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# Tortoise mortality along fence lines in the Karoo region of South Africa

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ABSTRACT

Fencing, including electric fencing, is widely used across South Africa for livestock and game ranching practices. Leopard tortoises (*Stigmochelys pardalis*) are particularly prone to being killed by electric fences, but no published studies have assessed the impact of fence structure or quantified tortoise mortality along non-electric fences. This is a conservation concern, especially because South Africa is home to more tortoise species than any other country. This study relates tortoise mortality associated with electrified and non-electrified fences to fence structure, and uses transects away from fences as a comparison to estimate the impact of fences on mortality. All fence types had significantly higher tortoise mortality than open veld transects. Leopard tortoise mortalities were greatest along electric fences (56 % of mortalities), even though these comprised only 4% of fences in the study. By comparison, most angulate tortoises (*Chersina angulata*) died after becoming wedged in mesh fences. The distribution and abundance of fence types along 2200 km of roads was used to extrapolate the impacts of different fence types on tortoises in the southeastern Karoo, South Africa. A survey of land-use types indicated that game farms were more likely to be associated with the presence of electric fences. Regulations are needed to limit mortality of vulnerable species (tortoises, pangolins) on electric fences by setting a minimum strand height and 'escape' periods implemented through randomized off times or thermostatic switches.

## 1. Introduction

Linear features such as fences can act as selectively permeable filters across landscapes with well-documented impacts on animals and the environment (Boone & Hobbs, 2004; Cassidy, Fynn, & Sethebe, 2013; Davies-Mostert, Mills, & Macdonald, 2013; Woodroffe, Hedges, & Durant, 2014). Seymour et al. (2019) highlighted the impact of fences on wildlife in a recent horizon scan of emerging and intensifying threats to biodiversity conservation in South Africa. The negative impacts of fencing include landscape fragmentation and isolation (Boone & Hobbs, 2004; Hayward & Kerley, 2009; Woodroffe et al., 2014), loss of connectivity and disruption of migratory movements and dispersal patterns (Cassidy et al., 2013; Vanak, Thaker, & Slotow, 2010; Woodroffe et al., 2014), reduced access to key resources (Hayward & Kerley, 2009), increased mortality rates, both as a direct (e.g. entanglement or electrocution) or indirect (e.g. increased predation) result of the fence (Beck, 2009; Boone & Hobbs, 2004), altered predator-prey dynamics (Davies-Mostert et al., 2013; Scofield, Cullen, & Wang, 2011), localised overgrazing (Boone & Hobbs, 2004; Kesch, Bauer, & Loveridge, 2014), and cascading effects leading to ecological meltdown (Kesch et al., 2014; Vanak et al., 2010). Most of these concerns have focused primarily on larger animals; few studies have investigated the direct impact of fencing on small animals as it is generally assumed that they pass freely through fences (Kesch et al., 2014; but see Ley & Tynan, 2008; Pietersen, McKechnie, & Jansen, 2014).

Tortoises may be particularly prone to adverse impacts from fences due to their limited agility (Ferronato, Roe, & Georges, 2014). Although fences have been used to reduce tortoise road mortality (Boarman & Sazaki, 1996), other studies have highlighted the threat posed to tortoises by fences (Beck, 2009; Burger & Branch, 1994). South Africa is the most species-rich tortoise country, with 13 species from six genera (Bates et al., 2014; Hofmeyr et al., 2017), and is a global biodiversity hotspot for tortoises (Spitzweg, Hofmeyr, Fritz, & Vamberger, 2019). Of these 13 species, one is listed as Critically Endangered using IUCN criteria, two as Endangered, two as Vulnerable and one as Near Threatened (Tolley et al., 2019). Key threats to tortoises in South Africa include illegal collection, road mortality, altered fire frequency, pollution, and habitat transformation due to farming activities, urban sprawl and invasive alien vegetation (Alexander & Marais, 2007; Bates et al., 2014). The local increase in pied crows (*Corvus albus*) across parts of

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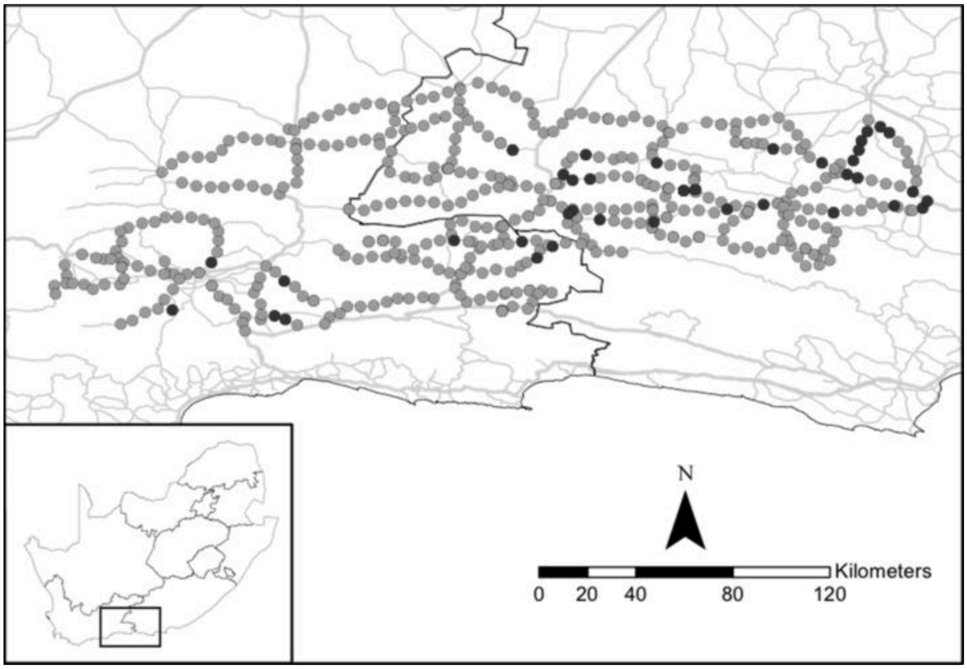


**Fig. 1.** Map of study area showing fence distribution data in the southeastern Karoo region of South Africa. Black dots = electric fences; grey dots = non-electric fences. Black lines show the boundaries between the Western and Eastern Cape provinces; grey lines are roads. Inset indicates the location of the study area in South Africa.

