



Research Article

Unexpected Decline in a Population of Speckled Tortoises

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ABSTRACT Long-lived, iteroparous species exhibit various mechanisms to overcome temporary unfavorable conditions and promote adult survival and population persistence. Consequently, populations may appear relatively stable while subtle and slow-progressing threats cause their decline. The speckled tortoise (*Homopus signatus*) is a long-lived, iteroparous species in South Africa that is thought to be secure in areas that meet the species' known requirements. To verify its stability, I monitored a dense speckled tortoise population, integrating 2 mark-recapture studies (2000–2004 and 2012–2015) in long-term joint live and dead encounters and POPAN population models. From 2000 to 2015, the study site remained fenced, ungrazed, and was not modified in any way, yet the size-class frequency distribution, sex ratio, and abundance of speckled tortoises drastically changed. Population numbers decreased 66%, mainly because of the disappearance of juveniles and males. Modeling results identified a reduction in the number of entrants into the population (via births and immigration) as the likely cause of population changes, whereas apparent survival remained high. Observations, in part anecdotal, of increasing numbers of pied crows (*Corvus albus*) on the study site suggest that increased predation on speckled tortoise hatchlings contributed to the population decline. Examination of rainfall data for 1990–2015 did not reveal evidence of aridification in the study area, a documented cause of reduced reproduction in speckled tortoises. The results of this study caution against the assumption that areas in the range of the speckled tortoise that meet its known requirements can maintain healthy populations. © 2017 The Wildlife Society

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Populations of long-lived, iteroparous species may appear relatively stable and unaffected by changes in their environments, because of a suite of mechanisms that promote adult survival and population persistence (Begon et al. 1990). For example, female edible dormice (*Glis glis*) can increase female survival by flexibly adjusting reproduction to available resources (Ruf et al. 2006), desert lizards (*Sauromalus ater*) survive drought by exhibiting physiology and behavior that reduces water loss (Nagy 1972), roaches (*Rutilus rutilus*) reduce winter predation pressure by migrating (Skov et al. 2013), and (heterothermic) bats (*Chiroptera*) may increase their longevity by the use of torpor (Stawski et al. 2014). Although populations of long-lived, iteroparous species may thus overcome temporary unfavorable conditions, longer-term perturbations are more likely to lead to declines in populations, as was found in shark and skate populations that successfully coped with temporary changes in sea-surface temperature and chlorophyll—a concentration but not with repeated harvesting (Quetglas et al. 2016). Because population decline may be the result of subtle and slow-progressing

effects (e.g., long-term depressed reproduction, juvenile survival, or resource diversity; Peakall 1993, Anders et al. 1997, Merrick et al. 1997, Tomillo et al. 2008), early detection requires long-term population monitoring, particularly in species with extreme longevity, slow growth to maturity, and low fecundity.

In the animal kingdom, tortoises are among the species with the longest life spans, exceeding 150 years in giant tortoises and >50 years in smaller taxa (Orenstein 2012). Although the International Union for Conservation of Nature (IUCN, 2016) has categorized 54% of the world's extant tortoise species (Turtle Taxonomy Working Group 2014) as threatened with extinction, surprisingly few long-term monitoring studies have been published and most deal with managed populations (Bertolero et al. 2007, Tuberville et al. 2008, Fernández-Chacón et al. 2011, Couturier et al. 2014, Gibbs et al. 2014). Consequently, threats to natural tortoise populations from perturbations in their environments may go unnoticed. Twenty-five percent of the world's tortoise species occur in South Africa (Turtle Taxonomy Working Group 2014). Recognized threats to tortoises in South Africa include anthropogenic land transformation, climate change, invasive alien species, and poaching for the pet trade (Branch 2008, Bates et al. 2014). In addition, predation by expanding pied crow (*Corvus albus*) populations

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has been suggested as a potential threat (Fincham and Lambrechts 2014, Fincham and Nupen 2016). However, the lack of long-term monitoring hinders understanding tortoise population dynamics in light of recognized and unknown threats.

