Tortoise mortalities along fences in the southeastern Karoo, South Africa

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Abstract

Fencing, particularly electric fencing, is widely used across South Africa for livestock and game ranching practices. Recent studies found that leopard tortoises (*Stigmochelys pardalis*) are more prone to dying from electrocution along electric fences than any other taxa. However, no studies have quantified tortoise mortality along non-electric fences or assessed the impact of fence structure. With South Africa being home to more tortoise species than anywhere else in the world, thus is a conservation concern. This study quantifies tortoise mortalities associated with electrified and non-electrified fences and relates these rates to fence structure (mesh or strand). Open veld transects are used as controls to estimate background mortality. This study also reports the distribution and abundance of different fence types along 2200 km of roads in the southeastern Karoo, allowing the cumulative impacts of different fence types to be estimated. All fence types had significantly higher tortoise mortalities than open veld transects. Leopard tortoise mortalities were significantly higher along electric fences than non-electric fences. Despite forming only approximately 4 % of all roadside fencing, electric fences account for 56 % of leopard tortoise mortalities. This study validates concern for increased electric fence use in the future and the potential impacts on leopard tortoises. When considering the current abundance of fence types and their associated mortalities, the total number of leopard tortoise mortalities along electric and non-electric fences are similar. Angulate tortoise (*Chersina angulata*) mortalities were significantly higher along mesh fences than strand fences, but did not differ between electric and non-electric fences. Angulate tortoises appear to wedge themselves in mesh fences and are unable to escape. This study highlights the current threat of non-electric fencing on tortoises as no similar findings have been reported. These additional tortoise mortalities should be considered alongside other emerging threats when questioning the longevity of these tortoise populations, not only in the Karoo, but globally. The implementation and practicality of previously suggested mitigation strategies are discussed and alternative mitigation strategies are suggested. This study concludes that raising of the electric strands is impractical and the implementation of rock aprons are ineffective. Live tortoises displayed active behavior when temperature was above 20 °C, thus thermostatic switches for electric fences could potentially reduce tortoise mortalities without compromising fences function.

Introduction

Tortoise conservation

The family Testudinidae contains 59 extant species of terrestrial tortoises in 14 genera, which are found on every continent (except Australia where they have gone extinct, and Antarctica) and on several islands in the Indian Ocean and Galapagos (van Dijk et al. 2014; Reptile database 2017). Many tortoises contribute to the biodiversity of their respective ecosystems, often serving as keystone species (Turtle conservation fund 2002; Hansen et al. 2010; Catano & Stout 2015). The IUCN (2017) lists many of these species as threatened (Critically Endangered = 9, Endangered = 5, Vulnerable = 17, Near Threatened = 3) largely as a result of over-exploitation for the pet trade, food and medicine (Lau & Shi 2000; UNEP-WCMC 2014; van Dijk et al. 2014). Concern for high numbers of road mortalities has also been reported for tortoises in North America (Ruby et al. 1994; Baxter-Gilbert et al. 2015). Currently, all tortoise species are protected by CITES, with 9 species in Appendix I and the remainder in Appendix II (CITES 2016). This led to a global conservation action plan with numerous international partners and contributors, the goal of which was to fund conservation projects aimed at protecting tortoises and turtles (Turtle Conservation Fund 2002).

South Africa is the most species-rich tortoise region in the world, with 13 species from five genera (Bates et al. 2014). In addition to being collected and suffering from road mortalities, tortoises face additional threats across South Africa. Habitat transformation from farming activities, encroachment of urban sprawl, establishment of invasive alien vegetation, increased fire frequency and pollution have led to decreasing populations (Alexander & Marais 2007; Watson et al. 2008). The local increase in pied crows (*Corvus albus*) across parts of South Africa (Cunningham et al. 2016; Joseph et al. 2016) has resulted in increased predation on juvenile and small tortoises (Fincham & Lambrechts 2014; Loehr 2017). Electric fences are an emerging threat to tortoises as they are more prone to dying from electrocution along electric fences than are any other taxa (Beck 2010).

Fencing in South Africa

Fences are used to demarcate ownership of animals and different land practices, and are considered a necessity for wildlife conservation, game ranching and livestock farming, which are the main land practices that utilize fencing in South Africa (Boone & Hobbs 2004; Beck 2010; Cumming et al. 2015; Farber 2016). Landowners engage in many land-use practices (Taylor & Van Rooyen 2015), but each practice has specific objectives and different rationales for the use of fences. Wildlife conservation uses fences to contain and formally protect a variety of wildlife species within protected areas (Hoare 1992). However, the use of fences to achieve conservation goals is controversial as fences have many negative impacts on wildlife (Hoare 1992; Bode & Wintle 2010; Scofield et al. 2011S; Woodroffe et al. 2014). Livestock farming uses fences primarily to exclude predators, while fences are used to constrain animals within camps and limit the spread of diseases in game ranching (Beck 2010; Cumming et al. 2015). Most of South Africa's native fauna persist outside of protected areas, with game ranching playing an increasingly important role in biodiversity conservation (Cumming et al. 2015; Taylor & van Rooyen 2015; Tayor et al. 2015). Private game ranches cover approximately 17million hectares, roughly 2.2 times greater than formally protected areas in South Africa (Taylor & van Rooyen 2015).

Electric fencing, is increasingly being used across South Africa since 1992 due to an increase in livestock farming and game ranching (Beck 2010; Brandt & Spierenburg 2014; Pietersen et al. 2014; Taylor & van Rooyen 2015; Farber 2016). Electric fences deliver an electric shock when the electrified strand is contacted. Thus, they 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 (Burger & Branch 1994; Kesch 2014; Kesch et al. 2014). Predators threaten livelihoods for some game ranchers and particularly livestock farmers across South Africa (van Niekerk 2010; Pietersen et al. 2014). It is estimated that 3 – 6 % of all livestock and 6 – 13 % of juvenile livestock are lost to predators each year (depending on the province), with black-backed jackal (*Canis mesomelas*) and caracal (*Felis caracal*) being responsible for most losses (53 – 65 % and 9 – 36 %, respectively) (van Niekerk 2010).

The structure of electric fences varies greatly (e.g. the number of electric strands, heights between strands, voltage and whether one or both sides are electrified) depending on the land use and animals to be contained or excluded (Cape Nature 2014). One common feature is an offset, single low-lying electrified strand designed to prevent problem animals from digging underneath fences (Beck 2010; Pietersen 2013). The height of this strand typically varies from 30-300 mm (Burger & Branch 1994, Beck 2010; Pietersen 2013). Fences that lack this electrified strand will hereafter be referred to as non-electric fences. Typical structure, uses and functioning of electric fencing is described in further detail by Macdonald (2005) and Beck (2010).

There are few national regulations regarding fence type, structure and abundance, although local policies may be found (e.g. Cape Nature 2014). In 2011, the Department of Labor 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 are primarily focused on security fencing in urban areas (Mcdonald 2011; Department of Labour 2011). Local/provincial departments, organizations or privately-owned fencing companies have policies regarding minimum requirements for effective containment of different animal categories and species (Beck 2010; Todd et al. 2009: Ndlovu Fencing 2011; Cape Nature 2014). A review of these policies shows that suggested designs often vary greatly, depending on the type of animals to be confined or excluded (Beck 2010). However, these policies are difficult to implement and regulate in remote areas where wildlife conservation, game ranching and livestock farming practices occur.

Regardless of whether a fence is electrified or not, fences are primarily comprised of either a diamond shaped mesh or horizontal strands that run between fence poles (hereafter referred to as mesh and strand fences, respectively). Many fences have a combination of strands above mesh, because most animals push through between the lower horizontal strands. The environmental impacts of both electrified and non-electrified fencing are of great concern as more fences continue to be erected without regulations managing the range of fence designs.

Impacts of fences on South African fauna

Linear features across a landscape, such as fences, can act as selectively permeable filters, obstructions and ecological traps for animals (Boone & Hobbs 2004; Beck 2010). The impacts that these features have on animals and the environment have been well-documented across a wide range of taxa (e.g. Boone & Thompson Hobbs 2004; Cassidy et al. 2013; Davies-Mostert 2013; Woodroffe et al. 2014). However, these studies are primarily concerned with larger animals and the resulting effects on the environment. Few studies investigate the impact of fencing on small animals, as it is generally assumed that they pass through fences freely (Kesch 2014). However, a few studies have investigated the impacts of electric fencing on pangolins (Pietersen 2013; Pietersen et al. 2014).

