.R., 1988. South African Red Data Book–Reptiles and Amphibians. vol. 151. South African Natl. Sci. Program, pp. 1–241.

Butchart, S.H.M., Akçakaya, H.R., Chanson, J., Baillie, J.E.M., Collen, B., Quader, S., Turner, W.R., Amin, R., Stuart, S.N., Hilton-Taylor, C., 2007. Improvements to the Red List Index. PLoS One 2 (1), e140. https://doi.org/10.1371/journal.pone.0000140.

Ceballos, G., Ehrlich, P.R., Barnosky, A.D., Garcia, A., Pringle, R.M., Palmer, T.M., 2015. Accelerated modern human-induced species losses: entering the sixth mass extinction. Sci. Adv. 1, e1400253. https://doi.org/10.1126/sciadv.1400253.

Collinson, W., Parker, D., Patterson-Abrolat, C., Alexander, G., Davies-Mostert, H., 2015. Chapter 54. Setjhaba SA, South Afrika: a South African perspective of an emerging transport infrastructure. In: Van der Ree, R., Grilo, R., Smith, D. (Eds.), Handbook of Road Ecology. John Wiley & Sons, Ltd., pp. 439–447. https://doi.org/10.1002/9781118568170.ch54.

Conrad, O., Bechtel, B., Bock, M., Dietrich, H., Fischer, E., Gerlitz, L., Wehberg, J., Wichmann, V., Böhner, J., 2015. System for Automated Geoscientific Analyses (SAGA) v. 2.1.4. Geosci. Model Dev. 8, 1991–2007. https://doi.org/10.5194/gmd-8-1991-2015.

Conradie, W., Bittencourt-Silva, G.B., Engelbrecht, H.M., Loader, S.P., Menegon, M., Nanvonamuquitxo, C., Scott, M., Tolley, K.A., 2016. Exploration of the hidden world of Mozambique's sky island forests: new discoveries of reptiles and amphibians. Zoosystematics Evol. 92 (2), 163–180. https://doi.org/10.3897/zse.92.9948.

Cressey, E.R., Measey, G.J., Tolley, K.A., 2014. Fading out of view: the enigmatic decline of Rose's mountain toad Capensibufo rosei. Oryx 49, 521–528. https://doi.org/10.1017/S0030605313001051.

Cunningham, S.J., Madden, C.F., Barnard, P., Amar, A., 2015. Electric crows: powerlines, climate change and the emergence of a native invader. Divers. Distrib. 22, 17–29. https://doi.org/10.1111/ddi.12381.

DEA, 2011. National Environmental Management: Biodiversity Act (10/2004): list of ecosystems that are threatened and in need of protection. In: Government Gazette 9 No. 34809:1002, (9 December 2011, Pretoria).

GeoTerraImage, 2015. Technical report: 2013/2014 South African National Land Cover Dataset version 5. Retrieved from. http://egis.environment.gov.za (Pretoria).

GeoTerraImage, 2016. Technical report: 1990 South African National Land Cover Dataset version 5.2. Retrieved from. http://egis.environment.gov.za (Pretoria).

Gerland, P., Raftery, A.E., Ševčíková, H., Li, N., Gu, D., Spoorenberg, T., Alkema, L., Fosdick, B.K., Chunn, J., Lalic, N., Bay, G., Buettner, T., Heilig, G.K., Wilmoth, J., 2014. World population stabilization unlikely this century. Science 346 (6206), 234–237. https://doi.org/10.1126/science.1257469.

Gibbons, J.W., Scott, D.E., Ryan, T.J., Buhlmann, K.A., Tuberville, T.D., Metts, B.S., Greene, J.L., Mills, T., Leiden, Y., Poppy, S., et al., 2000. The global decline of reptiles, Déjà Vu Amphibians: reptile species are declining on a global scale. Six significant threats to reptile populations are habitat loss and degradation, introduced invasive species, environmental pollution, disease, unsustainable use, and global climate change. Bioscience 50, 653–666.

Government of South Africa, 2010. National Protected Area Expansion Strategy for South Africa 2008, Priorities for Expanding the Protected Area Network for Ecological Sustainability and Climate Change Adaptation. Department of Environmental Affairs, Pretoria.