The speckled tortoise (*Homopus signatus*) is a small tortoise that is endemic to South Africa (Branch 2008). Its longevity is not known, but females mature when they are 11–12 years old (Loehr et al. 2007a) and an adult male from the wild survived for >20 years in captivity (V. J. T. Loehr, Homopus Research Foundation, unpublished data). Reproduction is slow, with mature females producing ≤ 5 eggs/year (Loehr et al. 2004, 2011). Much of the species' range appears relatively pristine as a result of the sparse human population (3.2 persons/km² for the Northern Cape Province; Tibane and Honwane 2015) and low precipitation (usually <150 mm/yr; Cowling et al. 1999), preventing any significant arable farming. Nevertheless, overgrazing by domestic stock (Bates et al. 2014) and aridification due to climate change (Loehr et al. 2009) may pose threats, and the behavior of the species (i.e., exposed activities when exploiting winter resources) suggests an intrinsic vulnerability to predation (Loehr et al. 2015). From 2000 to 2004, a speckled tortoise population in an area that met the species' requirements in terms of space, spatial variation, thermal environment, retreats, and vegetation (Loehr 2002a, 2006, 2012, 2015; Loehr et al. 2015) was monitored; the studies revealed that the tortoises occurred at a high density and had low mortality rates, even in a drought year (Loehr 2010). These findings seem to support the idea that these speckled tortoise populations are not threatened, but continued longer-term monitoring is required to detect potentially slow-progressing population changes.

From 2012 to 2015, I repeated the mark-recapture study in the speckled tortoise population that had been investigated previously, and integrated both datasets to generate a robust long-term analysis. My expectation was that the apparent lack of immediate threats to the population and its habitat would result in a size distribution, sex ratio, and demographic parameters similar to those documented in 2000–2004.

STUDY AREA

The study population inhabited a 37,220-m² site near Springbok, South Africa (coordinates deposited at the Scientific Services Unit, CapeNature, Western Cape Province, South Africa), 450 m from the nearest paved road. The site was situated in the Kamiesberg bioregion of Namaqualand, a semi-arid mountainous granite and gneiss landscape (Desmet 2007). Annual rainfall for 1990–2015 averaged 225 mm and peaked in winter (South African Weather Services, unpublished data). A combination of relatively predictable winter rainfall and moderate temperatures (average maximum winter and summer temperatures >18°C and <30°C, respectively) promoted a shrubland vegetation dominated by leaf succulents, geophytes, and annuals (Esler and Rundel 1999, Loehr 2002b, Desmet 2007). The topography of the study site consisted of a steep (i.e., 863–925 m above sea level), easterly facing rocky slope

with adjacent leveled areas, bare granite rock slabs, and dry river beds (Loehr 2002a). Use of the study site by people and livestock was virtually absent because the landowner had fenced the site and prohibited access. Speckled tortoises were the only tortoises occupying steep rocky slopes, but leveled areas were also inhabited by angulate tortoises (*Chersina angulata*). Other taxa that we often encountered near speckled tortoises were rock hyrax (*Procavia capensis*), dassie rat (*Petromus typicus*), western rock elephant-shrew (*Elephantulus rupestris*), western rock skink (*Trachylepis sulcata*), variegated skink (*Trachylepis variegata*), rock agama (*Agama atra*), and Karoo girdled lizard (*Karusasaurus polyzonus*).

METHODS

Field Recordings and Marking

Each spring from 2000 to 2004 and from 2012 to 2015, 1–4 assistants and I surveyed the study site for live and dead tortoises daily for approximately 8 hours between 0730–1800 hours. The surveys occurred between August and October for all years, but specific dates varied slightly (2000: 29 Aug–21 Sep, 2001: 7 Sep–1 Oct, 2002: 13 Sep–7 Oct, 2003: 5 Sep–7 Oct, 2004: 2 Sep–30 Sep, 2012: 21 Aug–6 Sep, 2013: 17 Sep–3 Oct, 2014: 24 Sep–9 Oct, 2015: 2 Sep–16 Sep). We measured live tortoises ± 0.01 mm for straight carapace length (SCL), maximum shell width (MSW), and maximum shell height (MSH) with digital sliding calipers. I used body dimensions to estimate shell volume (cm³) as $\pi \times \text{SCL} \times \text{MSW} \times \text{MSH} / 6,000$ (Loehr et al. 2004). I compared SCL frequency distributions between 2000–2004 and 2012–2015 using chi-square analysis (Zar 1999). We distinguished males from females by the smaller body size, larger tail, and concave plastron in males, and classified small individuals without clear sexual dimorphisms as juveniles. I used a *t*-test in SigmaPlot 12.0 (Systat Software, San Jose, CA, USA) to compare sex ratios between 2000–2004 and 2012–2015. For all statistical analyses, I considered tests significant if $P < 0.05$.