Most studies highlight the negative impacts of fencing as follows:

- Landscape fragmentation and isolation, loss of connectivity (Boone & Thompson Hobbs 2004; Hayward & Kerley 200; Woodroffe et al. 2014)；
- Disruption of migratory movements and dispersal patterns (Whyte 1988; Vanak et al. 2010; Cassidy et al. 2013; Woodroffe et al. 2014);
- Limits animal access to key resources or mates (Hayward & Kerley 2009);
- Skews demography of populations (Hoare 1992; Woodroffe et al. 2014);
- Isolated or confined populations (Whyte 1988; Cassidy et al. 2013; Woodroffe et al. 2014);
- Increased risk of local extirpation due to random demographic, genetic, and environmental events (e.g. inbreeding) ((Hayward & Kerley 2009; Kesch 2014; Woodroffe et al. 2014);
- Restriction of evolutionary potential (Hayward & Kerley 2009);
- Reduction of carrying capacity (Ben-Shahar 1993);
- Increased mortality rates, both as a direct (e.g. entanglement or electrocution) or indirect result (e.g. increased predation) of the fence (Boone & Thompson Hobbs 2004; Beck 2010);
- The potential to modify animal behavior (Vanak et al. 2010; Davies-Mostert et al. 2013);
- Altered predator-prey dynamics and interactions (Scofield et al. 2011; Davies-Mostert et al. 2013);
- Decreased habitat quantity and quality (Hoare 1992; Cassidy et al. 2013; Woodroffe et al. 2014);
- Overgrazing by confined livestock and wildlife (Boone & Thompson Hobbs 2004; Kesch 2014; Woodroffe et al. 2014);
- Provision of wire for the construction of illegal snares (Davies-Mostert et al. 2013);
- Cascading effects leading to ecological meltdown (Vanak et al. 2010; Kesch 2014).

Fences can also benefit conservation actions by helping to achieve desired goals such as:

- Control and management of animal populations (Woodroffe et al. 2014)
- Exclude or control human access or conflict (Hoare 1992; Hayward & Kerley 2009)
- Enable restoration and protection of threatened environments and species (Boone & Thompson Hobbs 2004)
- Reduce access to roads thus reducing road mortalities (Ruby et al. 1994)
- Prevent spread of diseases and invasive species (Day & Macgibbon 2007; Hayward & Kerley 2009; Ewen et al 2011; Cumming et al. 2015)

However, Woodroffe et al. (2014) note that fences often fail to deliver desired benefits due to lack of maintenance, poor design, construction challenges and location. Do the benefits of fencing outweigh the costs? This important question can be answered only against well-defined objectives.

Given the increased of electrified fencing, Beck (2010) tried to quantify the number of animals killed by electric fences across South Africa. He found individuals from 33 species that died as a direct result of electric fencing. Reptiles had an order of magnitude higher mortality rate than mammals had, with mortality rates up to 2.15 individuals/km/yr ($\bar{x}$ = 0.475 individuals/km/yr). Leopard tortoises (*Stigmochelys pardalis*) comprised 91 % of all reptile mortalities and Beck (2010) concluded that this species was most susceptible reptile species. He also found that more leopard tortoise mortalities happened in summer, when tortoises are more active, than in winter (May – August), when leopard tortoises were less active and had no mortalities.

Tortoises vulnerability to fencing

Beck's (2010) results supported findings of a previous study (Burger & Branch 1994) that investigated tortoise mortalities along electric fences in the Thomas Baines Nature Reserve, South Africa. After finding 36 tortoise carcasses along 8.4 km of electric fence, Burger and Branch (1994) measured mortality rates in summer (1 October 1990 – 9 February 1991) and found 22 tortoises (6 alive) along the same fence. They acknowledged that tortoises are more active in the warmer months and thus give a conservative mortality rate of approximately 3.5 individuals/km/yr. Of the 58 tortoises found, 56 were leopard tortoises.

Both South African studies related high mortalities of leopard tortoises to their behaviour, large size, wide distribution and reaction to electrocution (Burger & Branch 1994; Beck 2010). All tortoise mortalities were a direct result of tortoises contacting a single, low-lying electric strand. When leopard tortoises touched an electrified strand, they adopt their natural defense strategy, retracting their limbs and head into their shell (Beck 2010). Unfortunately, they remain part of the circuit and thus become trapped (Burger & Branch 1994; Todd et al. 2009; Beck 2010). Some urinate which increases the degree to which they are earthed and the amount of current that passes through them (Burger & Branch 1994). The tortoises eventually die of electrocution, dehydration or overheating (from exposure to the sun), or a combination of all three (Burger & Branch 1994).

Electric fences remove presumably reproductively active leopard tortoises, as mainly large tortoises were killed in both studies (Burger & Branch 1994; Beck 2010). Such mortality may threaten future populations given their low recruitment rates (Beck 2010; McMaster & Downs 2009; van Dijk et al. 2014). Considering leopard populations tend to be female-biased and to contain more adults than juveniles (Grobler 1982; Mason et al. 2000; McMaster & Downs 2009), demographic impacts may be further exacerbated as many adult females are likely to be killed, further threatening population size, recruitment and viability. Other tortoise species also are killed by electric fences, including angulate tortoises (*Chersina angulata*), Kalahari Tent Tortoises (*Psammobates oculiferus*) and Lobatse hinged-backed tortoise (*Kinixys lobatsiana*) (Burger & Branch 1994; Beck 2010), suggesting that all tortoise species could be at risk if the electric strands are low enough to contact small tortoises. The two primary mitigation strategies recommended to reduce tortoise mortalities include raising the height of the electric strand and building rock aprons along electric fences (Beck 2010). Rock aprons are rocks packed against the fence to prevent animals from digging beneath the fence and to maintain fence integrity. The rock aprons prevent tortoises from reaching the electric strand (Beck 2010).

A few studies conducted in the United States investigated desert tortoise (*Gopherus agassizii*) responses to various barriers, including mesh fences (Ruby et al. 1994), and found that the most effective tortoise barrier was a mesh screen fine enough to exclude a tortoise's head. No studies in South Africa have reported any tortoise mortalities along non-electric fences. Non-electric fence mortalities involve larger animals (only mammals?) that became entangled and were unable to escape (Kesch et al. 2014). It is unknown if non-electric fences kill tortoises or whether fence structure (i.e. mesh or strand) has any role. The mortality rates reported (Burger & Branch 1994, Beck 2010) were also not compared to natural mortality rates.

Tortoises in the southeastern Karoo

The Karoo is the most species-rich tortoise region in South Africa, with four genera of tortoises comprising nine species, of which six are endemic (Branch et al. 1995; Branch 1998; Milton et al. 1999; Boycott & Bourquin 2000, Branch 2012). The leopard tortoise is the largest (with exceptional individuals reaching lengths of 750 mm and masses of 40 kg), most abundant and widespread tortoise across South Africa (Alexander & Marais 2007; Branch 2012). In addition, leopard tortoises produce more offspring than other tortoises in the region. Angulate tortoises may be locally abundant, with exceptional individuals reaching carapace lengths of 300 mm and body masses of 2 kg (Alexander & Marais 2007). Of the three tent tortoise species, only the Karoo tent tortoise (*Psammobates tentorius*) occurs in the southeastern Karoo in low densities (Alexander & Marais 2007). Finally, of the five species of padloper tortoise, two occur in the southeastern Karoo: the parrot-beaked padloper (*Homopus areolatus*) and the rare Karoo padloper (*H. boulengeri*) (Boycott & Bourquin 2000; Alexander & Marais 2007). All the tortoises found in the southeastern Karoo have a conservation status of least concern, except the Karoo padloper which is listed as near threatened (Bates et al. 2014).

