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The desolation of Smaug: The human-driven decline of the Sungazer lizard (*Smaug giganteus*)

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ABSTRACT

The Sungazer (*Smaug giganteus*) is a threatened lizard species endemic to the Highveld grasslands of South Africa. The species faces risks from habitat loss and fragmentation, and illegal harvesting for traditional medicine and the pet trade. Despite these threats, the current conservation status of the species was poorly validated. We visited 79 Sungazer populations recorded in 1978 to assess population change since the initial surveys, and surveyed an additional 164 sites to better define the distribution and estimate the current population size. We interrogated all known historical trade data of the species. One-third of Sungazer populations have been extirpated over the past 37 years. The distribution includes two allopatric populations, with the smaller Mpumalanga population experiencing a significantly higher decline. The species has an extent of occurrence (EOO) of 34 500 km^2, and an area of occupancy (AOO) of 1149 km^2. The interpreted distribution is 17 978 km^2, and just under 60% remains untransformed grassland. We estimate a population size of 677 000 mature individuals, down 48% from the estimated historical population, prior to commercial agricultural development. A total of 1194 live Sungazers were exported under permit from South Africa between 1985 and 2014, with a significant increase in numbers exported over the last decade. Without any evidence of captive breeding, we believe that these animals are all wild-caught. Based on the AOO, level of decline, fragmentation within the distribution and suspected level of exploitation, we recommend classification of the species as Vulnerable under IUCN Red List Criteria A2acd and B2ab(ii–v). The establishment of a protected area network, genetic research and further investigations into the pet and traditional medicine trades are urgently needed.

1. Introduction

More than half of Earth's land-area has been transformed for agriculture, resource harvesting, transport networks, and human habitation (Hooke, Martin-Duque, & Pedraza, 2012). These processes result in habitat loss, degradation and fragmentation, and are the primary contributors to biodiversity loss worldwide (Driver, Maze, Lombard, Nel, Rouget, & Turpie, 2005; Lötter, 2010), particularly for reptiles (Branch, 1988; Böhm et al., 2013). While the conservation plight of charismatic taxa such as large mammals and birds are widely publicized and addressed by conservation bodies, smaller, cryptic fauna such as reptiles are often neglected (Tolley, Alexander, Branch, Bowles, & Maritz, 2016). Only 46% of reptiles have been risk-assessed by the International Union for Conservation of Nature (IUCN, 2016). Of those assessed, 20% are classified as threatened and 21% as data deficient, an indication of a lack of focus on reptiles (Böhm et al., 2013). Many reptile species have small ranges and narrow niche requirements (Anderson & Marcus, 1992), and are thus particularly susceptible to the threat processes of habitat destruction and harvesting.

Smaug giganteus, commonly known as the Sungazer, is an enigmatic cordylid lizard endemic to the Highveld grasslands of the Free State and Mpumalanga provinces of South Africa (Fig. 1; De Waal, 1978; Jacobsen, 1989). The species is atypical for the family in that it is an obligate burrower rather than being rupicolous, and is large and heavily armored. It is also distantly related to other members of the family (Stanley et al., 2011), and has recently been ranked as the 19th-most evolutionarily-distinct threatened squamate (top

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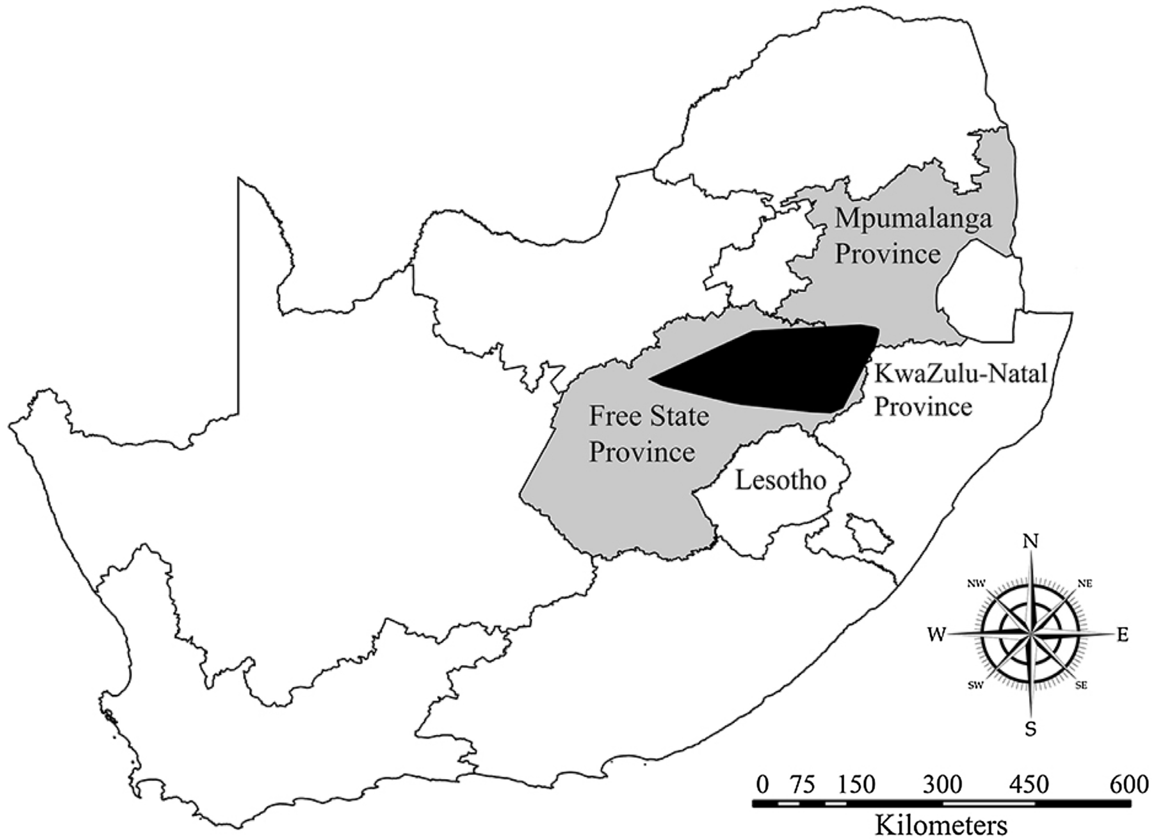