From 2000 to 2002, I uniquely marked tortoises with combinations of black nail polish dots on the carapace. From 2003 onwards, I marked the tortoises by notching the marginal scutes (Cagle 1939). I also photographed each tortoise's carapace and plastron for identification.

In 2003, 2012, and 2013, I equipped 19, 11, and 8 adult tortoises, respectively, with radio-transmitters (AVM Instrument Company, Colfax, CA, USA) and tracked them during the next yearly survey. Consequently, radio telemetry produced 14 tortoises in 2004, 6 in 2013, and 7 in 2014 ($n = 24$). However, I only included telemetered tortoises in mark-recapture analysis if they were located during surveys without the assistance of telemetry equipment. Therefore, 8 telemetered tortoises in 2004 and all telemetered tortoises in 2013 and 2014 could be included in the mark-recapture analysis.

Assistants and I handled tortoises in accordance with permits issued by the Northern Cape Department of Environment and Nature Conservation (permit numbers 019/2001, 152/2002, 168/2003, 158/2003, 633/2003,

152/2012, 153/2012, 460/2013, and 052/2015). In addition, the Research Ethics Committee of the University of the Western Cape approved my methods.

Mark-Recapture Analysis

I used 2 models in Program MARK version 8.1 (White and Burnham 1999) to analyze if apparent survival, entrance into the population (i.e., net births and immigration), and population size were similar through time: 1) the joint live and dead encounters model (Burnham 1993); and 2) the POPAN formulation (Schwarz and Arnason 1996). The joint live and dead encounters model estimated survival rate (S), recovery rate of dead individuals (r), and recapture rate (p). Because all recoveries of dead tortoises occurred within the study site, I fixed the model parameter fidelity (F) to 1. Consequently, S included emigration and should be interpreted as apparent survival. I fixed recovery rate after 2015 to 0 because 2015 was the final survey. The construction of the general model benefited from a previous analysis of the 2000–2004 portion of the dataset, which revealed a strong relationship between apparent survival and shell volume (Loehr 2010). Thus, I included shell volume in the current general model as a covariate affecting apparent survival. Individual covariate values consisted of the averages of minimum and maximum shell volume recordings for each tortoise to account for growth during the study. Because the dataset was too sparse for a fully time-dependent general model, I allowed apparent survival to vary among 3 time periods: between the 2001 and 2004 surveys (2001–2004), between the 2004 and 2012 surveys (2004–2012), and between the 2012 and 2015 surveys (2012–2015). Transient tortoises in the population (Loehr 2010) could violate the model assumption that every marked tortoise had the same probability of recapture; therefore, I ignored sampling intervals following first captures in estimations of apparent survival. As a result, I could not estimate apparent survival for the sampling interval 2000–2001. Sampling effort varied among yearly surveys, so I allowed recovery rate and recapture rate to vary over time. I included competing models that grouped the apparent survival time periods 2001–2004, 2004–2012, and 2012–2015 in all possible combinations. Moreover, I considered models with or without the shell volume covariate. I ranked models based on adjusted Akaike's Information Criterion (AIC_c , Sugiura 1978, Hurvich and Tsai 1989) and considered ranked models different if $\Delta AIC_c > 2$. To accommodate model uncertainty for models with $\Delta AIC_c \leq 2$, I investigated 95% confidence intervals of apparent survival values estimated by the most parsimonious model, and estimated recapture and recovery rates as model-averaged values (Buckland et al. 1997).

The POPAN formulation estimated (through model-averaging) 2 derived parameters (i.e., entrants into the population and population size) based on the most parsimonious joint live and dead encounters model. Because the POPAN formulation contained an additional model parameter, probability of entrance, I used a general model in which I allowed probability of entrance to vary through time, and assessed support for this model by ranking (based on

AIC_c , with ranked models considered different if $\Delta AIC_c > 2$) derived models with probability of entrance differing among time periods (between surveys) 2002–2004, 2004–2012, and 2012–2014, or between 2004–2012 and the other 2 time periods combined. I also constructed a model with constant probability of entrance. I removed the first encounters of all tortoises from the encounter histories to avoid transiency issues (Loehr 2010). Consequently, I could not estimate derived parameters for the sampling interval 2001–2002.