The Karoo exhibits all the fencing problems mentioned above that result from game ranching and livestock farming (Brandt & Spierenburg 2014; Farber 2016), making unregulated fencing a conservation concern for tortoises. The Karoo stretches across multiple provinces, making it difficult to monitor and regulate at a provincial level. Although landowners appreciate the threat posed to tortoises by electric fences, little has been done to address electric fence electrocution of tortoises. The problem recently received media attention to raise awareness to the public and generate pressure for change (Watson et al. 2008; Farber 2016).

Additional sources of anthropogenic mortality further threaten tortoise populations, especially the small, less common species with low reproductive rates. The spread and increase of pied crow

(*Corvus alba*) populations across the Karoo (Cunningham et al. 2016; Joseph et al. 2016) is an emerging threat that has been linked to decreases in tortoise populations (Fincham & Lambrechts 2014; Loehr 2017). Road mortalities are also common across the Karoo, but have been published only for greater padlopers (*Homopus femoralis*) (Loehr 2012). Overgrazing and habitat transformation also threaten many tortoise species in the Karoo (Watson et al. 2008). More than 80 % of the Karoo is privately owned and used for extensive livestock farming (Hoffman et al. 1999), implicating a great risk to tortoises and other wildlife in the region. Besides these few scientific publications, the impacts of livestock and other anthropogenic effects are scarcely published. More research is needed to improve our understanding of tortoise populations and consequently ensure their future existence.

Many farmers in the Karoo are converting their land to wildlife habitats for game ranching and conservation as they seek greater economic returns and wish to maintain ownership given post-apartheid land-reform and labor policies (Brandt & Spierenburg 2014). Nature-based tourism in Southern Africa is growing at 5 – 15 % per annum and contributes as much or more to gross domestic product (GDP) than livestock farming, which is growing at only about 2% per annum (Cumming et al. 2015). Although game ranching often results in more electrified fences being erected along property perimeters, internal fencing and farming infrastructure is being removed to create continuous landscapes (Brandt & Spierenburg 2014).

This study

This study expands on Beck's (2010) findings by investigating tortoise mortalities along all fence types and identifying which tortoise species and demographics are at risk, and what fence features are responsible. A key objective was to estimate the total number of fence related tortoise mortalities within the study area by quantifying tortoise mortalities associated with electrified and non-electrified fences and relating these rates to fence structure. Open veld transects were used are used as controls to estimate background mortality. This study also reports the distribution and abundance of different fence types in the southeastern Karoo, allowing the cumulative impacts of different fence types to be estimated. I also investigated the effectiveness of strategies to mitigate fence-related mortalities. Finally, the study aims to raise awareness and inform a code of best practice to reduce tortoise mortality on fences, thus benefiting game ranchers, livestock farmers and tortoises

Methods

Study area

The study was conducted in the southeastern Karoo between Calitzdorp and Kleinpoort (Fig. 1). The study area is diverse as it consists of four biomes. The study area was situated primarily in the Nama Karoo Biome, although some areas extended into Succulent Karoo and drier areas of Albany Thicket and Fynbos Biomes. However, many areas have been transformed due to overgrazing by livestock (Hoffman et al. 1999; Milton et al. 1999). The vegetation primarily consists of low-shrubs, although succulents are common in arid areas and grasses and fynbos shrubs are found in wetter areas with trees occurring along river beds (Milton et al. 1999). Annual rainfall varies between 120 – 200 mm, with March generally being the wettest month (20 – 30 mm) and June being the driest (0 – 12 mm), but this varies regionally (SA Explorer 2016). However, the area suffered a drought in 2016. January and February are the hottest months, with average daily maximum temperatures of 30 – 33 °C and minima of 14 – 16 °C (SA explorer 2016). June and July are the coldest months with average daily maxima temperatures ranging from 18 – 20 °C and minima from 3 – 6 °C. Data were collected during October and November 2016 using CyberTracker software, a mobile application (Steventon et al. 2015).

Data collection

Tortoise encounter survey

Transect data were collected in relation to fence type to identify what factors predicted the presence of tortoises along types of fences. I recorded data of live tortoises and the standing stock of dead tortoises along fences. A mortality rate of individuals/km/yr could not be measured as I did not have enough time to clear carcasses and recheck areas. Instead I recorded presence and number of tortoises along 1 km of fence. I walked transects along different fence types and transects in open veld to serve as a control (Fig. 2). I focused surveys on road verges for data consistency and time restrictions, because obtaining permission from every landowner for such a large area would be impractical. Transect lengths typically were 1-km long, but were occasionally shortened if the fence type changed. Distances were measured using a vehicle odometer and the mobile GPS application Galileo (Galileo 2016).

The following information on fence presence and design were recorded at 100 m intervals, as well as at each tortoise found during a transect: the structure of the fence (i.e. mesh or strand); presence of electrified strands; where these were present, the height of the lowest electric strand above the ground was recorded to the nearest 5 mm using a measuring tape (if obstructions were present such as rock aprons, the height from the ground under the obstruction to the strand was measured). Fence types were categorized into the following groups: No fence (open veld = control), Electric mesh, Electric strand, Mesh (non-electric) and Strand (non-electric). 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 could contact the fence. If a rock apron was present, it was recorded. A rock apron was recognized if there were rocks packed together with no observable gaps to a height of at least 5 cm and extended for 5 m either side from the data point. Roads bordering fences were categorized as tar or dirt. I recorded data from the roadside.

The following environmental data were recorded at 100 m intervals, as well as at each tortoise found during a transect: average vegetation height and percentage of open ground was estimated within a 5 m radius on side of the fence where the tortoise was found; presence of water within a 50 m radius; and proximity to a river (GPS locations were given a 50 m radius and intersected with a river map (Lotter 2014) in ArcGIS (ESRI 2016).

The following measurements were recorded for all tortoise encounters (both live and dead) along transects: species identity (based on scutes and carapace shape), sex (from plastron shape); standard carapace length (SCL, 5 mm) and carapace height (measured to the nearest 5 mm using a measuring tape); stage of decomposition of dead tortoises (adapted from Bourn & Coe 1979, see Table 1); and perpendicular distance to the fence (to the nearest 5 cm using a measuring tape or rangefinder to the nearest 0.5 m). All dead tortoises found within 10 m of a transect were included because scavengers or people may move a carcass.

It is possible that farmers move these tortoises far out of sight to maintain a positive reputation. For tortoises found on an electric fence, the electric strand height was recorded at point of contact and when point of contact could not be estimated, the reading was made where the fence was closest to the carcass.

The top three scutes (2nd, 3rd and 4th vertebrals; Fig. 3) were measured due to their distinctive shape, which allowed them to be easily identified among partial tortoise remains. These scute lengths, including loose ones that were warped by the sun, were measured using a string and a tape measure to the nearest 1 mm.

Spatial distribution of fences

Fence distribution data were collected to sample the distribution and abundance of different fence types in non-urban environments. Data points were collected every 5 km along public roads (for both sides of the road) across the study area (Fig. 1). Data points along each road were recorded independently from any existing data points on adjacent roads. The same information on fence presence and design described above were recorded, except the height of lowest electrified strand due to time constraints. I recorded the same environmental information described above.

Additional information

For any incidental tortoise encounters (not on a transect), the same fence presence and design, environmental and tortoise encounter information described above were recorded. Behavior of live tortoises was categorized as follows: Resting (inactive), Trapped at fence, Drinking, Feeding, Mating and Walking. In addition, temperature was recorded with a handheld Kestrel device for all incidental encounters. Live tortoises found trapped on a fence were removed by hand or using a wooden pole to push them away without touching the fence. Finally, personal field observations and informal conversations with landowners regarding tortoises, land-use, and wildlife conflict were noted.

Data analysis

Tortoise mortality along fence types

The data were filtered before conducting analyses. Nine transects that occurred in pure fynbos were excluded as tortoise diversity and abundance are known to be low in fynbos in the southeastern Karoo (Dr A. Lee 2016, pers. comm.). In addition, six transects that were less than 300 m in length were also excluded. The three live tortoises found trapped under an electric strand on a fence were treated as dead as it is assumed they would have died if they had not been rescued. I performed all statistics analyses using the statistical package R 3.2.4 (R core team 2015) unless specified otherwise. The potential for spatial autocorrelation for models regarding the average number of tortoises found along a 1-km transect were run to investigate the independence of transects, using the R package ncf (Bjornstad 2016). The x function and y function were specified to be the coordinates of each transect's midpoint. If spatial autocorrelation is found at a given distance, neighboring transects within this distance cannot be compared. Thus, only one transect should be used in analyses.