Fig. 1. Map of South Africa showing the convex hull (black) that defines the EOO of *S. giganteus.*

0.5% of all assessed squamate species; Tonini, Beard, Ferreira, Jetz, & Pyron, 2016). Forty percent of its distribution has been transformed for crop farming (DEAT, 2005) as it inhabits areas of rich loamy soils on gentle slopes that are ideal for crops (Van Wyk, 1992). Agriculture therefore presents a major threat to the species, destroying large tracts of habitat and fragmenting populations (Van Wyk, 1988; Jacobsen, 1989 Mouton, 2014). Additionally, many populations have been extirpated by the construction of roads, pipelines, electricity infrastructure and other developments (Van Wyk, 1992). Since there are currently no credible records of recolonization of fallow or rehabilitated land, habitat transformation is regarded as an irreversible loss of habitat (Van Wyk, 1992).

Illegal harvesting for the international pet trade and local traditional medicine trade are also significant threats (Branch, 1988 Loehr, Parusnath, & Gilchrist, 2016; McLachlan, 1978 Whiting, Williams, & Hibbitts, 2011). Sungazers are highly sought-after in the pet trade due to their rarity and dragon-like appearance (Auliya, Altherr, Ariano-Sanchez, Baard, & Brown, 2016), and the species is one of the top five reptile species exported from South Africa for the pet trade (CITES, 2016). High prices drive illegal trade and cases of poaching for the pet trade have been reported since the 1970s (McLachlan, 1978; Van Wyk, 1988; Auliya et al., 2016). There is no validated evidence that the species has been successfully bred in captivity and all specimens in the trade are thus suspected to be wild-caught (Loehr et al., 2016). Similarly, Sungazers are widely harvested for use in Sotho and Zulu traditional medicine, where their bodies are powdered for use in love potions (Peterson, Newbery, & Jacobsen, 1985). Whole Sungazer carcasses, skins, and body parts are frequently offered for sale in traditional medicine markets across South Africa (Whiting et al., 2011). Due to the illegal nature of these trades, the numbers of animals harvested annually remain unquantified, and their level of impact on wild populations is unknown.

Despite the obvious threats, little research has focused on quantifying their impact on *S. giganteus*. It was listed as vulnerable by McLachlan (1978) and has maintained this status since (Van Wyk, 1988; Mouton, 2014). The most recent conservation assessment (Mouton, 2014)) uses criterion A2c, based on a 30% decrease in abundance over the last three generations (assumed to be 27 years), inferred from modification of the Grassland Biome in South Africa. However, population size, population decline and habitat reduction have not been quantified for the species. Furthermore, the boundaries of its distribution are poorly defined, and the rate at which it occupies the landscape unknown. The need for a re-assessment of the conservation status based on an empirical data has long been recognized (Van Wyk, 1988; Van Wyk, 1992; McIntyre & Whiting, 2012). We used data collected in an extensive field survey to refine measures of the EOO and AOO, and created an interpreted distribution map of *S. giganteus*. We estimated population density and population size, and used population surveys and GIS land-cover analyses to assess population and habitat declines over the last 30 years. We also used Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) data to assess trends in numbers of Sungazers traded internationally. Finally, we integrated these measures to assess the conservation status of *S. giganteus* using the latest IUCN criteria, and make recommendations for the future conservation of the species.

2. Methods

Our approach focused on four aspects of Sungazer life history: geographic distribution, population size, population decline, and habitat decline. We relied heavily on measures of burrow density and occupancy as these are distinctive and easily identifiable, providing a useful proxy for direct counts of burrowing reptiles (McCoy & Mushinsky, 1992). We conducted surveys between February 2012 and December 2015 using a standardised survey technique in 1-ha quadrats. This quadrat size was chosen because Sungazers aggregate in 'colonies' that typically range from less than 1 ha to a few hectares in size. Surveys were initiated upon the sighting of a Sungazer burrow, or as informed by the landowners. For each site surveyed, we walked the quadrat for 1 h at a standard pace, in parallel line-transects 5 m apart so that the entire quadrate was evenly covered. We used a Garmin GPSmap 78 s (datum WGS1984) with real-time path-tracking to guide the length and spacing of transects. We classified burrows as occupied if there was evidence of claw or tail marks, or sloughed skin at the burrow entrance, and the entrance was unobstructed by debris. If the state of occupancy was uncertain, we inserted a closed-circuit borescope video-camera into the burrow to directly assess occupancy. We recorded coordinates and elevation for every burrow.

2.1. Geographic distribution

2.1.1. EOO

We extracted all occurrence records with point locality data (n = 101) from the Animal Demography Unit Reptile Map (ADU, 2016). Records from KwaZulu-Natal Province and the supposed type locality in Lesotho were excluded, as these records are regarded as invalid (Armstrong, 2011; Mouton, 2014). We also conducted population surveys at 84 sites across the distribution. We targeted Quarter Degree Cells (QDC: a grid system of 15′ longitude x 15′ latitude units ~680 km^2) where the species had been recorded, but for which no point locality data existed, along with QDCs adjacent to QDCs containing records (n = 42). Within these grid cells we targeted habitat that appeared to be ideal (flat/gentle slope, primarily *Themeda* grass cover; n = 42). A convex hull representing the EOO (IUCN, 2012) was created in ArcMap that included all Sungazer sites with point locality data (n = 185).

2.1.2. Ecological niche model

We produced a maximum entropy ecological niche model to identify optimal habitat for the species, to guide the delineation of an 'interpreted distribution' map. We used the presence-only modelling software MaxEnt (Version 3.3.3k; Phillips, Anderson, & Schapire, 2006) to create niche models, since presence-only models allow for the creation of niche models for species where true absences are difficult to verify (Phillips et al., 2006). We used the full dataset of point locality records (n = 761), and 24 environmental GIS layers representing all known aspects of the species' niche requirements. This included 19 bioclimactic variables (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005), altitude (Hijmans et al., 2005), vegetation type (Mucina et al., 2006), soil type (Dijkshoorn, Engelen, & Huting, 2008), underlying geology (AGIS, 2007), and land cover (DEA, 2015). To increase the precision of the model, the layers were cropped to a rectangle that included that EOO and a surrounding buffer zone. The model was run with 10 000 background points, 5 000 iterations and 15 replicates. The selected output grid format was 'logistic', in which pixel values ranged from 0 to 1.