Because of the individual covariates in the joint live and dead encounters general model, the only goodness-of-fit test available was inspection of Fletcher's \hat{c} (variance inflation factor; Fletcher 2011) in Program MARK for deviations from 1. I used several additional approaches to verify that the general model adequately fit the data. I removed the individual covariates and used the median- \hat{c} approach in Program MARK under the assumption that the covariates would only improve model fit. In addition, I ran the bootstrap procedure in Program MARK (100 simulations) and calculated \hat{c} by dividing the general model deviance and \hat{c} by the mean simulated deviance and \hat{c} . I assessed the sensitivity of the ranking of the derived models by manually increasing \hat{c} from 1.0 to 2.0 in 4 steps of 0.25. For the POPAN formulation, I examined Fletcher's \hat{c} and conducted the goodness-of-fit tests provided in U-CARE version 2.3 (Choquet et al. 2005) on a fully time-dependent model.

Rainfall

To analyze if population changes might relate to aridification, I tested if rainfall from January to December (total annual rainfall), September to July (affecting somatic growth and reproduction in speckled tortoises; Loehr et al. 2011), and March to July (affecting spring body condition; Loehr et al. 2007b) changed from 2000 to 2015 (study period), or from 1990 to 2015 (all available rainfall data), using linear regressions in SigmaPlot 12.0 (significant if $P < 0.05$). Rainfall data originated from a Springbok weather station situated within 2.5 km of the study site.

RESULTS

Study Site and Rainfall

From 2000 to 2015, the study site showed little change. The site remained fenced, ungrazed, and was not modified in any way. Rainfall data lacked any evidence of aridification. Rainfall from January to December, from September to July, and from March to July were not related to year, neither for 1990–2015 ($F_{1, 24} \leq 0.67$, $P \geq 0.42$) nor for 2000–2015 ($F_{1, 14} \leq 0.46$, $P \geq 0.51$). The 4 driest January to December periods all occurred relatively recently, between 2003 and 2015. However, the 4 driest periods for the biologically more meaningful periods (Sep–Jul [growth and reproduction] and Mar–Jul [spring body condition]) occurred earlier, between 1999 and 2004.

Tortoise Observations

The number of individually unique live tortoises encountered from 2000 to 2015 was 311. Twenty-seven of these (9%) were eventually recovered dead. The yearly surveys from 2000 to

2004 each yielded 82–119 live tortoises, but only 16–42 tortoises were encountered in the surveys from 2012 to 2015.

For all live tortoises combined, the SCL frequency distributions differed between 2000–2004 and 2012–2015 ($\chi^2_7 = 30.51$, $P < 0.001$; Fig. 1). Particularly in the smaller size classes of 30–70 mm, there were fewer tortoises in 2012–2015 than in 2000–2004. When examined for each group separately, the difference was significant for females ($\chi^2_6 = 13.92$, $P = 0.031$), but not for males and juveniles ($\chi^2_{\leq 4} \leq 5.86$, $P \geq 0.16$).

The sex ratio of the population also differed between 2000–2004 and 2012–2015. In 2000–2004, the population had a slightly male-biased average ratio of 1.1 ± 0.1 , whereas the average ratio of 0.5 ± 0.1 in 2012–2015 was strongly biased towards females ($T_7 = 3.75$, 2-tailed $P < 0.01$).

Population Modeling

Goodness-of-fit testing indicated that the general model that included live and dead encounters adequately fit the data, with a Fletcher's \hat{c} of 1.05. After removal of individual covariates, the median \hat{c} procedure produced a similar \hat{c} value of 1.19, and bootstrap simulations produced \hat{c} values of 0.72–1.30. Moreover, manual increases of \hat{c} left the ranking of derived models unchanged, indicating that modeling results were robust.