South Africa (Cunningham, Madden, Barnard, & Amar, 2016; Joseph, Seymour, & Foord, 2017) also has been associated with increased predation on small tortoises, including juveniles of larger species (Fincham & Lambrechts, 2014; Loehr, 2017). An emerging concern is the impact of electric fences because tortoises are more prone to dying from electrocution along electric fences than any other taxon (Beck, 2009; Seymour et al., 2019).

Fences are widely used in South Africa to control animal movements, and are considered essential for livestock farming, game ranching and wildlife conservation (Boone & Hobbs, 2004; Heard & Stephenson, 1987; Reidy, Campbell, & Hewitt, 2008). Livestock farming uses fences to constrain animals within camps, limit the spread of disease and exclude predators (Cumming, Osofsky, Atkinson, & Atkinson, 2015; McGahey, 2011). Wildlife conservation uses fences to contain wildlife within protected areas (Hoare, 1992). However, the use of fences to achieve conservation goals is controversial as fences have many negative impacts on wildlife (Bode & Wintle, 2010; Farber, 2016; Hoare, 1992; Scofield et al., 2011; Woodroffe et al., 2014). Fences typically are comprised of horizontal strands or diamond shaped mesh (hereafter referred to as strand and mesh fences, respectively). Some fences have strands above mesh, because most animals push through between the lower horizontal strands.

Electric fencing, which delivers a pulsed electric charge along electrified strands, is increasingly being used across South Africa in both livestock farming and game ranching (Brandt & Spierenburg, 2014). Electric fences provide an effective means of containing large animals (Hoare, 1992) and are a strong deterrent to predators and other 'problem animals' that attempt to dig under or make holes in a fence as they move through the landscape (Kesch et al., 2014). The structure of electric fences varies greatly in terms of the number of electric strands, gaps between strands, voltage and whether one or both sides are electrified, depending on the land-use and animals to be contained or excluded (Brown, Gildenhuys, Hignett, & van Deventer, 2014). One common feature is a single electrified strand offset from the fence, between 30−300 mm above the ground, designed to prevent animals from digging underneath fences (Beck, 2009; Nass & Theade, 1988; Pietersen et al., 2011). Here, we refer to fences with any such electric strand as 'electrified' and all other designs as 'non-electric' fences.

Beck (2009) reported 33 species of animals killed by electric fences in South Africa. Reptiles were particularly impacted, suffering an order of magnitude more deaths than mammals, with tortoises making up the majority of reptile casualties. When tortoises contact an electric strand, they tend to adopt their natural defence response, retracting their limbs and head into their shell (Beck, 2009). Unfortunately, this results in them remaining in contact with the electrified strand where they are repeatedly shocked (Burger & Branch, 1994). In these circumstances, some individuals urinate, increasing their conductivity and hence the current that passes through their bodies (Burger & Branch, 1994). These tortoises eventually die of electrocution, dehydration or overheating (from exposure to the sun), or a combination of these effects (Burger & Branch, 1994).

Four species of tortoises have been reported killed by electric fences in South Africa, with leopard tortoises (*Stigmochelys pardalis*) making up most of the deaths (Beck, 2009; Burger & Branch, 1994). This is likely the result of their large size, which makes them susceptible to electrocution by a wide range of strand heights. However, all tortoises are at risk if the electric strands are low enough to make contact with small tortoises. By electrocuting larger tortoises, electric fences selectively kill adult tortoises (Burger & Branch, 1994) which has an increased impact on the demography of populations given the high adult survivorship and low recruitment rates typical of tortoise populations (Beck, 2009; McMaster & Downs, 2009). Two mitigation strategies have been recommended to reduce tortoise mortalities: raising the height of the lowest electric strand and packing rocks against the fence as this prevents tortoises from reaching the electric strand and discourages other animals from digging beneath the fence (Beck, 2009).

We investigated tortoise mortalities along different fence types in the Karoo, the most species-rich tortoise region in South Africa, with nine species in five genera (Branch, 1998). We identified the tortoise species, sizes and sexes most at risk, and related these to fence features associated with tortoise mortality. By measuring the distribution and abundance of different fence types, we extrapolate the number of tortoises killed by different fence types, and compare these to natural mortality rates estimated from open veld transects. In order to direct conservation measures, we also surveyed fences across the Karoo to assess which land-uses are associated with electric fencing.

## 2. Methods

The main study was conducted in the southern Karoo between Calitzdorp and Kleinpoort (Fig. 1), home to five species of tortoise. The leopard tortoise is the largest species, reaching lengths of 750 mm and masses of 40 kg (Alexander & Marais, 2007; Branch, 2012). Angulate tortoises (*Chersina angulata*) are the next largest, with carapace lengths of up to 300 mm and masses of 2 kg (Alexander & Marais, 2007). The three smaller species are the Karoo tent tortoise (*Psammobates tentorius*), the parrot-beaked dwarf tortoise (*Homopus areolatus*) and the rare Karoo dwarf tortoise (*Chersobius boulengeri*) (Alexander & Marais, 2007; Boycott & Bourquin, 1988). These species are listed as Least Concern by the IUCN, except the Karoo dwarf tortoise, which is Endangered and Karoo tent tortoise which is Near Threatened (Tolley et al., 2019).

The study area is primarily in the Nama Karoo Biome, although some areas extended into the Succulent Karoo and drier areas of Albany Thicket and Fynbos Biomes (Mucina & Rutherford, 2006). The vegetation consists primarily of low-shrubs, with trees occurring along river beds (Milton, Davies, & Kerley, 1999). Average annual rainfall in the Nama Karoo varies between 120−200 mm, with rain most likely in late summer (Palmer & Hoffman, 1997). Average daily maximum temperatures range from 30−33 °C in summer and 18−20 °C in winter; daily minima are 14−16 °C in summer and 3−6 °C in winter (Palmer & Hoffman, 1997).