2.1.3. Interpreted distribution

We created an 'interpreted distribution' map to represent the actual range of *S. giganteus*. We created a polygon around optimal Sungazer habitat, as identified using the niche ecological model created in this study, then guided the shape around the full dataset of point locality records (n = 761). We excluded areas that have historically been devoid of records due to environmental boundaries, or areas that were found in this study to have not been colonized by Sungazer populations. We refined the perimeter of the shape using each of the environmental variables used in the niche model. For instance, we used the landcover map to cut around waterbodies, and highly developed urban areas, and the altitude map to remove extreme high and low areas.

2.1.4. AOO

Sungazers do not occur uniformly across their range, but rather in discrete aggregations that may be separated by several kilometers. To estimate the proportion of the interpreted distribution actually occupied by *S. giganteus* at a 1-ha resolution, we conducted population surveys at 92 randomly-selected sites in natural grassland within the interpreted distribution of the species, guided by the most recent national land-cover map (DEA, 2015). These sites were selected by generating random points in ArcMap and removing those that did not fall in natural grassland. Surveying these sites provided a proportional measure of suitable habitat where the species actually occurs.

2.2. Habitat decline

We used the most recent national land-cover map (DEA, 2015) to calculate the area of natural grassland within the interpreted distribution. We assumed that transformed land within the interpreted distribution was historically *Themeda* grassland, as this is the dominant land-cover type within the Highveld Agricultural Region (DEAT, 2005). The area of these land-cover feature classes was calculated and the proportion of natural grassland was used to calculate the percentage of natural area remaining after transformation. We also did this for the South African national land-cover 1990 dataset (DEA, 2015), to estimate the rate of change in land-cover over time.

2.3. Population density

We calculated population density by surveying 80 Sungazer colonies across the distribution (Fig. 2) (these included AOO survey sites where Sungazers were present) and counted the number of burrows in each 1-ha quadrat. We distinguished Sungazer burrows from those of other burrowing species by a) their distinctive ovular shape, b) the ~3 cm wide ridge running along the centre of the burrow floor and c) the bare patch of the earth where Sungazers forage and bask. We used published measures of occupancy (Jacobsen, Newbery, & Peterson 1990; Van Wyk, 1992) (Table 1) to relate Sungazer burrow densities (burrows/ha) to population density (lizards/ha).We weighted scores according to the number of burrow observations made per study to create a burrow occupancy index (BOI). An overall weighted mean (Mean Burrow Density per ha – MBD) was then derived using the formula:

$$\text{Weighten metascore for mean}$$

$$S.\ giganteus\ \text{burrow occupancy}$$

$$= \frac{A_n.A_{MBO}}{(A_n + B_n + C_n)} + \frac{B_n.B_{MBO}}{(A_n + B_n + C_n)} + \frac{C_n.C_{MBO}}{(A_n + B_n + C_n)}$$

A_n, B_n, C_n = number of observations per site

A_{MBO}, B_{MBO}, C_{MBO} = mean burrow occupancy at each site

2.4. Population size

We estimated the total number of burrows across the distribution by multiplying MBD by the AOO. Since previous demographic studies found that 14.3% (range 11.5–18.5) of burrows are unoccupied (Stoltz, & Blom, 1981; Jacobsen, 1989; Van Wyk, 1992), we subtracted the mean percentage of empty burrows (PEB) to derive the total number of occupied burrows within the distribution. We

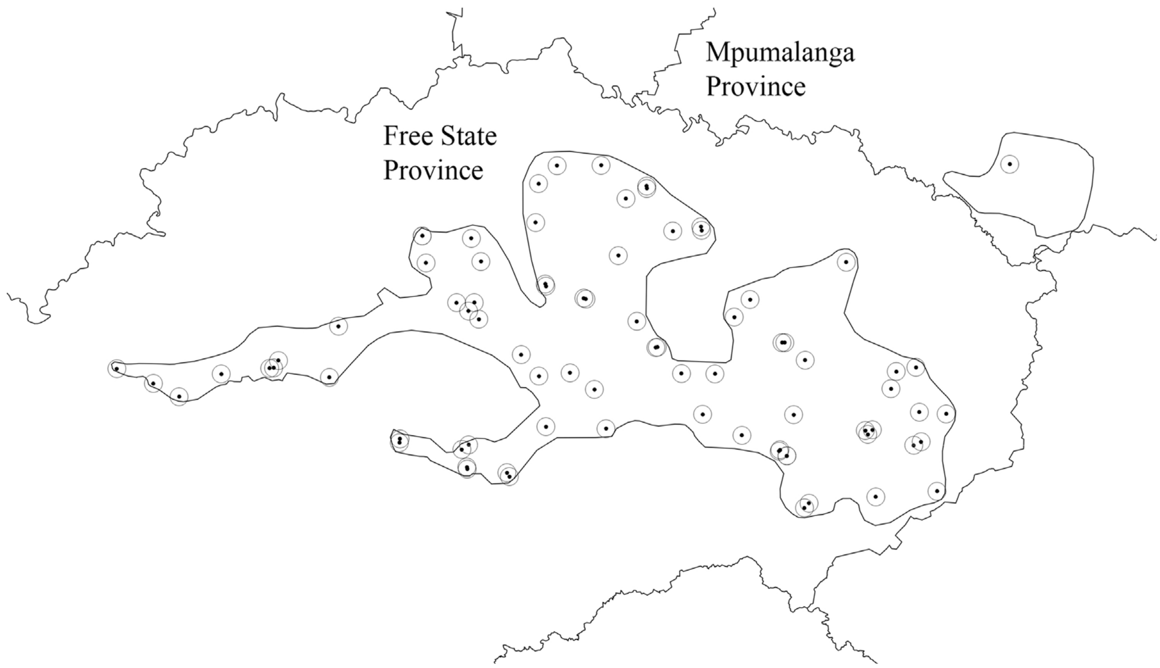

Fig. 2. Interpreted distribution showing the location of 80 sites surveyed for *S. giganteus* population density.