I generalized linear models (GLMs) to model the probability of finding a tortoise and the average number of tortoises found along a 1-km transect using presence and absence data from transects. Live and dead tortoise results were treated separately, as were analyses of different species of dead tortoises. Fence type and road type were used in GLMs as they were consistent along each transect. I used transect length as an offset to account for varying transect lengths. For probability models, a binomial distribution and a logit-link function were specified. For average number of tortoises along a 1-km transect, a negative binomial distribution and a logit-link function were specified. Both variables were initially included in the GLMs. If they did not have a significant effect, I removed from them from the model to increase power. Models were selected by using lowest AIC values and the smallest ratio between null deviance and residual deviance. Data were back-transformed respectively after analyses using the R package lsmeans (Lenth 2016).

A generalized linear mixed-effect model (GLMM) was used to analyze the impact of variables which could influence where a tortoise was likely to be found within transects (water presence, rock apron presence, vegetation height, percentage open ground), using the R package lme4 (Bates et al. 2015). Fence type was included as a category. The possibility of interaction terms between vegetation height and percentage open ground, between vegetation height and presence of water, and between fence type and presence of a rock apron were investigated.

Estimated number of tortoises killed

I estimated the total number of 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 tortoises (from the GLMs for each fence type) to estimate the total number of dead tortoises for each and all species.

Predictors of tortoise mortality

Regression models were fitted to predict carapace heights from SCL and scute lengths for each species (sex was not included as a category as sex could not be determined for all carcasses). All regressions were significant (Appendix Figs S1 and S2). For broken or disarticulated carcasses where carapace heights could not be measured, heights were calculated using regression equations (Appendix Table S1: Scute lengths and SCL regression equations used to predict height of tortoise carapaces. Regression equations that showed the strongest correlation were used if multiple scutes were found.

The impact of electric strand height relative to carapace height of dead tortoises was investigated as follows. Carapace heights of dead tortoises found along electric fences were scored as taller or shorter than the electric strand. The null hypothesis that electric strand height has no impact on size of tortoise killed, predicts an equal distribution of tortoises that are taller and shorter than the electric strand. A chi-squared test (with Yates' correction for continuity) was used to test the significance between observed and predicted (null) frequencies. Similarly, observed sex frequencies of dead tortoises were compared against an equal distribution of sexes using a chi-squared test with a Yates' correction for continuity.

Measurements where the electric strand height was above 400 mm were removed because they were not serving a functional purpose against problem animals (most of these were in dips of river beds). The heights of electric strands and tortoise carapace heights (of each species) were not normally distributed. Thus, a non-parametric Wilcoxon test using the R package exactRankTests (Hothorn & Hornik 2017) was used to test for significant differences between: electric strand heights where dead tortoises were found against strand heights recorded every 100 m; carapace heights of dead tortoises found along electric fences against all other tortoises (live and dead tortoises not found along electric fences); and carapace heights of dead tortoises found along electric fences against electric strand heights measured every 100 m.

Tortoise behavior

Tortoise behaviours were analyzed in relation to temperature using logistic regression GLMs, specifying a binomial distribution and a logit-link function. Feeding, mating and walking were considered to be active behaviours. A loess regression (which fits a smooth curve between variables) was run using the R package dyplr (Wickham & Francois 2016) and plotted using the R package ggplot2 (Wickham 2009).

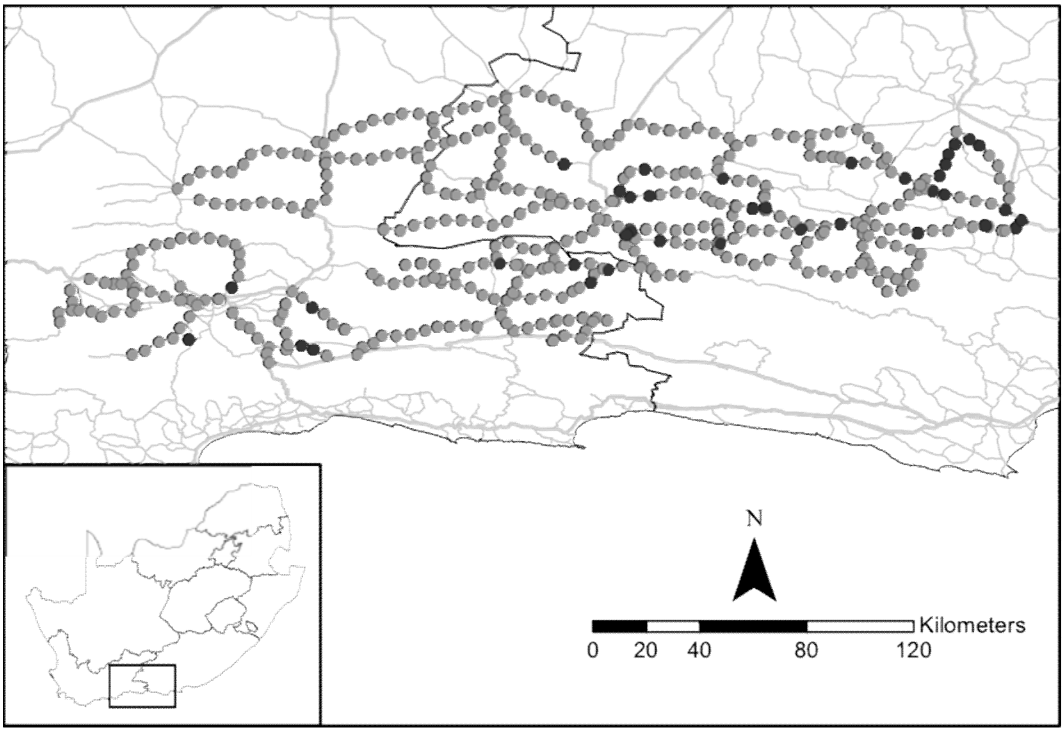


Figure 1: Map of study area showing fence distribution data. Black dots = electric fence; grey dots = lack of an electric fence. Black lines show provincial boundaries for the Western and Eastern Cape; grey lines indicate dirt or tar roads. Inset indicates the location of the study area in South Africa.

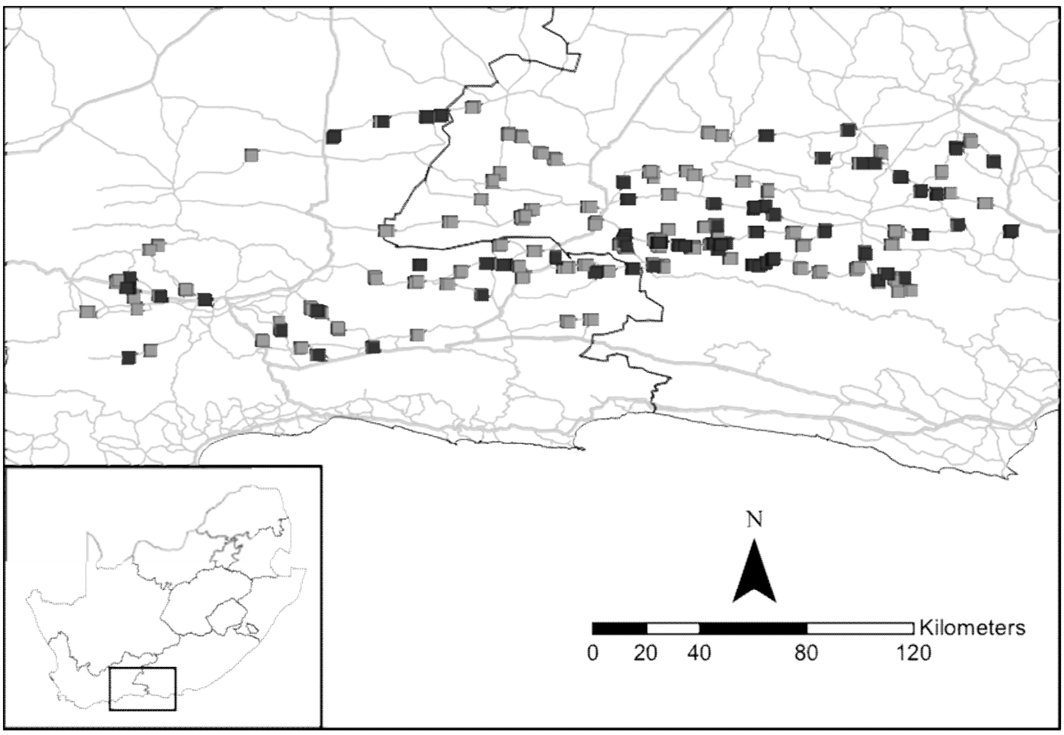


Figure 2: Map of study area showing location of transect points. Black squares indicate points where dead tortoises were found and grey dots indicate transect points where no dead tortoises were found; other conventions as in Fig. 1.