### 2.1. Tortoise encounter survey

Tortoises (live and dead) were recorded along 189 transects (163.9 km) along fences and in the open veld (Fig. S1 for sampling distribution, Fig. S2 for sample effort by fence type). Most transects were 1 km long but some were shorter if the fence type did not extend to 1 km. Distances were measured using the mobile GPS application Galileo (galileo-app.com). Data were collected during October and November 2016 using CyberTracker software, a mobile device application (Steventon, Liebenberg, Derbecker, Bapat, & Miles, 2011). The following information on fence presence and design were recorded at 100 m intervals and at each tortoise found during a transect: the structure of the fence (i.e. mesh or strand); presence of electrified strands; and where these were present, the height of the lowest electric strand above the ground was recorded to the nearest 5 mm. Four fence categories were recognised: Electric mesh, Electric strand, Mesh (non-electric) and Strand (non-electric), with No fence (open veld) as a control. In cases where multiple structures were used (e.g. bottom half mesh and top half strand), fences were categorized according to the bottom section of fence where tortoises would interact with the fence. The presence of a rock apron (rocks packed against the lower section of the fence) also was recorded. Environmental data recorded included the average vegetation height and estimated percentage of open ground within a 5-m radius of each point, and the presence/absence of water within a 50-m radius. Sampling was initially random, but then stratified to correct for the low number of electric fences encountered, resulting in 24 open veld transects, 26 electric mesh, 11 electric strand, 85 mesh only, and 43 strand-only transects.

The following measurements were recorded for all tortoise encounters (transect and incidental, both live and dead): species identity, sex (from plastron shape), standard carapace length (SCL) and carapace height (to the nearest 5 mm), stage of decomposition of dead tortoises (adapted from Bourn & Coe, 1979; see Table S1, Fig. S3) and perpendicular distance to nearest fence (to the nearest 50 mm using a measuring tape or rangefinder to the nearest 0.5 m). Three live leopard tortoises removed from electric fences were treated as dead, given that this was their likely fate failing intervention ($n < 1\%$ of total sample). Partial tortoise remains were identified from the 2nd, 3rd and 4th vertebral scutes (top three scutes), and these were measured to the nearest 1 mm to calculate tortoise height using allometric equations (Macray, 2017). All dead tortoises found within 10 m of a transect were included because carcasses are moved from fences to prevent short-circuits as part of standard fence maintenance: but most were within a few metres of the fence (see Fig. S4 for histogram of distances). It is possible that land-owners move fence-line casualties far out of sight to avoid attracting attention to the issue, and carcasses may also be shifted by scavengers.

### 2.2. Tortoise mortality along fence types

We first used generalized linear models (GLMs) to estimate the number of dead angulate or leopard tortoises found per kilometre using the presence of any electric fence type as the predictor variable. A negative binomial distribution with a logit-link function was chosen due to the large number of zeros and over-dispersion. The model was run using the glm.nb function from the MASS package (Venables & Ripley, 2002) with R 3.5.0 (R Core Team, 2019). The same approach was used to examine the effect of mesh fences on the number of dead angulate tortoises encountered.

Then, the probability of finding a leopard tortoise in each state (dead or alive) was calculated using the environmental data collected from transects. We used a generalized linear mixed-effects model (GLMM) with a binomial error distribution and log-link function implemented using the glmer function from the lme4 package (Bates, Mächler, Bolker, & Walker, 2015), with p values calculated using lmerTest (Kuznetsova, Brockhoff, & Christensen, 2017). For the full model, predictor variables included fence type (electric mesh, non-electric mesh, electric strand, non-electric strand, open veld), water presence, rock apron presence, vegetation height and percentage open ground. Transect was used as the random effect, as there were often multiple encounters per transect. We applied manual backward selection, removing non-significant variables to present a simpler version of this model. Spatial autocorrelation of each model was tested using the ncf package (Bjornstad, 2019) by examining model residuals as a function of latitude and longitude. This overall modelling approach did not work for angulate tortoise due to insufficient samples leading to convergence issues.

### 2.3. Morphometric predictors of tortoise mortality

A non-parametric Wilcoxon test was used to test for differences between: 1) electric strand heights where dead tortoises were found against strand heights recorded every 100 m; 2) carapace heights of dead tortoises found along electric fences against all other tortoises (live and dead tortoises not found along electric fences); and 3) carapace heights of dead tortoises found along electric fences against electric strand heights measured every 100 m. The tests were run in the R package exactRankTests (Hothorn & Hornik, 2017). Sex ratios of dead leopard tortoises were compared against an equal distribution of sexes using a chi-squared test with a Yates' correction for continuity. Differences in carapace height between sexes were tested with a Wilcoxon test.

### 2.4. Estimating mortality as a function of fence type distribution

Fence distribution data were collected to sample the distribution and abundance of different fence types. Data points were collected every 5 km along public roads (for both sides of the road) across the study area. We estimated the total number of leopard tortoise mortalities along the roads surveyed, assuming that the relative proportions of each fence type (measured every 5 km) were representative of fences along the roads sampled. The proportions of each fence type were multiplied by the total length of roads surveyed to estimate the total distance of each fence type in the study area. This was multiplied by the average density of dead leopard tortoises per fence type to estimate the total number of tortoises killed by fences in the survey area.

**Table 1**
Coefficient results of models explaining live and dead leopard tortoise presence as a function of environmental variables in the southeastern Karoo region of South Africa. Models were logistic regression mixed effects models that used transect as random effect. Model results shown here are the 'best' models by AIC, with difference from full models indicated (dAIC): full model results as Appendix A Table A1. Initial predictor variables in all cases included transect type (4 fences plus control of no fence), presence of rock apron, water, and percentage open ground and vegetation height. Vegetation height and percent open ground were centred and scaled using the scale function in R.

| Variable | Estimate | SE | Z | P |
|---|---|---|---|---|
| **Dead leopard tortoise, dAIC = 1.67** | | | | |
| Intercept (Electric + mesh, no rock apron) | −0.322 | 0.282 | −1.142 | 0.253 |
| Electric + strand | −0.966 | 0.527 | −1.833 | 0.067 |
| Mesh | −3.784 | 0.407 | −9.300 | <0.001 |
| Strand | −4.250 | 0.530 | −8.011 | <0.001 |
| No Fence | −5.725 | 1.088 | −5.261 | <0.001 |
| Rock apron present | −0.871 | 0.396 | −2.203 | 0.028 |
| Vegetation height | 0.220 | 0.086 | 2.549 | 0.011 |
| **Live leopard tortoise, dAIC = 10.4** | | | | |
| Intercept (Water absent) | −8.271 | 1.22 | −6.779 | <0.001 |
| Water present | 4.031 | 1.673 | 2.409 | 0.016 |
| Vegetation height | 0.495 | 0.175 | 2.821 | 0.005 |