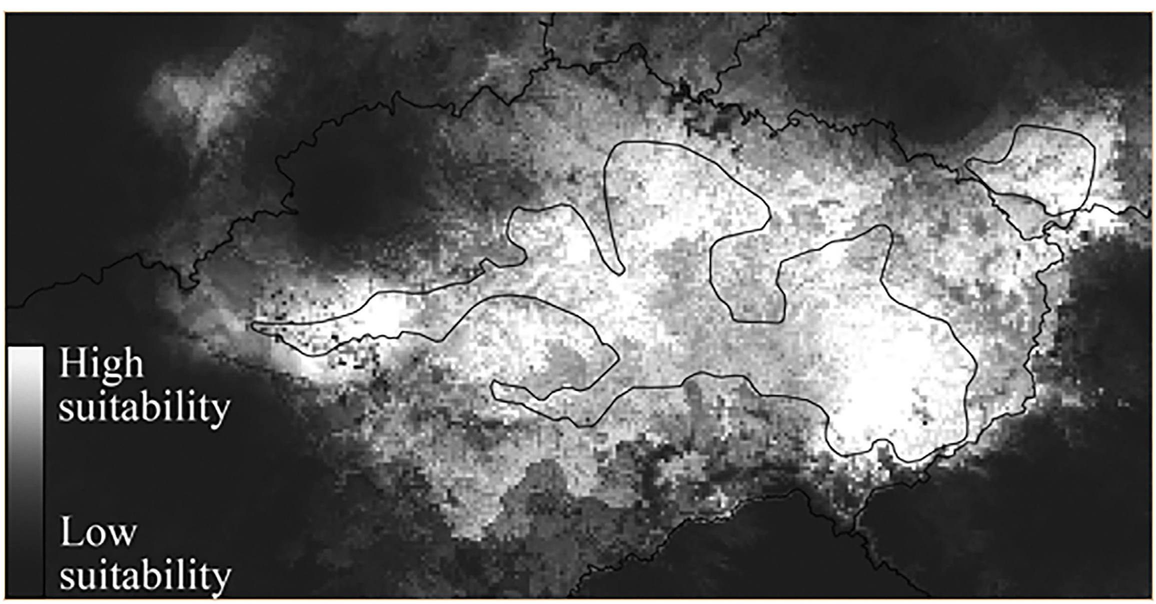

Fig. 3. Ecological niche model for *S. giganteus* showing areas of high suitability (white) and low suitability (black) across the interpreted distributed of the species.

Table 1
Weighted metascore of mean Sungazers per burrow derived from previous studies.

Study	Mean burrow occupancy	No. burrows recorded	% of total burrow count	Weighted contribution
Jacobsen et al. (1990)	1.83	841	73.8	1.35
Van Wyk (1992) – Greenlands	2.11	180	15.8	0.33
Van Wyk (1992) – Middelpunt	1.42	118	10.4	0.15
Total		1139	100	1.83

applied the weighted burrow occupancy index (BOI) to the total number of occupied burrows to calculate total population size. For purposes of IUCN conservation assessments, 'population size' is defined as the total number of individuals in a population capable of reproduction (IUCN, 2012). Van Wyk (1992) recorded the percentage of mature individuals (PMI; SVL > 165 mm) to be 62.4% (range 53.6–74.2). Thus, we calculated the number of mature individuals using the formula:

Total mature individuals = ((MBD ± 95% CI x AOO)-PEB) x BOI x PMI

Where the 95% confidence interval around the mean burrow density is 1.96 x Standard Error of the mean MBD.

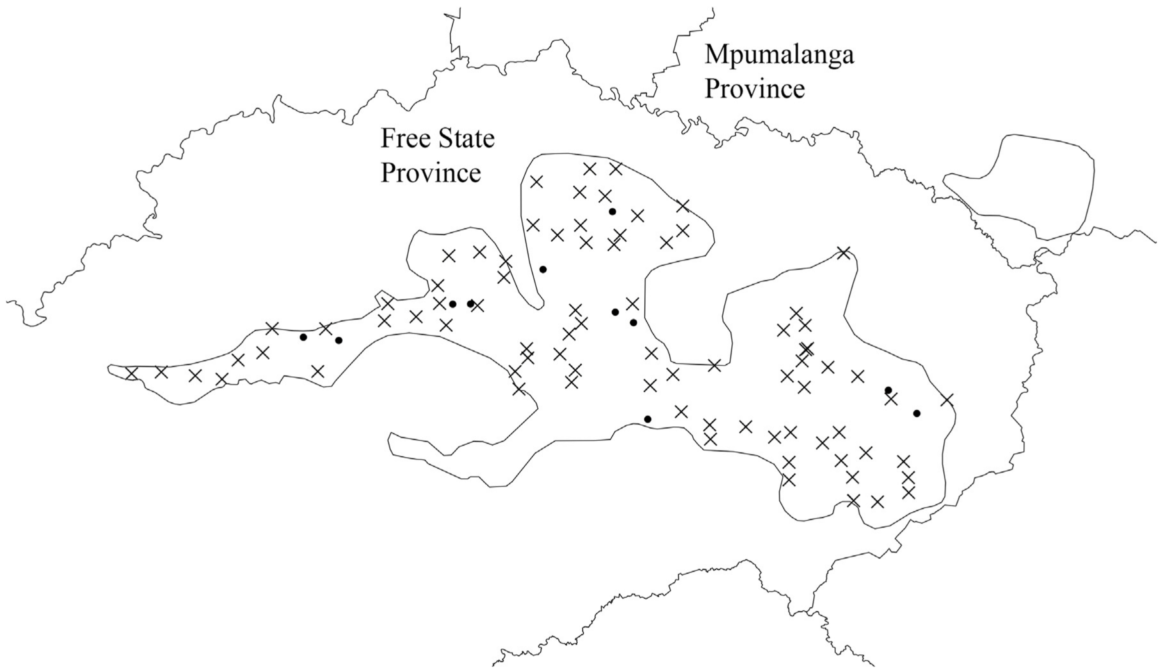

Fig. 4. Randomly chosen sites within the interpreted distribution showing presence (●) and absence (x) of *S. giganteus* used for the calculation of AOO.