Table 1: Decomposition categories for tortoise carcasses (from Bourn & Coe 1979).

Stage	Description
Flesh intact	Tortoise recently dead; shows little to no signs of decomposition. No odour of decomposing material
Recent decay	Decomposing soft tissue with putrid odour.
Scutes present	All soft tissue decomposed with little to no odour. Most scutes firmly attached, but a couple scutes may be missing.
Carapace intact	Most scutes missing from carapace. Carapace intact, but starts showing early signs of decay. Exposed bones may be bleached white.
Carapace decay	Bones separating along sutures, but most are still connected. Carapace may have collapsed.
Fragments	Most bones separated

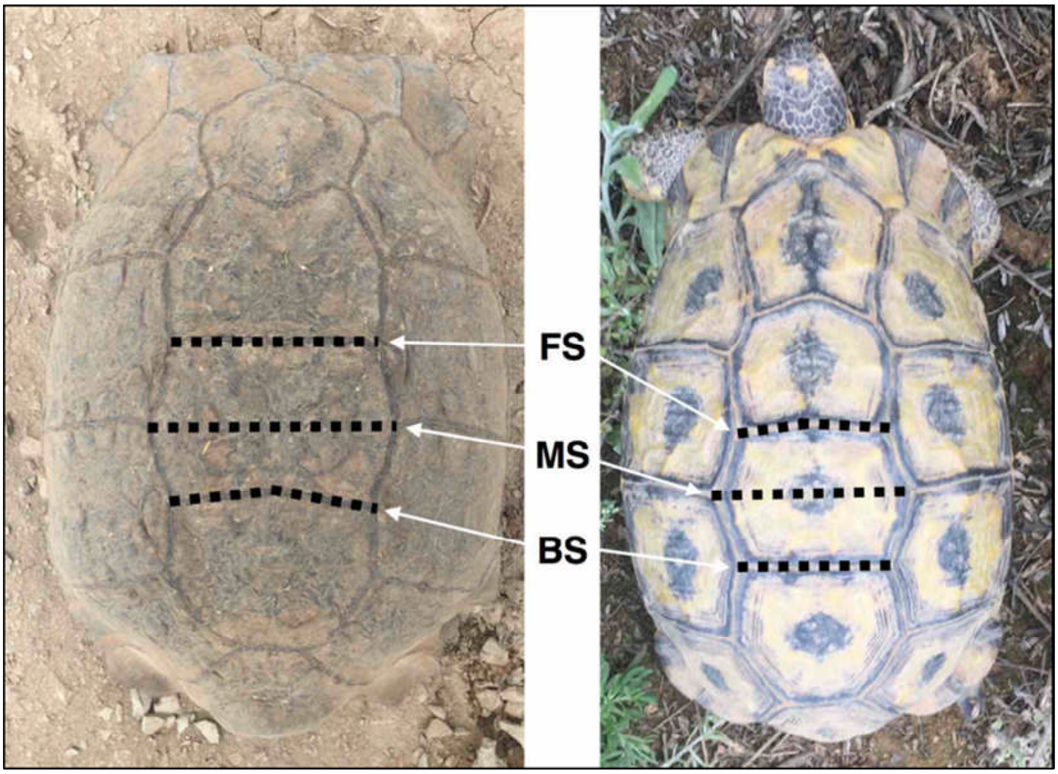


Figure 3: Dashed lines show the lengths recorded of the top three carapace scutes for leopard tortoises (left) and angulate tortoises (right). Relevant scute codes indicated by arrows (FS = length along the edge between the top front scute and top middle scute, MS = length of middle scute, BS = length along the edge between the top back scute and top middle scute).

Results

Fence type abundance

The fence distribution data consisted of 442 points spanning approximately 2200 km, each with information for both sides of the road (884 points in total). Electric fences were uncommon in the southeastern Karoo (relative proportions: electric mesh = 0.010, electric strand = 0.033) compared to non-electrified fences: mesh (0.604) and strand (0.258; Figure 4). The proportion of road verges lacking fencing (0.095) was more than double the proportion with electric fencing (0.043). Mesh fence proportions were higher than strand fences for both non-electric and electric fences. Rock aprons were uncommon as they were present on 7.2 % of fences.

Tortoise presence along fences

Transect data used in analyses comprised of 189 transects covering 163.85 km (Appendix Fig. S3). I found 403 tortoises were found on transects, only 40 of which were alive (Fig. 5). Leopard tortoises were most commonly found (344 individuals, 35 alive), followed by angulate tortoises (54 individuals, 5 alive) and tent tortoises (5, all dead). Thus, many of the statistical analyses could be done only for leopard tortoises.

The GLMs (Appendix Table S2, Table S3, Table S4 and Table S5) show that the probability of finding a live tortoise was significantly lower than finding a dead tortoise for all fence types, excluding the control (No fence transects) (Fig. 6A). Similar patterns were found in the average number of live and dead tortoises found per km, with the only exception being that the average number of live and dead tortoises were not significantly different on non-electric strand fences (Fig. 6B, Appendix Table S6, Table S7, Table S8 and Table S9). No live tortoises were found along electric strand fences. Road type was not a significant predictor for any of the GLMs and was removed from final models.

The GLMs (Appendix Tables S10, S11, S12 and S13) show that the probabilities of finding a dead leopard tortoise on an electric fence were significantly higher than finding a dead angulate tortoise on an electric fence, with no significant difference between non-electric fences (Fig. 7A). Similar patterns are seen in the average number of dead leopard and angulate tortoises found per km (Fig.7B, Appendix Tables S14, S15, S16 and S17).

The probability of finding a dead leopard tortoise on an electric fence was significantly greater than on a non-electric fence (Fig. 7A, Appendix Table S11). Electric mesh fences had a significantly higher probability of having a dead leopard tortoise than electric strand fences, but there was no difference between these fence types when they were not electrified. All fences had significantly higher probabilities of a dead leopard tortoise than open veld transects. Similar patterns were found for the average density of leopard tortoises, with the only exception being a significant difference between the two non-electric fences (Fig. 7B, Appendix Table S15). A notable observation is the two transects with the highest number of mortalities (54 dead tortoises in 1km and 45 dead tortoises in 0.7km) were on opposite ends of a single property (approximately 20km apart) which had electric mesh fences.

No dead angulate tortoises were found along electric strand fences or in open veld transects, and there was no significant difference between the probability of a dead angulate tortoise between electric mesh and non-electric mesh fences (Fig. 7A, Appendix Table S12). However, both mesh fence types have a greater probability of having a dead angulate tortoise than a strand fence. Similar patterns were found for the average density of angulate tortoises (Fig. 7B, Appendix Table S17). GLMs could not be run for tent tortoises due to paucity of data (n = 5); four dead tent tortoises were found along non-electric mesh fences and one was found dead in open veld.

Spatial autocorrelation between transects was not significant for all GLMs at smaller distances (Figure 8, 9, 10 and 11). However, live tortoises showed significant spatial autocorrelation at distances greater than 2.7° (approximately 300 km) (Fig. 8). There is no biologically meaningful reason for spatial autocorrelation at this distance. This is most likely a result of sampling clusters. Of the variables which varied within transects, only vegetation height was significant with dead tortoises associated with tall vegetation (Table 2).