Derived model-ranks confirmed that apparent survival was related to shell volume ($\Delta AIC_c \geq 50.80$ for models without shell volume; Table 1). The most parsimonious model (37%

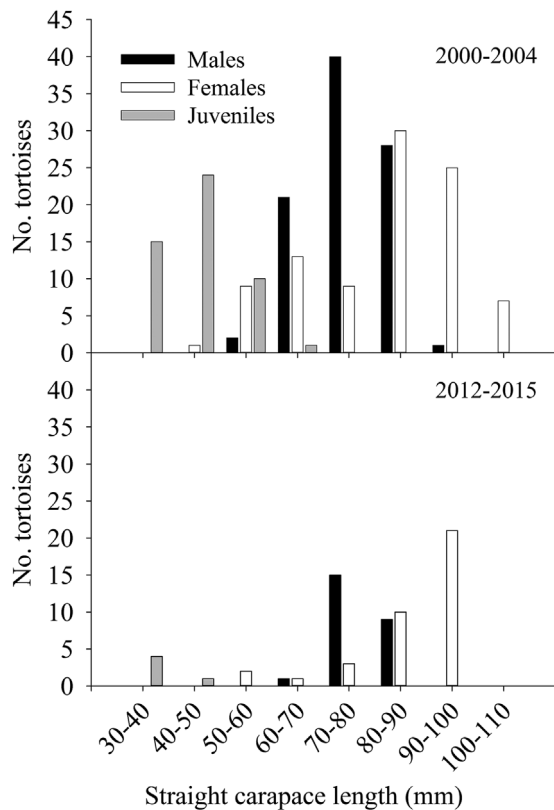


Figure 1. Frequency distributions of straight carapace length for male, female, and juvenile speckled tortoises encountered alive in a study population near Springbok, South Africa, 2000–2004 and 2012–2015.

support by the data) suggested that apparent survival was greater from 2001 to 2012 than from 2012 to 2015 (Table 1). However, there was also considerable support ($\Delta AIC_c < 2$) for models in which apparent survival differed among other time periods (total 34%) or was equal for all time periods (29%). Thus, there was no obvious pattern of differences in apparent survival among time periods. Graphical examination of apparent survival as a function of shell volume for 2001–2012 and 2012–2015 (most parsimonious model) corroborated the lack of differences in apparent survival among time periods; the 95% confidence intervals for the relationships showed large overlaps (Fig. 2). Annual recapture and recovery rates averaged for all models were 0.33–0.90 and 0.03–0.75, respectively (Table 2). Although recapture rates showed no trends, recovery rates increased toward the end of the study.

The POPAN general model (apparent survival dependent on shell volume, and time-dependent recapture rates and probabilities of entrance into the population) fit the data, as indicated by a Fletcher's \hat{c} of 1.04. In addition, extending the model to a fully time-dependent model led to all goodness-of-fit tests being passed in U-CARE ($P \geq 0.22$). Ranking of derived models strongly supported (81% support by the data) differences in probability of entrance among years, with little support (18%; $\Delta AIC_c = 3.01$) for differences in probability of entrance among the 3 time periods (2002–2004, 2004–2012, and 2012–2014). All other derived models resulted in a $\Delta AIC_c \geq 10.42$. The averaged POPAN models showed that the number of entrants into the population decreased from 2002 to 2014 (Fig. 3). Moreover, the number of (resident) speckled tortoises in the population just prior to the 2002–2004 surveys was greater than prior to the 2012–2014 surveys (Fig. 3).

DISCUSSION

Despite the apparent lack of change on the study site, and contrary to my expectations, the initially dense resident speckled tortoise population decreased 66% between 2000–2004 and 2012–2015. There was a fairly large time gap between the 2004 and 2012 surveys, but site visits in February 2005, March 2008, and October 2011 confirmed that the landscape remained unmodified. Small individuals and males, the smaller sex in speckled tortoises (Loehr et al. 2006), were most affected, resulting in a population that was skewed toward large individuals and females in 2012–2015. The relatively high recapture rates (O'Brien et al. 2005) throughout the study indicated that the population changes were not the result of our shorter surveys in 2012–2015 compared to 2000–2004. Moreover, the increasing recovery rates of dead tortoises toward the end of the study were indicative of our increased effort to include rock crevices and other retreats in which tortoises might hide in our daily searches.

Cause of the Population Decline

Population changes are ultimately caused by imbalances between births and immigration, and deaths and emigration (Case 2000). In my population of speckled tortoises,

Table 1. General and derived models with corrected Akaike’s Information Criterion values (AIC_c), change in AIC_c (ΔAIC_c), AIC_c weights (w_i), estimable model parameters (K), and deviances, generated to estimate apparent annual survival (S), recapture (p), and dead recovery (r) for a population of speckled tortoises near Springbok, South Africa. Fidelity (F) was fixed to 1. Model variables for S included shell volume (SV) and time period (subscript numbers), parameters p and r included year (t). All models also modeled S for the time period after first captures (to separate transient tortoises from the rest of the analysis) and after the last sampling period (a model artifact).