2.5. Generation length

Generation length is used as an IUCN metric for the assessment of the rate of decline in a species. In lieu of detailed age- and sex-specific information on survival and fecundity of wild-living Sungazers, we calculated generation length using the following formula:

Generation Length = AFR + (ML-AFR)/2

AFR = age of first reproduction

ML = maximal longevity

AFR – Van Wyk (1992) estimated age of first reproduction to be late in the fourth year, or early in the fifth year of life. Thus, we assume the age of first reproduction to be 5 years.

ML – There are no measures or estimates of longevity for free-ranging Sungazers, but records from captive specimens indicates a longevity of at least 25 years (HAGR, 2016), and we have thus assumed a ML of 25 years.

2.6. Population decline

Previous herpetological surveys recorded the presence of Sungazer populations at 39 sites in the Free State (De Waal, 1978), and 40 sites in Mpumalanga (G. Theron, unpublished survey data). The majority of these sites were on privately owned farmlands. We visited each of these sites to assess the current status of these populations. At each site, the landowner was interviewed and if the population was still present, we surveyed a 1-ha quadrat within the colony. We also visited 37 sites in the Free State that De Waal (1978) surveyed but did not find Sungazers, to assess for the presence of new Sungazer populations, and/or errors of omission of that survey. We scored population declines across the distribution per QDC, and used an independent-sample T-test to compare the number of extant populations between 1978 and 2013.

2.7. Pet trade

We used the CITES trade database (CITES, 2016) to assess trends in the trade in Sungazers between 1983 and 2014. We totalled the number of live Sungazers exported from South Africa each year, as well as Sungazers exported from other countries over this period. We tested for differences in the numbers of Sungazers exported from South Africa over the past three decades with a Kruskal-Wallis ANOVA.

2.8. Analyses

All statistical analyses were performed with STATISTICA v8.0 (Statistica Data Analysis Software System 2001). All GIS analyses were performed with ArcMap v10.2 (ESRI Inc., Redlands, CA, USA).

3. Results

3.1. Geographic range

3.1.1. EOO

EOO was estimated to be over 34 500 km^2 (Fig. 1). Just over half (56%) remains natural grassland, while the balance is either unsuitable natural habitat (3%), or is transformed (41%).

3.1.2. Ecological niche model

The area-under-curve (AUC) value of 0.915 achieved for the niche model reflects a high predictive ability of species presence in geographic space. The niche model shows several distinct areas that are predicted to represent optimal Sungazer habitat (Fig. 3), with extremely high probabilities of Sungazer presence (pixel value >0.85). In between, and connecting these zones are large contiguous patches that are modelled as being highly suitable habitat, with a high probability (pixel value >0.7) of Sungazer presence.

3.1.3. Interpreted distribution

The interpreted distribution is 17 978 km^2; 16 546 km^2 in the Free State, and 1 432 km^2 in Mpumalanga (Fig. 2). The two polygons that make up the interpreted distribution are separated by 44 km at their closest borders, and indicate that the species occurs in two allopatric populations. Large wetlands along major rivers appear to be unsuitable for Sungazers and were excluded from the interpreted distribution polygon. Just under half (47%) of the interpreted

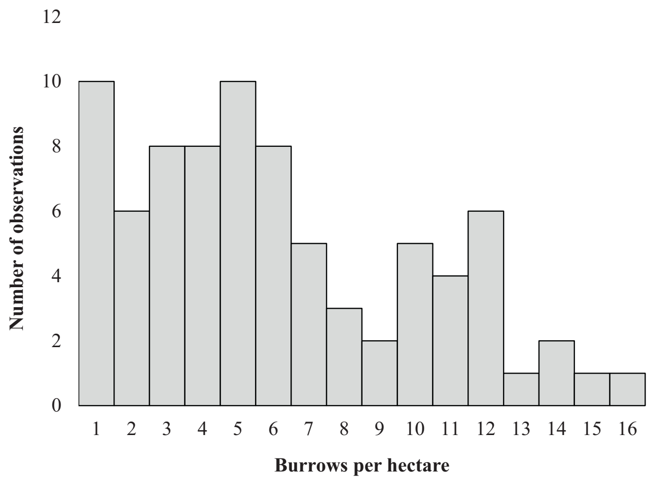

Fig. 5. Number of *S. giganteus* burrows observed per hectare.

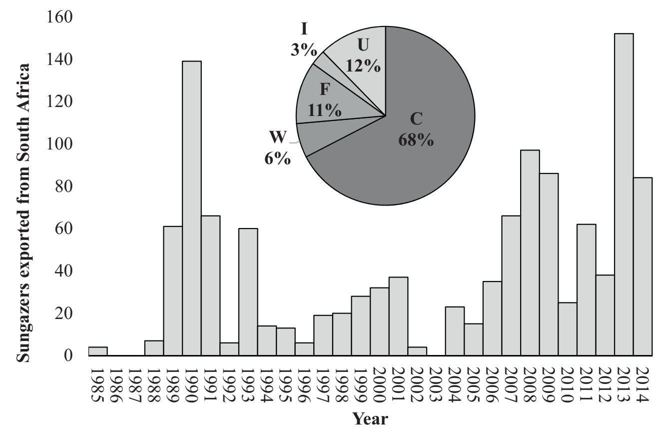

Fig. 6. Reported number of *S. giganteus* exported out of South Africa per year between 1985 and 2014 (Source: CITES, 2016). The pie diagram indicates the reported sources of exported *S. giganteus* over this period (C = captive bred, U = source unknown, F = born in captivity, W = wild-caught, I = confiscated; CITES, 2016).

distribution has been transformed through human modification, leaving 9 578 km^2 as suitable natural grassland.

3.1.4. AOO

We found Sungazers at 11 of the 92 (12%) random sites surveyed in natural grassland across the interpreted distribution (Fig. 4). Thus we calculated the AOO to be 12% of the natural grassland within the interpreted distribution, resulting in an area of 1 149 km^2.