Halley, J.M., Monokrousos, N., Mazaris, A.D., Newmark, W.D., Vokou, D., 2016. Dynamics of extinction debt across five taxonomic groups. Nat. Commun. 7, 1–6. https://doi.org/10.1038/ncomms12283.

Hanski, I., Ovaskainen, O., 2002. Extinction debt at extinction threshold. Conserv. Biol. 16, 666–673. https://doi.org/10.1046/j.1523-1739.2002.00342.x.

Hofmeyr, M.D., Loehr, V.J.T., Baard, E.H.W., 2018. *Chersobius signatus*. The IUCN Red List of Threatened Species 2018: e.T10241A115650943. https://doi.org/10.2305/IUCN.UK.2018-2.RLTS.T10241A115650943.en. (Downloaded on 26 January 2019).

IUCN, 2012. IUCN Red List Categories and Criteria: Version 3.1, second edition. IUCN, Gland, Switzerland and Cambridge, UK.

IUCN Standards and Petitions Subcommittee, 2017. Guidelines for using the IUCN Red List Categories and Criteria. Version 13. Prepared by the Standards and Petitions Subcommittee. http://www.iucnRed. List.org/documents.

Jenkins, R.K.B., Tognelli, M.F., Bowles, P., Cox, N., Brown, J.L., Chan, L., Andreone, F., Andriamazava, A., Andriantsimanarilafy, R.R., Anjeriniaina, M., et al., 2014. Extinction risks and the conservation of Madagascar's reptiles. PLoS One 9. https://doi.org/10.1371/journal.pone.0100173.

Kuussaari, M., Bommarco, R., Heikkinen, R.K., Helm, A., Krauss, J., Lindborg, R., Öckinger, E., Pärtel, M., Pino, J., Rodà, F., Stefanescu, C., Teder, T., Zobel, M., Steffan-Dewenter, I., 2009. Extinction debt: a challenge for biodiversity conservation. Trends Ecol. Evol. 24, 564–571. https://doi.org/10.1016/j.tree.2009.04.011.

Loehr, V.J.T., 2017. Unexpected decline in a population of speckled tortoises. J. Wildl. Manag. 81, 470–476. https://doi.org/10.1002/jwmg.21217.

Lombard, A.T., N, A.O., August, P.V., 1995. Where should nature reserves be located in South Africa? A snake's perspective. Conserv. Biol. 9, 363–372.

Loyd, K.A.T., Hernandez, S.M., Carroll, J.P., Abernathy, K.J., Marshall, G.J., 2013. Quantifying free-roaming domestic cat predation using animal-borne video cameras. Biol. Conserv. 160, 183–189. https://doi.org/10.1016/j.biocon.2013.01.008.

Mace, G.M., Collar, N.J., Gaston, K.J., Hilton-Taylor, C., Akçakaya, H.R., Leader-Williams, N., Milner-Gulland, E.J., Stuart, S.N., 2008. Quantification of extinction risk: IUCN's system for classifying threatened species. Conserv. Biol. 22, 1424–1442. https://doi.org/10.1111/j.1523-1739.2008.01044.x.

Macray, M.B., 2017. Tortoise Mortalities Along Fences in the Southeastern Karoo, South Africa. University of Cape Town, Cape Town, South Africa (M.Sc. Thesis, 76 pp.).

Maritz, B., Turner, A.A., 2018. *Bitis armata*. The IUCN Red List of Threatened Species 2018: e.T22473777A115666580. (Downloaded on 19 November 2018).

Maritz, B., Penner, J., Martins, M., Crnobrnja-Isailović, J., Spear, S., Alencar, L.R.V., Sigala-Rodriguez, J., Messenger, K., Clark, R.W., Soorae, P., Luiselli, L., Jenkins, C., Greene, H.W., 2016. Identifying global priorities for the conservation of vipers. Biol. Conserv. 204, 94–102. https://doi.org/10.1016/j.biocon.2016.05.004.

Marques, M.P., Ceríaco, L.M.P., Blackburn, D.C., Bauer, A.M., 2018. Diversity and distributions of the amphibians and terrestrial reptiles of Angola. Atlas of historical and bibliographic records (1840–2017). Proc. Calif. Acad. Sci. 4 (65), 1–501 (Supp. II).

Morling, F., 2014. Cape Town's Cats: Reassessing Predation Through Kitty-cams. University of Cape Town, Cape Town, South Africa (M.Sc. Thesis, 77 pp.).