### 2.5. Distribution of electric fence use across the Karoo

During 2017 and 2018, the spatial distribution of electric fence use across the entire Karoo Biome south of the Orange River was examined in a separate survey quantifying bird use patterns in relation to landscape features (Lee & Wright, 2019). In brief, 150 grid cells measuring 5′ latitude x 5′longitude (~9 × 7 km) were randomly selected using latin hypercube sampling, and the presence of any electric fence observed at up to 20 observation points 0.5−1 km apart in the pentad was recorded, together with the presence of land-use type: sheep or game farming. The probability of the presence of electric fence in a pentad was modelled as a function of the proportion of sheep and game counts in the pentad in a logistic regression glm. Here we present measures of the proportion of pentads with electric fences.

## 3. Results

A total of 403 tortoises were recorded during transects, of which only 40 (10 %) were alive. Leopard tortoises were most commonly found (344 individuals, 35 alive), followed by angulate tortoises (54 individuals, 5 alive) and tent tortoises (5, all dead). Our models suggested that 2–3 times more dead leopard tortoises were found per kilometre of electric fence compared to other transect types (nb.glm coefficient estimate ± se for 'electric fence': 3.51 ± 0.32, Z = 11.01, $p < 0.001$; intercept = -1.24 ± 0.20, df = 188). Electric mesh fences had a significantly higher probability of being associated with a dead leopard tortoise than electric strand fences, but there was no difference between these fence types when they were not electrified (Table 1, Appendix A, Fig. 2). The two transects with the highest number of mortalities (54 dead tortoises in 1 km and 45 dead tortoises in 0.7 km) were along electric mesh fences. All fences had significantly higher probabilities of a dead leopard tortoise than open veld transects. There was no difference in electric strand height between locations where dead leopard tortoises were found (175 ± 7 mm) and average electric strand height measurements along transects (185 ± 85 mm, W = 89676, p = 0.202).

Dead leopard tortoises usually were taller than the electric strand where they were found, with 93 being taller and 19 being shorter (Fig. 3). The carapace heights of leopard tortoises found dead next to an electric fence (196 ± 50 mm, n = 40) were not significantly different from those of tortoises found elsewhere (dead and alive from transects and incidental data which were not on electric fences) (211 ± 41 mm, n = 90, W = 4930.5, p = 0.100). However, small size classes were poorly represented. Of the dead leopard tortoises where sex could be assessed, significantly more females (n = 61) were found than males (n = 26) ($\chi^2 = 14.08$, df = 1, $p < 0.001$). By comparison, of the live tortoises, 15 were male and 9 females. There was no significant difference in carapace height between sexes (W = 2743, p = 0.84), so this factor did not explain the higher prevalence of female tortoises on fences.

Fences with rock aprons had lower probabilities of being associated with dead leopard tortoises, and more dead tortoises were associated with taller vegetation. Live tortoise encounters were also significantly associated with taller vegetation, as well as with the presence of water, but not fence type (Table 1, Appendix A). Interestingly, water was not associated with the presence of dead tortoises, possibly because there were fewer electric fences associated with water. Spatial autocorrelation was not significant for all GLMs (Fig. S5).

Angulate tortoise encounters were not explained by the presence of an electric fence (nb.glm coefficient estimate ± se for 'electric fence': 0.31 ± 0.55, Z = 0.62, p = 0.58, df = 188) but significantly more dead angulate tortoises were found along mesh fences than other transect types; no dead angulate tortoises were found along electric strand fences or in open veld transects (nb.glm coefficient estimate ± se for 'mesh

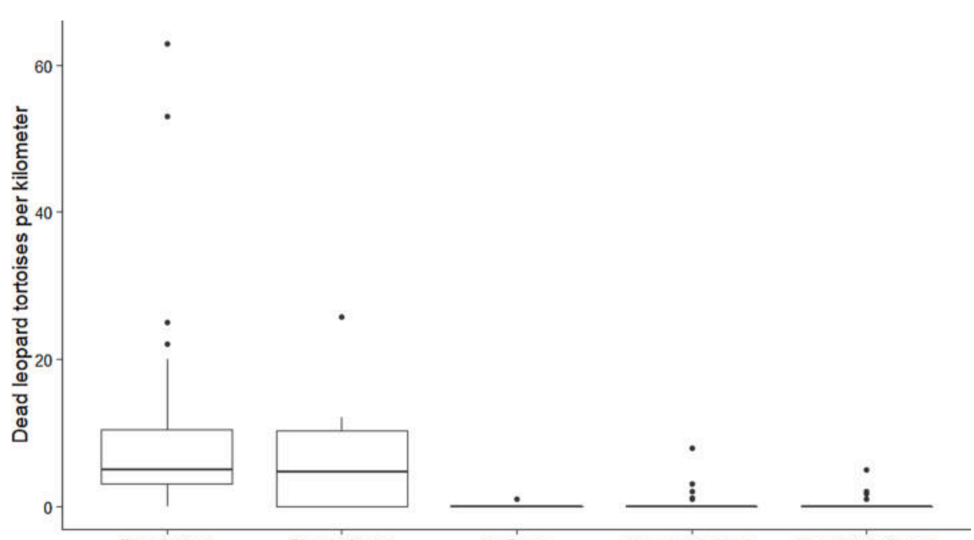


**Fig. 2.** Boxplots of the density of dead leopard tortoises along different transect types in the southeastern Karoo region of South Africa.