3.2. Habitat decline

Fifty-eight percent of *S. giganteus* distribution is currently in a natural state, while 40% is cultivated for crop farming. The remaining 2% is classified as plantations (0.6%), waterbodies (0.3%), degraded (0.3%), and mines (0.2%). Natural grassland increased by 0.5% between 1990 and 2013/4, balanced by a 0.6% decrease in cultivated land. Importantly, neither the 1990 or 2013/4 land-cover maps differentiates between primary and secondary grassland.

3.3. Population density

A total of 491 Sungazer burrows were recorded at 80 occupied sites, with a mean density of 6.14 (SD 0.87) burrows/ha (range: 1–16). Data for burrow density were not normally distributed (Shapiro-Wilk normality test W = 0.9, $p < 0.001$). Lower population densities (<6 burrows/ha) are more common than high-density populations (>6 burrows/ha) (Fig. 5). On average burrows were observed 3.6 m from the observer, with 83% of observations within 5 m of the observer. The mean number of Sungazers per burrow was 1.83 animals (Table 1), resulting in a range of 1.8–29.3 Sungazers/ha.

3.4. Population size

We estimate a total of 705 000 (SE 100 000) burrows across the distribution of the species. Of these, 605 000 (SE 86 000) are estimated to be occupied. Thus, we estimate that the total current population of Sungazers is 1 107 000 (SE 157 000), with 677 000 (SE 96 000) of these being mature individuals. Based on the historical extent of natural grassland within the interpreted distribution, the historical population size of *S. giganteus* is estimated as 1 301 000 (SE 184 000) mature individuals. This computes to a 48% decrease in the total population size due to habitat loss.

3.5. Population declines

We found that 25 of the 79 populations recorded by De Waal (1978) and Theron (G. Theron, unpublished survey data) have been extirpated (32% decline over 37 years; Two-sample *T*-test; $t = 3.6$; $p < 0.001$). There was a significantly higher rate of extirpation in the Mpumalanga polygon (17/40) than in the Free State polygon (8/39) (Two-sample T-test; $t = 7.4$; $p < 0.001$). Importantly, none of these extirpations were directly due to habitat transformation, as the habitat of each of these extirpated populations had not been obviously transformed, and remained primary grassland. We found Sungazer populations at three of the 37 sites where De Waal (1978) did not find Sungazers. At each of these localities, we interviewed the landowner and found that, without exception, the colony existed in 1978 during the time of De Waal's survey, suggesting that these were due to errors of omission as opposed to the formation of new colonies.

3.6. Generation length

We estimated generation length for *S. giganteus* to be 15 years. Thus, the length of time over which declines should be assessed under IUCN Criterion A is 45 years.

3.7. Pet trade

A total of 1194 live Sungazers were exported under permit from South Africa between 1985 and 2014 ($\bar{x} = 40$ per year). There was a significant difference (Kruskal-Wallis ANOVA; $H_{(2,27)} = 9.0$; $p < 0.05$) between the number of Sungazers exported from South Africa between decades (1985–1994; n = 357, 1995–2004; n = 182, 2005–2014; n = 660). The most recent decade had the highest number of exports, representing 55% of total export numbers on record. Sungazers were exported to 15 countries, with Japan, North America and Germany being the main recipients, collectively receiving 74.8% of imports (Fig. 6). Just under 70% of Sungazers exported were reported to be captive bred (although this is unlikely to be true), 11.3% born to wild-caught females in captivity, 6.2% as wild-caught, and the remainder of unknown source (12%) or confiscated (3%) (Fig. 6 inset). Between 1982 and 2014, 853 Sungazers were exported from countries other than South Africa (outside the species natural distribution; $\bar{x} = 28$ per year). Of these, Mozambique was the greatest contributor, exporting 350 animals in 1988 and 50 in 2009, making up 47% of non-South African exports. Indonesia

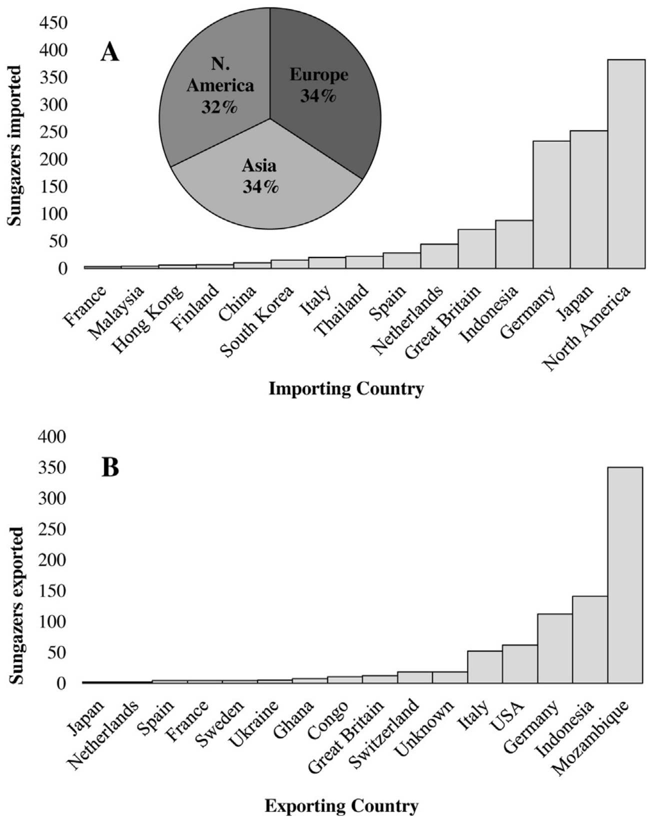

Fig. 7. A) Number of *S. giganteus* exported from South Africa 1983 and 2014. The pie diagram indicates the percentages destined to different continents (CITES, 2016). B) Number of *S. giganteus* exported from countries other than South Africa between 1982 and 2014 (CITES, 2016).

and Germany were also important exporters, exporting a total of 141 and 112 animals respectively. In the cases of Mozambique, Indonesia, Italy, Switzerland, Congo, Ghana, Ukraine, Sweden and Spain, more Sungazers were exported from the respective country than were reported to have been imported over the same period (Fig. 7a, b).