Model	AIC_c	ΔAIC_c	w_i	K	Deviance
$S(SV+time\ period_{2001-2012\ vs.\ 2012-2015})\ p(t)\ r(t)\ F(1)$	1,192.17	0.00	0.37	20	1,150.66
$S(SV+time\ period_{2001-2015})\ p(t)\ r(t)\ F(1)$	1,192.63	0.46	0.29	19	1,153.26
$S(SV+time\ period_{2001-2004,\ 2012-2015\ vs.\ 2004-2012})\ p(t)\ r(t)\ F(1)$	1,193.25	1.08	0.21	20	1,151.74
$S(SV+time\ period_{2001-2004\ vs.\ 2004-2015})\ p(t)\ r(t)\ F(1)$	1,194.76	2.59	0.10	20	1,153.25
$S(SV+time\ period_{2001-2004\ vs.\ 2004-2012\ vs.\ 2012-2015})\ p(t)\ r(t)\ F(1)$	1,197.27	5.11	0.03	21	1,153.61
$S(time\ period_{2001-2012\ vs.\ 2012-2015})\ p(t)\ r(t)\ F(1)$	1,242.97	50.80	0.00	19	1,203.60
$S(time\ period_{2001-2004,\ 2012-2015\ vs.\ 2004-2012})\ p(t)\ r(t)\ F(1)$	1,243.40	51.23	0.00	19	1,204.03
$S(time\ period_{2001-2004\ vs.\ 2004-2015})\ p(t)\ r(t)\ F(1)$	1,244.03	51.86	0.00	19	1,204.66
$S(time\ period_{2001-2015})\ p(t)\ r(t)\ F(1)$	1,244.03	51.87	0.00	19	1,204.67
$S(time\ period_{2001-2004\ vs.\ 2004-2012\ vs.\ 2012-2015})\ p(t)\ r(t)\ F(1)$	1,249.81	57.64	0.00	21	1,206.14

apparent survival (combining deaths and emigration) was relatively high, particularly for the larger size classes, and population modeling failed to identify consistent differences among time periods. Thus, deaths and emigration seemed fairly constant throughout the study. In contrast, entrance into the population, which is related to hatching success, hatchling survival between hatching and the following yearly survey, and immigration, showed a decreasing trend. Therefore, decreasing entrance into the population was a likely cause for the decline.

For some (sink) populations to persist, regular additions of entrants through immigration are essential (Pulliam 1988); however, there is little evidence for this process in reptiles (Furrer and Pasinelli 2016). In addition, we can rule out effects of aridification as a cause of reduced entrance in the population, despite the fact that fertility, egg size, hatchling size, and possibly hatching success and hatchling survival of speckled tortoises are sensitive to drought (Loehr et al. 2009), because rainfall patterns did not indicate aridification. Population declines in birds and amphibians can be influenced by a reduction in entrants through predation on eggs and hatchlings (Gamradt and

Kats 1996, McLennan et al. 1996, Wilson et al. 1998). The same pathway has also been identified for chelonians (Thompson 1983, Epperson and Heise 2003, Smith et al. 2013), and I propose that the decline of the speckled tortoise population may also have been influenced by predation on hatchlings.

Corvids prey on tortoises and may have played a role in the reduction of entrants into the study population. Although the effect of corvids on European and North American bird populations was smaller than perceived (Madden et al. 2015), survival of hatchling and juvenile North American desert tortoises (*Gopherus agassizii*) may be affected by predation by common ravens (*Corvus corax*; Kristan and Boarman 2003, Nagy et al. 2015), to the extent that ravens can become a determining factor for desert tortoise population densities and distribution (Berry et al. 2013). In South Africa, pied crows may extensively predate tortoises (Fincham and Lambrechts 2014). Pied crows are an adaptive species that benefit from human activities and favor habitat near roads (Dean and Milton 2003, Dean et al. 2006) such as the speckled tortoise study site. We often counted groups of 1–8 pied crows during the 2012 survey (average 47% of the time during 37 9-hour observation days; T. Stark and C.