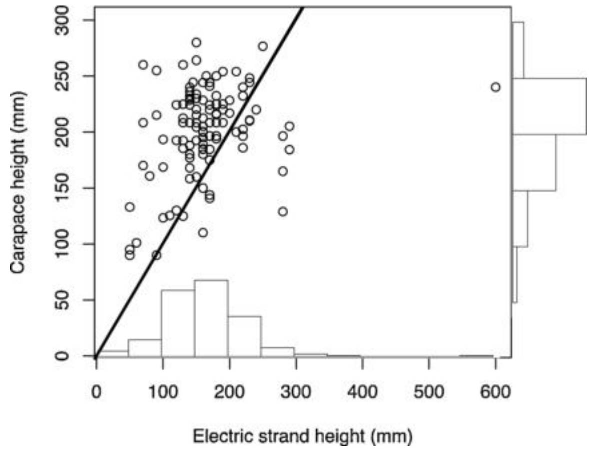


**Fig. 3.** Plot showing leopard tortoise carapace heights (circles) found dead alongside electric fences in relation to electric strand height in the southeastern Karoo region of South Africa. Bars highlight distribution of points as data is right skewed in each case. Line shows where carapace height equals strand height ($y = x$), indicating that most tortoises were taller than the electric strand height since most points are to the left of this line.

**Table 2**
Estimates of the number of dead leopard tortoises for each fence type along 2200 km of road sampled in the southeastern Karoo.

| Fence type | Proportion fence type | Length of fence surveyed (km) | Dead leopard tortoises per km | Estimated number of dead leopard tortoises |
|---|---|---|---|---|
| Electric mesh | 0.033 | 72.6 | 8.67 | 629 |
| Mesh | 0.604 | 1328.8 | 0.33 | 445 |
| Strand | 0.258 | 567.6 | 0.20 | 112 |
| Electric Strand | 0.010 | 22.0 | 4.74 | 104 |
| No fence | 0.095 | 209.0 | 0.04 | 9 |

fence': $2.52 \pm 0.66$, $Z = 3.83$, $p < 0.001$; intercept = $-3.26 \pm 0.62$, $df = 188$). All angulate tortoises were shorter than the electric strands, with carapace heights from 60−100 mm. No dead small angulate tortoises were found. Too few dead angulate tortoises were sexed to reach a meaningful conclusion regarding sex ratio: where sex could be ascertained, 8 were male, 4 were female. Similarly, too few dead tent tortoises were found to run statistical models; four were found along non-electric mesh fences and one in open veld.

Electric fences were uncommon in the study area (electric mesh = 1%, electric strand = 3.3 %, N = 442 points, over 2200 km) compared to non-electrified fences: mesh (60.4 %) and strand (25.8 %). The proportion of road verges lacking fencing (9.5 %) was more than double the proportion with electric fencing (4.3 %). Rock aprons were uncommon, present on 7.2 % of fences. The estimated number of dead leopard tortoises represented by the fence types across the 2200 km of roads surveyed was 1300 individuals, with 56 % of these modelled mortalities along electric fences and 43 % along nonelectric fences (Table 2). Less than 1% of leopard tortoise mortality was predicted to be on unfenced areas.

Across the greater South Africa Karoo region, electric fence use was recorded in 27 % of grid cells (n = 40 of 150). The presence of electric fence use was predicted by game farming activities, but not by sheep farming activities (coefficient estimate of electric fence as a function of game: $0.03 \pm 0.01$, $Z = 3.3$, $p = 0.001$; sheep: $0.002 \pm 0.009$, $Z = 0.23$, $p = 0.82$).

## 4. Discussion

All fences had higher mortality rates for tortoise than open veld transects, highlighting the threat posed by fences to tortoises. Tortoises move considerable distances in the Karoo (>5 km, Grobler, 1982) and thus likely encounter fences that might prevent them from accessing key resources such as water or food plants (Farber, 2016; Milton, 1992; Milton et al., 1999). Indeed, by separating different land-use practices that differ in vegetation type, fences create incentives for tortoises to attempt to cross fences. Tortoises often walk along fences until they find a way through, increasing their energy expenditure and making them vulnerable to exposure (Peaden, Nowakowski, Tuberville, Buhlmann, & Todd, 2017), as well as making them vulnerable to other threats e.g. fire or predation (Ferronato et al., 2014; Ruby, Spotila, Martin, & Kemp, 1994).

Leopard tortoises may be particularly at risk because they feed in disturbed areas in the Karoo, such as road verges or water points used by livestock (Milton, 1992). The shift to electrified fence use greatly increases the threat to this species (Beck, 2009; Burger & Branch, 1994; Farber, 2016). Despite comprising only 4% of roadside fencing in the study area, our results suggest that electric fences account for 56 % of fence-related mortalities of leopard tortoises. Electric strands along mesh fences cause more tortoise mortalities than strand fences, possibly because the mesh is more of a barrier, making it harder for tortoises to escape. Large leopard tortoises are particularly at risk because their taller carapaces make contact with the electric strand more likely. The selective mortality of large, female leopard tortoises have also been reported in other populations (Grobler, 1982; Mason, Kerley, Weathreby, & Branch, 2000; McMaster & Downs, 2009). Possible reasons for the sex-biased mortality include behavioural differences (faster retraction times, slower escape rates) or differences in movement patterns.

There has been a growing realisation that turtles and tortoises are in trouble (Stanford et al., 2020). The collapse of tortoise and turtle populations on a global scale has greatly diminished their ecological roles (Lovich, Ennen, Agha, & Gibbons, 2018). By killing larger reproductive individuals (especially females), fence mortalities have the maximum demographic impact on leopard tortoises (Beck, 2009). The loss of these herbivores from the landscape may have significant ecological impacts, including habitat conversion and plant extinction (Froyd et al., 2014). Leopard tortoises are key disperses of the seeds of various grasses, succulents and forbs belonging to 26 plant families and thus have an important function in shaping the Karoo flora (Milton, 1992). Many plants eaten by leopard tortoises are avoided by sheep, goats and antelope because they are unable to metabolize the toxins in these plants (Milton, 1992). Leopard tortoises thus provide an ecological service to the game and agricultural industries (Milton et al., 1999).