Mucina, L., Rutherford, M.C. (Eds.), 2006. The vegetation of South Africa, Lesotho and Swaziland. Strelitzia, vol. 19 South African National Biodiversity Institute, Pretoria.

Parusnath, S., Little, I.T., Cunningham, M.J., Jansen, R., Alexander, G.J., 2017. The desolation of Smaug: the human-driven decline of the Sungazer lizard (*Smaug giganteus*). J. Nat. Conserv. 36, 48–57. https://doi.org/10.1016/j.jnc.2017.02.002.

Petrozzi, F., Amori, G., Franco, D., Gaubert, P., Pacini, N., Eniang, E.A., Akani, G.C., Politano, E., Luiselli, L., 2016. Ecology of the bushmeat trade in west and central Africa. Trop. Ecol. 57 (3), 545–557.

Pimm, S.L., Jenkins, C.N., Abell, R., Brooks, T.M., Gittleman, J.L., Joppa, L.N., Raven, P.H., Roberts, C.M., Sexton, J.O., 2014. The biodiversity of species and their rates of extinction, distribution, and protection. Science 344, 1246752. https://doi.org/10.1126/science.1246752.

QGIS Development Team, 2018. QGIS Geographic Information System (version 2.18.2). Open Source Geospatial Foundation Projecthttps://qgis.org/.

R Core Team, 2017. R: a language and environment for statistical computing. https://www.R-project.org/.

Roll, U., Feldman, A., Novosolov, M., Allison, A., Bauer, A.M., Bernard, R., Böhm, M., Castro-Herrera, F., Chirio, L., Collen, B., et al., 2017. The global distribution of tetrapods reveals a need for targeted reptile conservation. Nat. Ecol. Evol. 1, 1677–1682. https://doi.org/10.1038/s41559-017-0332-2.

Taylor, G., Scharlemann, J.P.W., Rowcliffe, M., Kümpel, N., Harfoot, M.B.J., Fa, J.E., Melisch, R., Milner-Gulland, E.J., Bhagwat, S., Abernethy, K.A., Ajonina, A.S., 2015. Synthesising bushmeat research effort in West and Central Africa: a new regional database. Biol. Conserv. 181, 199–205. https://doi.org/10.1016/j.biocon.2014.11.001.

Tilman, D., May, R.M., Lehman, C.L., Nowak, M.A., 1994. Habitat destruction and the extinction debt. Nature 371, 65.

Tolley, K.A., Alexander, G.J., Branch, W.R., Bowles, P., Maritz, B., 2016. Conservation status and threats for African reptiles. Biol. Conserv. 204, 63–71. https://doi.org/10.1016/j.biocon.2016.04.006.

Venter, O., Sanderson, E.W., Magrach, A., Allan, J.R., Beher, J., Jones, K.R., Possingham, H.P., Laurance, W.F., Wood, P., Fekete, B.M., Levy, M.A., Watson, J.E.M., 2016. Sixteen years of change in the global terrestrial human footprint and implications for biodiversity conservation. Nat. Commun. 7, 1–11. https://doi.org/10.1038/ncomms12558.

Watson, J.E., Dudley, N., Segan, D.B., Hockings, M., 2014. The performance and potential of protected areas. Nature 515 (7525), 67–73. https://doi.org/10.1038/nature13947.

Whitfield, S.M., Bell, K.E., Philippi, T., Sasa, M., Bolaños, F., Chaves, G., Savage, J.M., Donnelly, M.A., 2007. Amphibian and reptile declines over 35 years at La Selva, Costa Rica. Proc. Natl. Acad. Sci. U. S. A. 104, 8352–8356. https://doi.org/10.1073/pnas.0611256104.

Williams, V.L., Moshoeu, T.J., Alexander, G.J., 2016. Reptiles sold as traditional medicine in Xipamanine and Xiquelene Markets (Maputo, Mozambique). S. Afr. J. Sci. 112, 1–9. https://doi.org/10.17159/sajs.2016/20150416.

Woinarski, J.C.Z., Murphy, B.P., Palmer, R., Legge, S.M., Dickman, C.R., Doherty, T.S., Edwards, G., Nankivell, A., Read, J.L., Stokeld, D., 2018. How many reptiles are killed by cats in Australia? Wildl. Res. 45, 247–266.