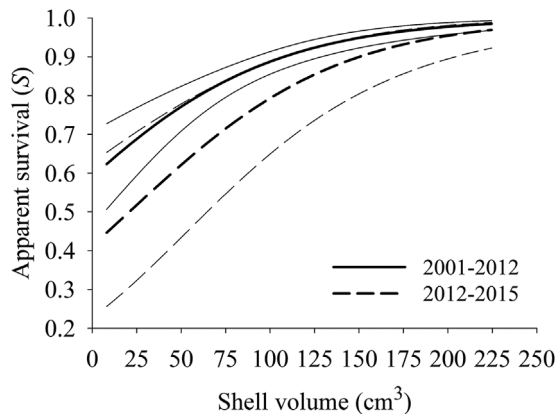


Figure 2. Relationships between apparent annual survival (S) and shell volume (bold lines) in a study population of speckled tortoises near Springbok, South Africa, 2001–2012 and 2012–2015. Thin lines represent 95% confidence intervals.

Table 2. Model-averaged estimates of annual recapture and dead recovery rates in a speckled tortoise study population near Springbok, South Africa, 2000–2015.

Period	\bar{x}	SE
Recapture rate		
2001	0.62	0.07
2002	0.79	0.05
2003	0.90	0.04
2004	0.51	0.06
2012	0.55	0.09
2013	0.73	0.08
2014	0.33	0.08
2015	0.53	0.10
Recovery rate		
2000–2001	0.05	0.04
2001–2002	0.03	0.03
2002–2003	0.05	0.05
2003–2004	0.09	0.05
2004–2012	0.05	0.02
2012–2013	0.10	0.09
2013–2014	0.44	0.17
2014–2015	0.75	0.31

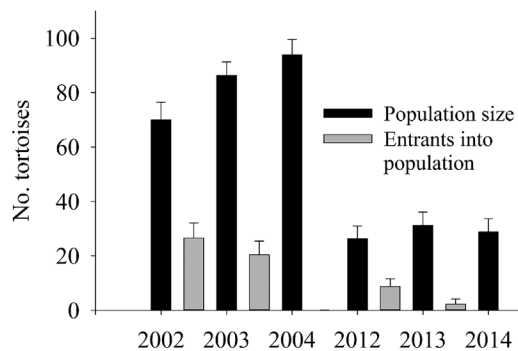


Figure 3. Net (resident) population size just prior to yearly surveys, and the number of entrants into the population (i.e., net births and immigration) between surveys, in a speckled tortoise study population near Springbok, South Africa, 2002–2014. Error bars represent standard errors.

Laurijssens, Homopus Research Foundation, unpublished data; Loehr et al. 2015), whereas pied crows were estimated to be present <5% of the time in 2000–2004.

My interpretation that predation played a role in the decline of the speckled tortoise population in the study site needs verification. Regardless whether predation or other factors caused the reduction in entrants, additional issues need to be addressed: 1) to what extent speckled tortoise populations are declining throughout the species' range; and 2) whether the decline is a temporary phenomenon. It is also important to assess if current entrance rates are sufficient to allow recovery of the study population (Epperson and Heise 2003), or if the study population can persist in its current composition.

MANAGEMENT IMPLICATIONS

In this study, population changes occurred unexpectedly and would not have been noticed if long-term monitoring had been absent. Therefore, I emphasize the importance of long-term monitoring of tortoise populations, particularly in South Africa with its rich tortoise fauna (Branch 2008) and poorly understood conservation status of some taxa (e.g., Karoo tortoise [*Homopus boulengeri*]; Bates et al. 2014, Juvik and Hofmeyr 2015).

With regards to the speckled tortoise, the species has historically been considered a fairly common species, not directly threatened, and occurring in relatively high densities (Branch 1988, 2008; Boycott 1989). In a recent red list assessment, the status of speckled tortoise populations was related to habitat quality (Bates et al. 2014), suggesting that populations would have a favorable status in areas with suitable habitat. Moreover, predation was not identified as a possible threat. I demonstrate that knowledge of factors used to determine conservation status of speckled tortoise populations may be insufficient. I caution that the persistence of apparently suitable habitat in the range of the speckled tortoise may not guarantee the presence of healthy, stable populations.

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