Compared to leopard tortoises, angulate tortoises generally are small enough to pass beneath the lowest electric strand. The largest angulate tortoise heights recorded in our study (100 mm), are well below the interquartile range of the electric strand heights measured (140−210 mm, 78 % of strands >100 mm), partly explaining why we found none dead on electric fences. Angulate tortoise mortalities were mainly associated with mesh fences. Some 64 % of roadside fences in the study area have mesh structures, which accounted for 93 % of angulate tortoise mortalities. They become trapped if the mesh size is slightly smaller than the tortoise's height. This issue likely affects other small tortoise species: all but one dead tent tortoises (80 %) were found along mesh fences. Even if not trapped by the mesh, small tortoises may be more vulnerable to predators along fences, because fences provide lookout posts for crows and other predatory birds, increasing predation pressure (Andersson, Wallander, & Isaksson, 2009). Predation risk may be further increased by clearing of vegetation along fence lines, increasing the visibility of small tortoises. Conversely, clearing thick vegetation along fences, a standard maintenance activity, my remove thermal refuges that tortoises seek to escape extreme temperatures.

*Mitigation strategies*

The environmental impacts of both electrified and non-electrified fencing are of great concern as fences continue to be erected without regulation of their use or design. Although the problem of wildlife electrocution has been known for 25 years (Burger & Branch, 1994), there are few national regulations regarding fence type, structure and abundance. In 2011, the South African Department of Labour made amendments to the Electrical Machinery Regulations within the Health and Safety Act of 1993, which sets minimum standards for all electrified fences (Department of Labour, 2011). However, these regulations primarily focus on fencing in urban areas (McDonald, 2011). Local/-provincial departments, organizations or privately-owned fencing companies have policies regarding minimum requirements for effective containment of different animal categories and species (Brown et al., 2014).

Raising the minimum height of the electrified strands to 200−250 mm would greatly reduce unintentional animal mortalities (Beck, 2009). This would of course only be of use to chelonians <200 mm high. Unfortunately, raising the height of the lowest electric strand reduces the effectiveness of restricting the movements of problem animals that go under fences, so this mitigation measure is poorly implemented, creating tension between farmers and conservationists when suggested (Pietersen et al., 2014; Woodroffe et al., 2014).

Rock aprons are used to prevent animals digging under fences as rocks will fall in place of dispersed soil (Beck, 2009). However, rock aprons require considerable labour to install and are present on only 7% of fences in the study area. Their use should be to form an effective barrier between tortoise and fence, and thus discourage movement towards fences. However, when used in combination with electric strands, rock aprons reduce the effective height of the electric strand height, effectively placing smaller tortoises that climb onto the apron at risk of electrocution.

We advocate the best way to reduce tortoise mortality on electric fences is to switch fences off during the day, when they pose the greatest risk to tortoises, and there is lower threat of movement of problem animals such as jackals and caracals. This could be achieved using either light-levels or thermostatic switches. Alternatively, fences could be programmed to switch off randomly to provide an opportunity for tortoises to recover and escape (Beck, 2009; Burger & Branch, 1994). Leopard tortoises may survive up to an hour or longer once caught on an electric fence (Burger & Branch, 1994).

In terms of non-electric fences, strand fences result in fewer tortoise mortalities. However, removal of fences is the most effective mitigation measure, with benefits to all animals negatively impacted by fences (Beck, 2009; Boone & Hobbs, 2004). There is a push towards removing fences for conservation efforts with former farmland being successfully converted into reserves (Cumming et al., 2015). In South Africa, fence removal has helped to restore large mammal populations (Woodroffe et al., 2014). Fence removal could have the same effect for tortoise populations. Alternative approaches to fencing include traditional farming practices such as crop guarding, livestock heading and planned grazing (Woodroffe et al., 2014).

Conservation programmes with a focus on landowner outreach and education are desperately required. Our survey of the Karoo Biome in South Africa suggests that wildlife ranching (game farming) industry would be a primary candidate for an outreach program. However, we also detected that there were regions with 'cultures' of electric fence use. For instance, in the far Northern Cape, electric fences were used across a variety of land-use types, across thousands of kilometres. According to one farmer AL spoke to "We are killing tortoises in their thousands".

## 5. Conclusions

Fences pose a significant danger to tortoises in the semi-arid rangelands of the Karoo and beyond. Electric fences threaten leopard tortoise populations and mesh fences also pose problems for tortoises of smaller body-size species. Such fences should be removed when possible such as on land that has been converted to conservation or wildlife practices. Considering the numerous negative effects of fencing, not only on tortoises, installing fencing should be an action of last resort when all other options have been exhausted (Woodroffe et al., 2014). Major conservation campaigns will be required to create legislation to protect wildlife imperilled by electric fencing and to educate landowners, but to date we are unaware of any such institutionalized programs.

**Table A1**
Coefficient results from the full GLMM that investigated environmental and fence variables explaining presence of leopard tortoise in the southeastern Karoo region of South Africa. Transect was the random effect. Vegetation height and percent open ground were centred and scaled using the scale function in R.

| Variable | Estimate | SE | Z | P |
|---|---|---|---|---|
| **Dead leopard tortoise** | | | | |
| Intercept (Electric mesh) | −0.325 | 0.280 | −1.158 | 0.247 |
| Electric strand | −0.961 | 0.524 | −1.835 | 0.067 |
| Mesh | −3.782 | 0.405 | −9.341 | <0.001 |
| Strand | −4.331 | 0.543 | −7.973 | <0.001 |
| No Fence | −5.724 | 1.087 | −5.265 | <0.001 |
| Rock apron | −0.863 | 0.398 | −2.171 | 0.023 |
| Vegetation height | 0.207 | 0.089 | 2.341 | 0.019 |
| Water presence | 1.281 | 1.049 | 1.220 | 0.222 |
| Open ground (%) | −0.038 | 0.112 | −0.337 | 0.736 |
| **Live leopard tortoise** | | | | |
| Intercept (Electric mesh) | −6.312 | 1.022 | −6.174 | <0.001 |
| Electric strand | −0.798 | 1.799 | −0.443 | 0.658 |
| Mesh | 0.020 | 1.000 | 0.020 | 0.984 |
| Strand | −0.670 | 1.223 | −0.548 | 0.584 |
| No Fence | −0.803 | 1.471 | −0.545 | 0.585 |
| Rock apron | −1.472 | 1.086 | −1.356 | 0.175 |
| Vegetation height | 0.403 | 0.175 | 2.299 | 0.021 |
| Open ground (%) | 0.140 | 0.251 | 0.558 | 0.577 |
| Water presence | 3.857 | 1.350 | 2.856 | 0.004 |

## Declaration of Competing Interest

There are no issues related to economical conflict of interests, or other that we are aware of.