Estimated number of tortoises killed

The estimated number of dead leopard tortoises across the 2200 km of roads surveyed was 1300 individuals, with 56% of these mortalities along electric fences and 43% along nonelectric fences (Table 3). Less than 1% of leopard tortoise mortalities was predicted to be on unfenced areas. The estimated number of dead angulate tortoises was approximately 630 individuals, with 93% of mortalities along mesh fences and 7% along strand fences (Table 4).

Predictors of tortoise mortality

Significantly more dead leopard tortoises were taller than, rather than shorter than, the electric strand where they were found (χ^2 = 48.9, df = 1, $p < 0.001$), with 93 being taller and 19 being shorter (Fig. 12). The same test could not be run for angulate tortoises due to the small dataset (n = 5). However, all angulate tortoises were shorter than the electric strand where found and carapace heights ranged from 60 – 100 mm.

The electric strand heights with dead leopard tortoises were significantly lower compared to the electric strand heights measured every 100 m along transects (W = 48272, p = 0.025; Fig. 13). However, when outliers > 400 mm high were removed, the result was not significant (W = 45298, p = 0.084). The carapace heights of leopard tortoises that were found dead next to an electric fence were not significantly different from those of tortoises found elsewhere (dead and alive from transects and incidental data which were not on electric fences) (W = 4930.5, p = 0.100; Fig. 14). In both cases, small size classes were represented poorly. The carapace heights of leopard tortoises not found on electric fences were significantly higher than electric strand heights measured every 100 m along transects (W = 9125, p-value = <0.001). This is reflected in the interquartile ranges (carapace heights = 190 – 235 mm, electric strand heights = 140 – 220 mm) (Figs 13 and 14). The same tests described above could not be run for angulate tortoises due to lack of data (only 5 dead animals), but all were shorter than the electric strand where they were found. Of all the angulate tortoises found, carapace heights ranged between 60 – 100 mm, with SCL ranging from 80 – 200 mm.

Of the leopard tortoises where sex could be determined, significantly more females (n = 61) were found than males (n = 26) (χ^2 = 14.08, df = 1, p < 0.001). Due to paucity of data for angulate tortoises (8 males and 4 females) the same test was not performed.

Most of the carcasses were old as the frequency increased with later stages of decomposition (Fig. 15). There was a notable increase in frequency between “scutes present” to “carapace intact” stages and again between “carapace decay” and “fragments” stages. However, this is not a linear time scale and is thus purely descriptive. Tortoise carcasses were found predominantly within the first 0.5 m of a fence (Fig. 16) with decreasing frequencies with increased distance from the fence.

Tortoise behaviour

There was a significant negative relationship between probability of recording a tortoise resting and increasing temperature (Z = -4.064, df = 168, p = <0.001). Conversely, a significant positive relationship was found between probability of tortoise being active and increasing temperature (Z = 3.283, df = 168, p = 0.001). In both cases tortoise behaviour appears to change at 20 °C (Figs 17 and 18). Of the 16 live tortoises trapped on fences, none were able to free themselves off the electric strand without assistance as all retracted in their shell, flinching with every shock.

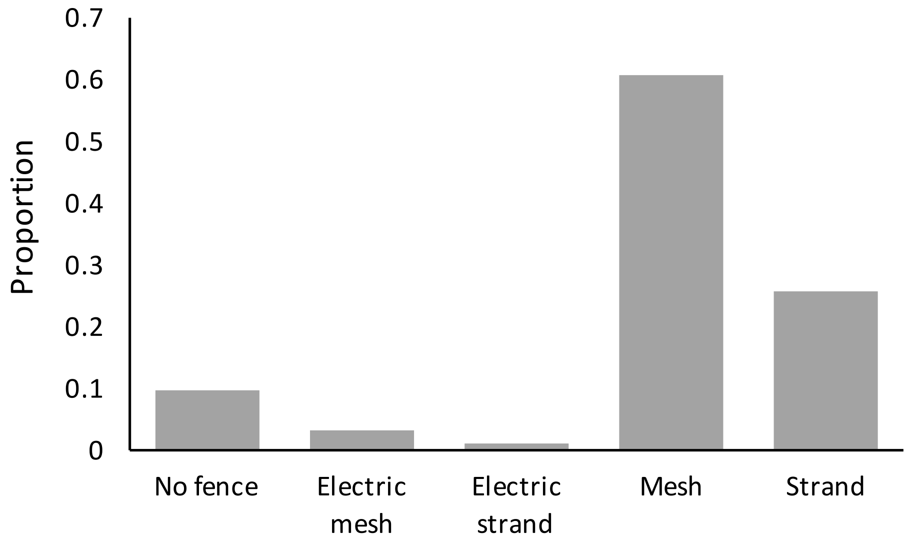


Figure 4: Proportion of fence types from points recorded every 5km along major and minor public roads, spanning approximately 2200 km in the southeastern Karoo (n=440).

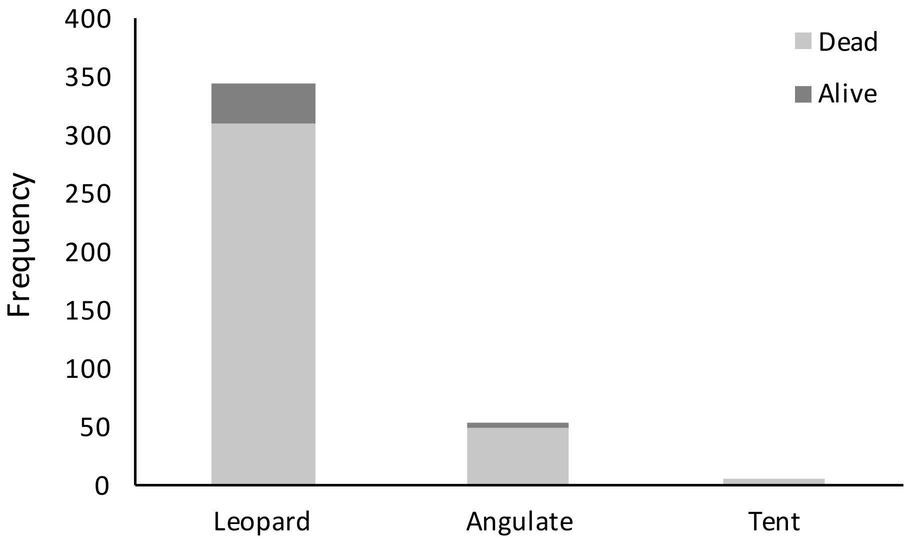


Figure 5: Encounter frequency for tortoise species along 2200km of transects walked in the southeastern Karoo during October and November 2016.