4. Discussion

Almost half of the original Sungazer habitat has been transformed, fragmenting the remaining habitat. This broad-scale habitat loss appears to have occurred more than two decades ago since recent land-cover maps show little further loss of grassland. However, we detected a significant decline in Sungazer populations over the past 37 years, ranging from 24 to 32%, depending on the reason that De Waal (1978) had not recorded Sungazers at the sites where we later found them. We believe that these are errors of omission, since in each case, landowners verified that the populations were long established and had been present in 1978. Thus, our best estimate of decline is 32% over the last 37 years, with no evidence of any newly established populations. Importantly, none of the recorded extirpations appeared to be due to habitat loss, as in each case of extirpation, the habitat remained untransformed. Rather, it is likely that extirpations are the result of harvesting and habitat fragmentation. We estimate that only 4% of the EOO is occupied by the species. Our study suggests that the most important landscape-scale limiting factors to occurrence are rivers, wetlands and mountain ranges. The distribution consists of two allopatric population and this disjunction appears to be natural – Sungazers have never been reported from the intervening area. It is possible that these two populations are genetically distinct. Our estimation of population size is one of the first for any African reptile species. We derived this by multiplying measures of burrow density by area of occupancy, while taking burrow occupancy, the percentage of unoccupied burrows, and mature individuals into account. While we acknowledge that there is a compounding error margin around this estimate with each step of the calculation, our means are derived from large sample sizes, and we are therefore confident about the numbers presented here.

Our calculation of EOO (34 500 km^2) exceeds the 20 000 km^2 limit for classification as "Vulnerable" under IUCN Red List Criterion B1 (IUCN, 2012). Our measure is 25% smaller than Van Wyk's (1992) estimate (45 623 km^2), and 27% smaller than Mouton's (2014) (47 450 km^2). These differences are the result of the different resolutions used in the analyses and the accumulation of new data in our study. Our AOO estimate (1149 km^2) falls below the 2000 km^2 for assessment as "Vulnerable" but above the 500 km^2 for "Endangered" under IUCN Criterion B2. Mouton's (2014) AOO estimate (3352 km^2) was calculated as 10% of the cumulative area of QDCs in which the species had been recorded (50 QDCs; P.le.F.N. Mouton, personal communication). Our measure is 66% smaller than Mouton's (2014) estimate, due primarily to the finer resolution and more direct measure of suitable habitat for our measure. However, our measure may still be an overestimate due to the difficulty in differentiating primary and secondary grassland using satellite land-cover imagery.

There was little net change in the area of grassland cover over the distribution of Sungazers from 1990 to 2014. Thus, the 48% loss of natural habitat occurred prior to 1990, supporting Branch's (1988) contention that ~50% of the arable grassland within the Sungazer's range was already irreversibly transformed prior to 1988. The mean burrow density recorded for *S. giganteus* in our study (6.14 burrows/ha) falls within the upper end of the range of burrow densities recorded for the species in previous studies (4–6.8 burrows/ha, Stolz & Blom, 1981; Jacobsen, Newbery, & Peterson 1990; Van Wyk, 1992), and higher than the mean burrow density calculated from these studies. The range of burrow densities recorded (1–16 burrows/ha) was similar to the range reported by Van Wyk (1992) (1–19 burrows/ha). As in our study, Van Wyk (1992) noted that despite high densities in some areas, large tracts of adjacent land were devoid of burrows.

One-third of Sungazer populations have been extirpated within the last four decades. The 31.6% decline recorded between 1978 and 2015 translates to a compounded rate of 1.03% per year. Assuming a constant rate of decline, populations have declined by 38.7% over the last 45 years (three generations). While decline was recorded across the distribution, Mpumalanga populations were more than twice as likely to become extirpated than were Free State populations. The cause of this differential decline is unclear and none of the extirpations recorded in our study could be directly linked to habitat loss through recent habitat transformation, as none of these sites had been ploughed since the initial surveys. Many landowners were able to pinpoint the exact areas where Sungazer colonies were once present, and in some instances, the remnants of inactive burrows were still visible. In four cases, the landowners suspected that the local extirpations were due to illegal harvesting, based on the presence of poaching tools and excavated burrows coinciding with recently extirpated colonies. Our estimates of decline may well underestimate the actual decline as our measures are at the resolution of entire populations. It is possible that there has also been a within-population decrease of abundance.

The majority of permitted Sungazer exports from South Africa over the past three decades were reported to have been captive-bred individuals (70%), while only 6% were reported as wild-caught. Seemingly, this suggests that the captive-breeding industry has boomed since the mid-1980s, but Sungazers are notoriously difficult to breed in captivity and there is only a single published case of captive-breeding (Langerwerf, 2001). Besides this case, the popular literature on Sungazer husbandry (McKeown, 2001; Schwier, 2007) and captive studbooks (Gilchrist & Zwartepoorte, 2014) are devoid of any records of breeding and there are no verified breeding facilities in South Africa. We agree with (Loehr et al., 2016) that the vast majority, if not all, 'captive-bred' Sungazers are actually wild-caught animals laundered for trade. The discrepancy between import and export numbers from countries such as Mozambique, Indonesia, Italy, also suggest unreported illegal trade. Investigative studies on other reptile species have revealed illegal trade in wild-caught laundered through 'breeding farms' (Lyons & Natusch, 2011; Bennett, 2012; Mucci, Mengoni, & Randi, 2014) as trade in captive-bred animals is less strictly regulated than trade in wild-caught animals (Auliya et al., 2016).