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## Appendix A

## Appendix B. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.jnc.2020.125945.

## References

Bourn, D., & Coe, M. J. (1979). Features of tortoise mortality and decomposition on Aldabra. *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences, 286*(1011), 189–193.

Alexander, G. J., & Marais, J. (2007). *A guide to the reptiles of southern Africa*. Cape Town: Struik.

Andersson, M., Wallander, J., & Isaksson, D. (2009). Predator perches: A visual search perspective. *Functional Ecology, 23*(2), 373–379.

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software, 67*(1), 1–48.

Bates, M. F., Branch, W. R., Bauer, A. M., Burger, M., Marais, J., Alexander, G. J., et al. (2014). *Atlas and red list of the reptiles of South Africa, Lesotho and Swaziland*. Pretoria: South African National Biodiversity Institute.

Beck, A. (2009). *Electric fence induced mortality in South Africa. MSc dissertation*. Johannesburg: University of the Witwatersrand.

Bjornstad, O. N. (2019). *Ncf: Spatial covariance functions. R package version 1.2-8*. https://CRAN.R-project.org/package=ncf.

Boarman, W. I., & Sazaki, M. (1996). *Highway mortality in desert tortoises and small vertebrates: Success of barrier fences and culverts*. Florida Department of Transport Report: No. FHWA-PD-96-041.

Bode, M., & Wintle, B. (2010). How to build an efficient conservation fence. *Conservation Biology, 24*(1), 182–188.

Boone, R. B., & Hobbs, N. T. (2004). Lines around fragments: Effects of fencing on large herbivores. *African Journal of Range & Forage Science, 21*(3), 147–158.

Boycott, R. C., & Bourquin, O. (1988). *The South African tortoise book: A guide to South African tortoises, terrapins and turtles*. Gauteng: Southern Book Publishers.

Branch, B. (2012). *Tortoises, terrapins & turtles of Africa*. Cape Town, South Africa: Struik.

Branch, W. R. (1998). *Field guide to snakes and other reptiles of southern Africa*. Cape Town: Struik.

Brandt, F., & Spierenburg, M. (2014). Game fences in the Karoo: Reconfiguring spatial and social relations. *Journal of Contemporary African Studies, 32*(2), 220–237.

Brown, C. J., Gildenhuys, P. S., Hignett, D. L., & van Deventer, J. D. (2014). *Policy on fencing and enclosure of game, predators and dangerous animals in the Western Cape province*. Stellenbosch: CapeNature, Biodiversity Support Services.

Burger, M., & Branch, W. R. (1994). Tortoises mortality caused by electrified fences in the Thomas Baines Nature Reserve. *South African Journal of Wildlife Research, 24* (1–2), 32–37.

Cassidy, L., Fynn, R., & Sethebe, B. (2013). Effects of restriction of wild herbivore movement on woody and herbaceous vegetation in the Okavango Delta botswana. *African Journal of Ecology, 51*(4), 513–527.

Cumming, D. H. M., Osofsky, S. A., Atkinson, S. J., & Atkinson, M. W. (2015). Chapter 21. Beyond fences: Wildlife, livestock and Land use in Southern Africa. In J. Zinsstag, E. Schelling, D. Waltner-Toews, M. Whittaker, & M. Tanner (Eds.), *One health: The theory and practice of integrated health approaches* (pp. 243–257). Pretoria: CABI.

Cunningham, S. J., Madden, C. F., Barnard, P., & Amar, A. (2016). Electric crows: Powerlines, climate change and the emergence of a native invader. *Diversity & Distributions, 22*(1), 17–29.

Davies-Mostert, H. T., Mills, M. G. L., & Macdonald, D. W. (2013). Hard boundaries influence African wild dogs' diet and prey selection. *The Journal of Applied Ecology, 50*(6), 1358–1366.

Department of Labour. (2011). *ZA government notices 34154* (pp. 3–33).

Farber, T. (2016). *Shell-Shocked: A tortoise massacre*. Sunday Times. p. 8.

Ferronato, B. O., Roe, J. H., & Georges, A. (2014). Reptile bycatch in a pest-exclusion fence established for wildlife reintroductions. *Journal for Nature Conservation, 22*(6), 577–585. https://doi.org/10.1016/j.jnc.2014.08.014.

Fincham, J. E., & Lambrechts, N. (2014). How many tortoises do a pair of Pied Crows *Corvus albus* need to kill to feed their chicks? *Biodiversity Observations, 5*, 135–138.

Froyd, C. A., Coffey, E. E. D., van der Knaap, W. O., van Leeuwen, J. F. N., Tye, A., & Willis, K. J. (2014). The ecological consequences of megafaunal loss: Giant tortoises and wetland biodiversity. *Ecology Letters, 17*(2), 144–154.

Grobler, J. H. (1982). The leopard tortoise in the Mountain Zebra national Park. *Koedoe, 25*(1), 49–53.

Hayward, M. W., & Kerley, G. I. H. (2009). Fencing for conservation: Restriction of evolutionary potential or a riposte to threatening processes? *Biological Conservation, 142*(1), 1–13.

Heard, H. W., & Stephenson, A. (1987). Electrification of a fence to control the movements of black-backed jackals. *South African Journal of Wildlife Research-24-Month Delayed Open Access, 17*(1), 20–24.

Hoare, R. E. (1992). Present and future use of fencing in the management of larger African mammals. *Environmental Conservation, 19*(2), 160–164.

Joseph, G. S., Seymour, C. L., & Foord, S. H. (2017). The effect of infrastructure on the invasion of a generalist predator: Pied crows in southern Africa as a case-study. *Biological Conservation, 205*, 11–15.

Kesch, K. M., Bauer, D. T., & Loveridge, A. J. (2014). Undermining game fences: who is digging holes in Kalahari sands? *African Journal of Ecology, 52*(2), 144–150.

Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2017). lmerTest package: Tests in linear mixed effects models. *Journal of Statistical Software, 82*(13), 1–26.

Lee, A. T. K., & Wright, D. R. (2019). Patterns of bird species richness at two sampling scales in the Karoo biome of South Africa. *Journal of Arid Environments*, Article 104077.

Ley, A. J., & Tynan, B. (2008). Bird casualties in fences in Diamantina National Park, Queensland, 1996-2008. *Australian Field Ornithology, 25*(2), 96.

Loehr, V. J. T. (2017). Unexpected decline in a population of speckled tortoises. *The Journal of Wildlife Management, 81*(3), 470–476.

Lovich, J. E., Ennen, J. R., Agha, M., & Gibbons, J. W. (2018). Where have all the turtles gone, and why does it matter? *BioScience, 68*(10), 771–781.

Macray, M. (2017). *Tortoise mortalities along fences in the southeastern Karoo, South Africa*. University of Cape Town.

Mason, M. C., Kerley, G. I. H., Weathreby, C. A., & Branch, W. R. (2000). Angulate and leopard tortoises in the Thicket Biome, Eastern Cape, South Africa: Populations and biomass estimates. *African Journal of Ecology, 38*(2), 147–153.

McDonald, C. (2011). New certificate requirement for electric fence systems. *SANS10400 building regulations*. Available from http://sans10400.co.za/new-electric-fence-law (accessed on 12 January 2017).

McGahey, D. J. (2011). Livestock mobility and animal health policy in southern Africa: The impact of veterinary cordon fences on pastoralists. *Pastoralism Research Policy and Practice, 1*(1), 215–234.

McMaster, M. K., & Downs, C. T. (2009). Home range and daily movement of leopard tortoises (*Stigmochelys pardalis*) in the Nama-Karoo, South Africa. *Journal of Herpetology, 43*(4), 561–570.

Milton, S. J. (1992). Plants eaten and dispersed by adult leopard tortoises *Geochelone pardalis* (Reptilia: Chelonii) in the southern Karoo. *South African Journal of Zoology, 27*(2), 45–49.

Milton, S. J., Davies, R. A. G., & Kerley, G. I. H. (1999). Population level dynamics. In W. R. Dean, & S. Milton (Eds.), *The karoo: Ecological patterns and processes* (pp. 183–207). Cambridge University Press Cambridge.

Mucina, L., & Rutherford, M. C. (2006). *The vegetation of South Africa, Lesotho and Swaziland*. Pretoria: South African National Biodiversity Institute.

Nass, R. D., & Theade, J. (1988). Electric fences for reducing sheep losses to predators. *Rangeland Ecology & Management/Journal of Range Management Archives, 41*(3), 251–252.

Palmer, A. R., & Hoffman, M. T. (1997). Nama-karoo. In R. M. Cowling, D. M. Richardson, & S. M. Pierce (Eds.), *Vegetation of southern Africa* (pp. 167–188). Cambridge: Cambridge University Press.

Peaden, J. M., Nowakowski, A. J., Tuberville, T. D., Buhlmann, K. A., & Todd, B. D. (2017). Effects of roads and roadside fencing on movements, space use, and carapace temperatures of a threatened tortoise. *Biological Conservation, 214*, 13–22.

Pietersen, D. W., McKechnie, A. E., & Jansen, R. (2014). A review of the anthropogenic threats faced by Temminck's ground pangolin, *Smutsia temminckii,* in southern Africa. *African Journal of Wildlife Research, 44*(2), 167–179.

R Core Team. (2019). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. https://www.R-project.org/.

Reidy, M. M., Campbell, T. A., & Hewitt, D. G. (2008). Evaluation of electric fencing to inhibit feral pig movements. *The Journal of Wildlife Management, 72*(4), 1012–1018.

Ruby, D. E., Spotila, J. R., Martin, S. K., & Kemp, S. J. (1994). Behavioral responses to barriers by desert tortoises: Implications for wildlife management. *Herpetological Monograph, 8*, 144–160.

Scofield, R. P., Cullen, R., & Wang, M. (2011). Are predator-proof fences the answer to New Zealand's terrestrial faunal biodiversity crisis? *New Zealand Journal of Ecology, 35*, 312–317.

Seymour, C. L., Gillson, L., Child, M. F., Tolley, K. A., Curie, J. C., da Silva, J. M., & Egoh, B. N. (2019). Horizon scanning for South African biodiversity: A need for social engagement as well as science. *Ambio, 49*, 1–11. https://doi.org/10.1007/s13280-019-01252-4.

Spitzweg, C., Hofmeyr, M. D., Fritz, U., & Vamberger, M. (2019). Leopard tortoises in southern Africa have greater genetic diversity in the north than in the south (Testudinidae). *Zoologica Scripta, 48*(1), 57–68. https://doi.org/10.1111/zsc.12328.

Stanford, C. B., Iverson, J. B., Rhodin, A. G. J., van Dijk, P. P., Mittermeier, R. A., Kuchling, G., … Blanck, T. E. G. (2020). Turtles and tortoises are in trouble. *Current Biology, 30*(12), R721–R735.

Steventon, J., Liebenberg, L., Derbecker, M., Bapat, V., & Miles, D. G. (2011). *CyberTracker*. www.cybertracker.com. Retrieved 23rd August.

Tolley, K. A., Weeber, J., Maritz, B., Verburgt, L., Bates, M. F., Conradie, W., … Alexander, G. J. (2019). No safe haven: Protection levels show imperilled South African reptiles not sufficiently safe-guarded despite low average extinction risk. *Biological Conservation, 233*, 61–72.

Vanak, A. T., Thaker, M., & Slotow, R. (2010). Do fences create an edge-effect on the movement patterns of a highly mobile mega-herbivore? *Biological Conservation, 143* (11), 2631–2637. https://doi.org/10.1016/J.BIOCON.2010.07.005.

Venables, W. N., & Ripley, B. D. (2002). Random and mixed effects. *Modern applied statistics with S* (pp. 271–300). New York, NY: Springer.

Woodroffe, R., Hedges, S., & Durant, S. M. (2014). To fence or not to fence. *Science, 344* (6179), 46–48.