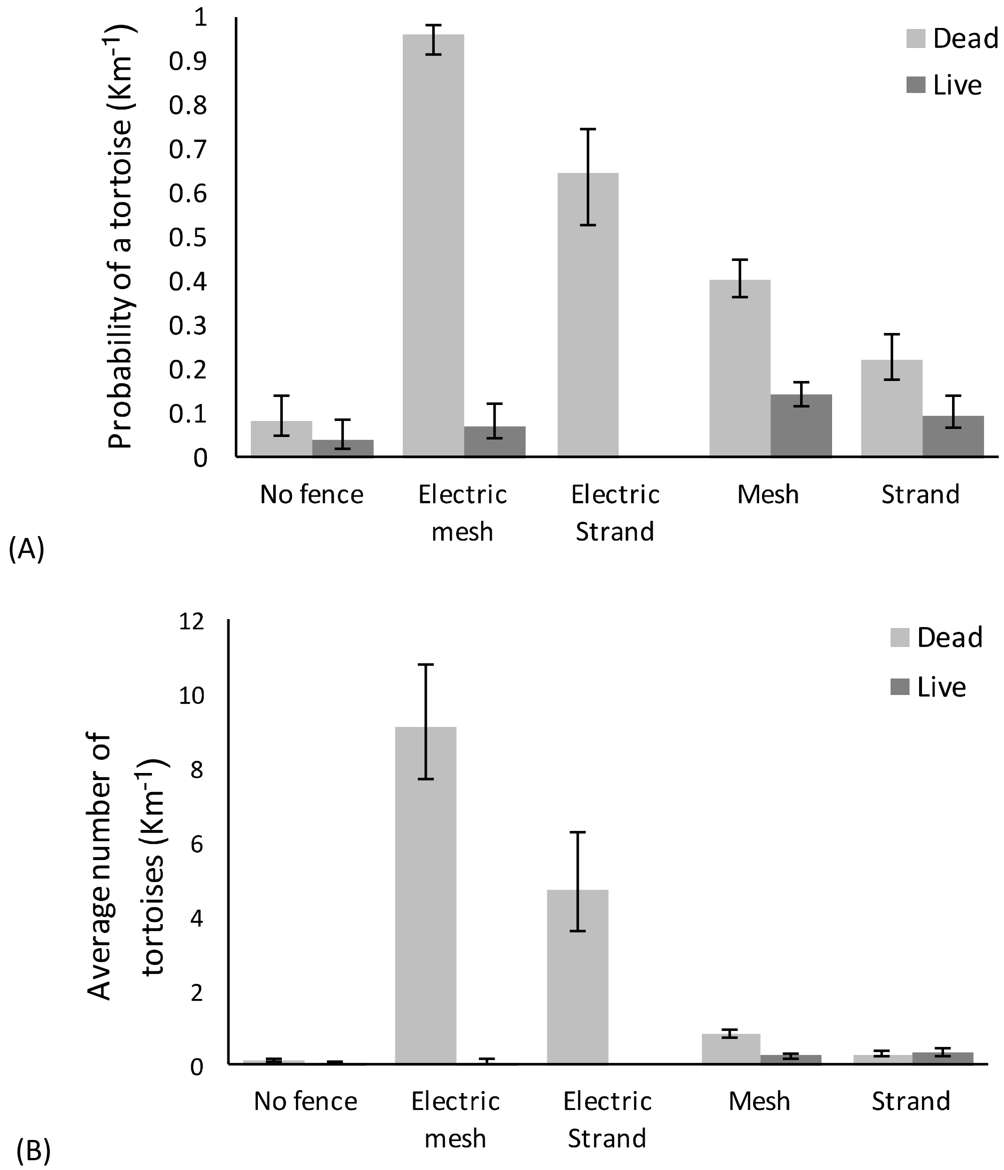
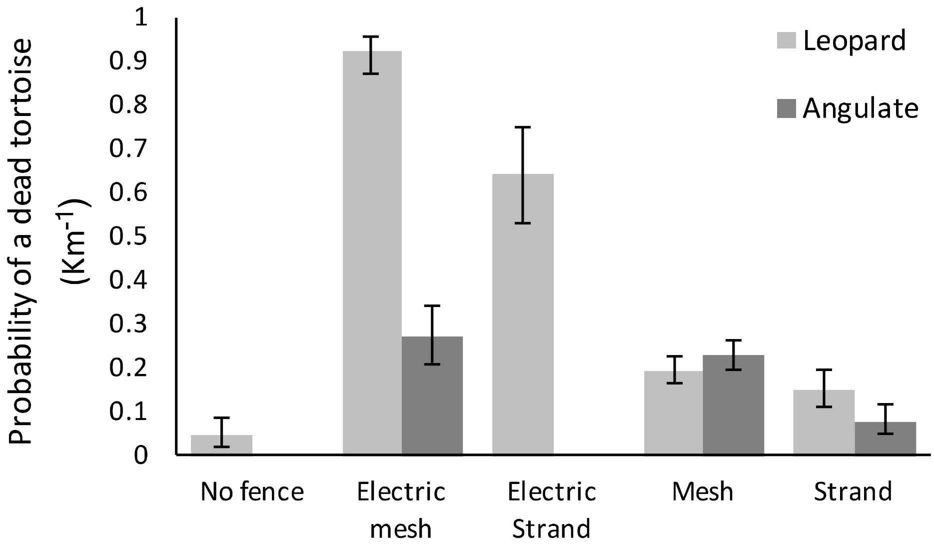
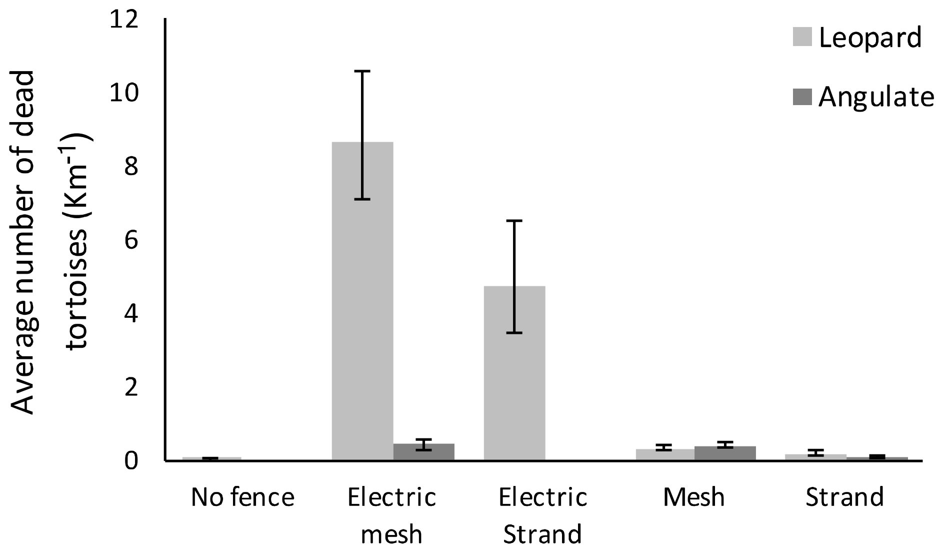


Figure 6: (A) Probability of live and dead tortoise occurrence per kilometre for each fence type. (B) The average density of live and dead tortoises along different fence types. Error bars indicate 95% confidence intervals.



(A)



(B)

Figure 7: (A) Probability of dead leopard and angulate tortoise occurrence per kilometre for each fence type. (B) Average number of dead leopard and angulate tortoises per kilometre of fence type. Error bars indicate 95% confidence intervals.

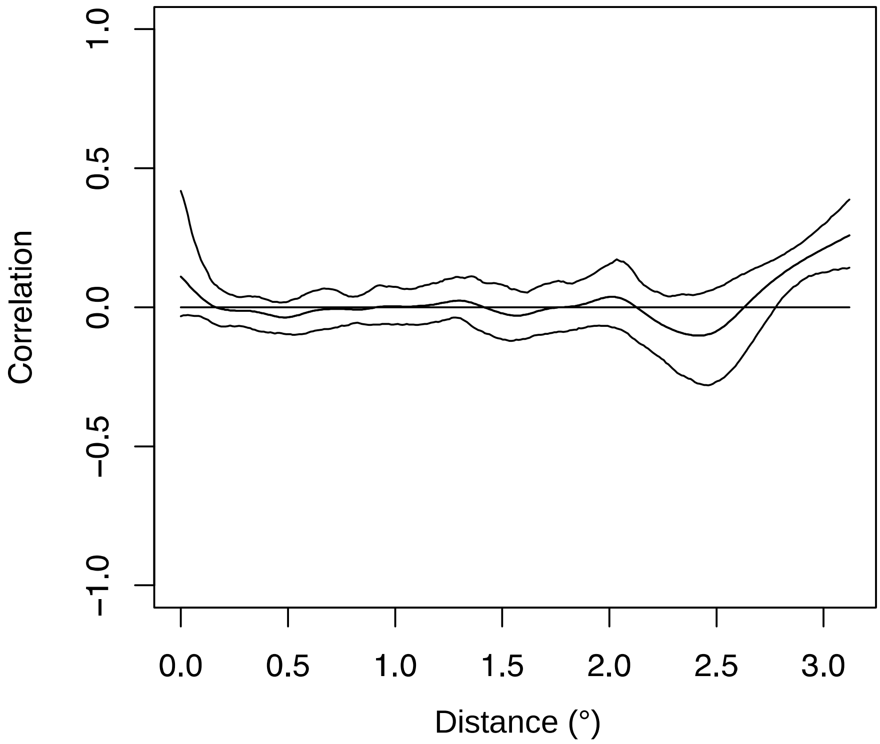


Figure 8: Spatial autocorrelation plot testing independence of transects for the GLM investigating the number of live tortoises per km.