The lack of a direct correlation between habitat loss and extirpations over the past several decades indicates that habitat transformation is unlikely to be the direct, primary agent behind the recent population declines. Rather, it is likely the combined effect of habitat fragmentation and illegal harvesting that are the most important causal factors. Many of the colonies recorded in this study exist within tiny fragments of natural grassland in a complex mosaic of human-altered land. It is likely that colonies in highly fragmented areas suffer considerably from ecophysiological edge effects such as drought stress, flooding, prey shortages, as well being exposed to pollution, and pesticides. Juveniles (<2 years of age) are highly susceptible to predation and this might be increased in fragmented areas (Van Wyk, 1992). Dispersal is reduced in fragmented habitats (Saunders, Hobbs, & Margules, 1991; Couvet, 2002) resulting in increasingly isolated populations (Slatkin, 1987; Frankham, Ballou, & Briscoe, 2002) and a loss of genetic diversity within fragments (Frankham, 2006; Keyghobadi, 2007). Given the heavy fragmentation across the distribution, gene flow between colonies is also likely to be compromised. However, since Sungazers are long-lived and have low fecundity, it is likely that these effects will be slow to manifest and the impacts of habitat transformation in the early 1900s may only now being shown. It is also likely that the actual numbers of Sungazer traded is very significantly higher than those traded through legal channels, given that South Africa is known to be a hotspot for reptile poaching (Auliya et al., 2016). Harvesting for the local traditional medicine trade is not monitored and there are no data on this trade due to its illicit nature.

4.1. Conclusion and recommendations

The major threats that *S. giganteus* faces – agricultural expansion, linear infrastructure development and illegal harvesting – are driven by national or international market dynamics and government policy, and are likely to impact populations across the entire distribution. The small AOO, population decline of 38.7% over three generations, the apparently irreversible impact of habitat transformation, and the levels of exploitation, make a classification of 'Vulnerable' under IUCN Red List Criteria A2acd and B2ab(ii–v) appropriate for the species. It has been listed as 'Vulnerable' since the first Red List in 1978 (McLachlan, 1978), but ours is the first study to use empirical data for the assessment. Furthermore, our data allow for the assessment of rates of decline and the extinction risk faced by the species. Despite the Sungazer being a charismatic, endemic, protected species, no conservation management initiatives have been implemented over the past century for its protection. We make the following recommendations to promote the conservation of the species:

1) *Protected areas.* – A protected area network is urgently needed to conserve the Sungazer in its habitat, since the species does not currently occur within any proclaimed conservation areas. We suggest that national and provincial biodiversity and conservation agencies, along with NGOs, target areas with intact, high density Sungazer populations as priority reserve sites. Since Sungazers only occupy pristine grassland, we identify the Sungazer as both an indicator species of optimal grassland, and a flagship species, whereby Sungazer reserves would help conserve other threatened species that are currently not found within protected areas (Botha's Lark *Spizocorys fringillaris*, Yellow-breasted Pipit *Anthus chloris*, Highveld Golden Mole *Amblysomus septentrionalis*, Hottentot's Golden Mole *Amblysomus hottentotus*). Formal reserves, however, are unlikely to be of sufficient size to guarantee persistence and maintenance of genetic diversity in Sungazers. In addition, we therefore suggest the implementation of a stewardship programme, whereby private landowners agree to restrictions on transformation of their land in return for benefits from protected area status. Stewardship efficiency can be maximised if these sites form an interconnected network allowing for dispersal of animals between sites. Any reserve, either governmental or private, will require dedicated staff to ensure suitable habitat management and close monitoring of populations to deter illegal harvesting.
2) *Fine-scale monitoring programme.* – The QDC resolution at which the species was previously mapped is too coarse to detect colony-level declines. We suggest a fine-scale (farm-level) monitoring programme for both reserve and stewardship sites. Ideally, landowners participating in stewardship programmes would report annually on the population dynamics of colonies on their property. This will allow for the early detection of extirpations, and mitigation of causal factors.
3) *Genetic research.* – The population declines reported in this study are potentially a result of long-term habitat fragmentation. A fine-resolution genetic study investigating the genetic diversity of colonies within highly fragmented and minimally fragmented areas will allow for an assessment of the effects of fragmentation on the genetic health of the Sungazer. Further, genetic studies are needed to investigate the processes of gene flow and dispersal in the species.
4) *Translocation protocol.* – Ongoing, high priority developments such as highways, pipelines, and power stations, will continue to impact on Sungazer populations. It is therefore important to develop means to minimise and mitigate these impacts. Previous translocation attempts have been unsuccessful (Groenewald, 1992), likely because Sungazers live in distinctive self-excavated burrows that they appear to use for decades, and may not readily adopt artificially created burrows. Furthermore, Ruddock (2000) found that Sungazers chemically mark their burrows, exhibit site defence, and show differential recognition of neighbours. These social aspects are therefore important additional considerations for future translocation attempts. We recommend the testing and development of translocation protocols that aim to replicate the morphometric dimensions of burrows animals were captured from, using small colonies in protected areas, followed by a regular long-term monitoring programme. Timing of relocation relative to reproductive cycles should also be considered.
5) *Genetic barcoding for trade.* – Despite the Sungazer being a CITES Appendix II listed species, few regulatory measures are enforced when applying for export permits from South Africa, with no proof of captive-breeding required. We recommend a comprehensive overhaul of the current permit application process for the species. Following CITES regulations, all Sungazers to be exported from South Africa should be barcoded using species-specific microsatellite markers to provide incontrovertible proof of captive-breeding, by providing tissue samples from the F0, F1 and F2 generations of captive populations. Barcoded Sungazers should be permanently tagged with a passive integrated transponder (PIT tag) allowing positive identification in subse-

quent trades. This will limit the export of wild-caught Sungazers laundered as captive-bred.

6) *Investigation of illegal trade*.– Thorough legal investigations into the illegal pet and traditional medicine trades are essential to further understand the effects of these harvests on wild populations. Monitoring of social-media websites such as Facebook and Instagram, as well as other online fora may provide an insight to the number of Sungazers exported from South Africa, since both adults and neonates are frequently advertised for sale through these platforms.
7) *Quantification of primary vs secondary grassland*. – A noted limitation in this study is that current satellite imagery does not distinguish between primary and secondary grassland. This poses the risk of gross overestimation of current Sungazer population size and AOO, since there is no evidence that Sungazers colonise secondary grassland. Ludick and Wooding (1991) estimated the extent of primary and secondary grassland in the Highveld region, however this is outdated and requires updating. We recommend the digitisation of aerial photographs documenting these agricultural regions, such that areas of secondary grassland can be discarded when generating population and distribution estimates for the species.

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