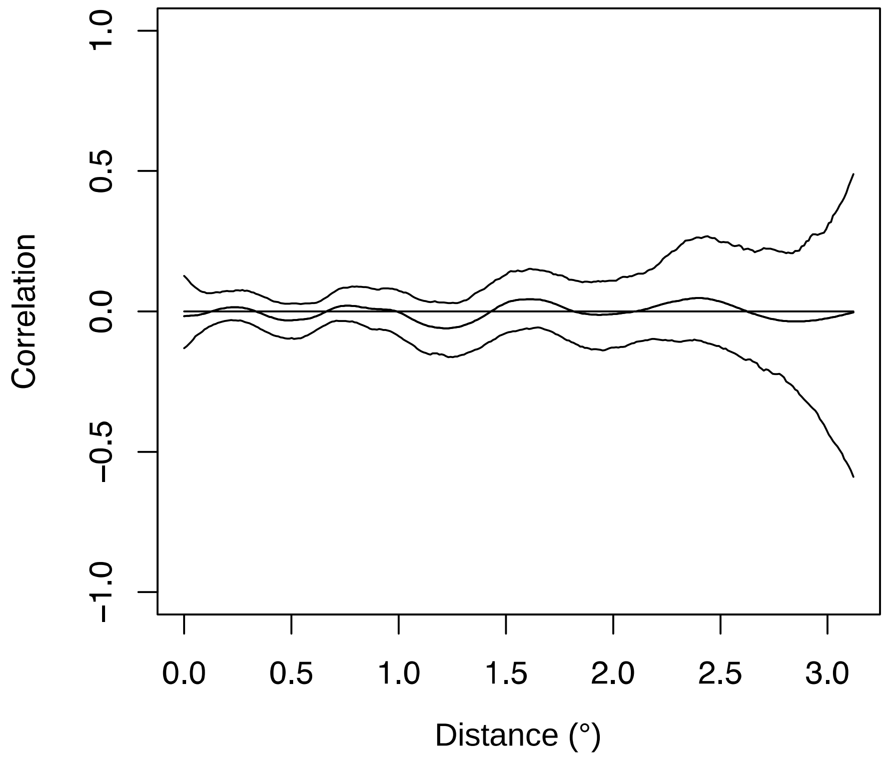


Figure 9: Spatial autocorrelation plot testing independence of transects for the GLM investigating the number of dead tortoises per km.

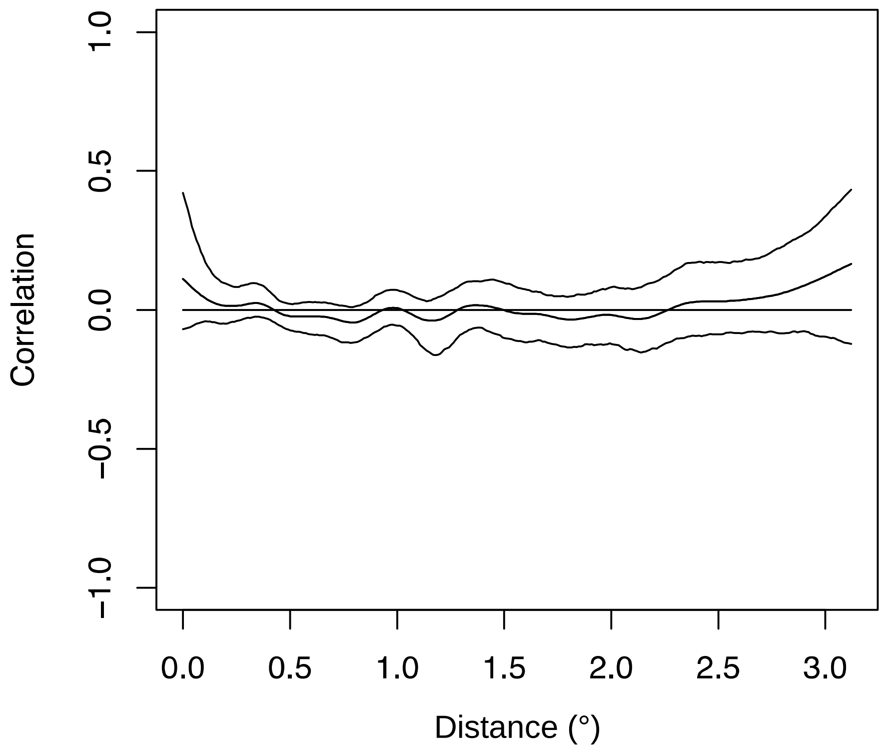


Figure 10: Spatial autocorrelation plot testing independence of transects for the GLM investigating the number of dead leopard tortoises per km.

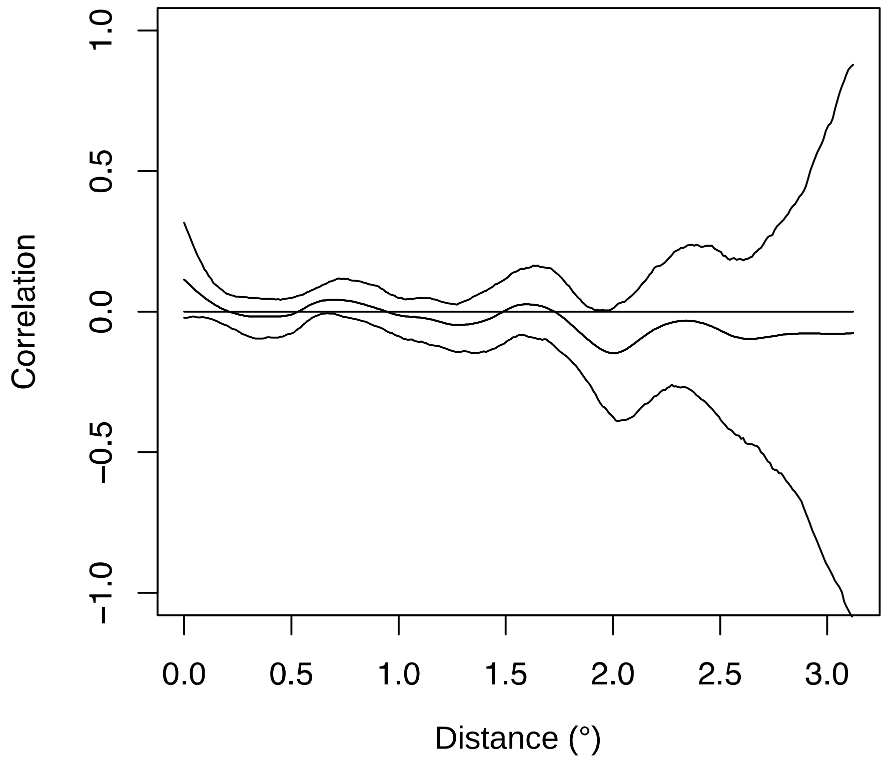


Figure 11: Spatial autocorrelation plot testing independence of transects for the GLM investigating the number of dead angulate tortoises per km.

Table 2: Statistical results for GLMM that investigated environmental and fence variables and interaction terms between variables explaining presence of a dead tortoise (df = 875).

Variable	Estimate	SE	Z	P
No fence	-7.172	1.431	-5.013	<0.001
Electric mesh	5.109	0.766	6.670	<0.001
Electric strand	4.058	0.813	4.991	<0.001
Mesh	2.194	0.749	2.931	0.003
Strand	1.204	0.813	1.481	0.139
Rock apron	1.484	1.418	1.047	0.295
Vegetation height	0.612	0.303	2.019	0.044
Water presence	1.711	2.326	0.735	0.462
Open ground (%)	0.012	0.019	0.638	0.523
Electric mesh: Rock apron	-2.758	1.485	-1.857	0.063
Electric strand: Rock apron	-20.693	209.025	-0.099	0.921
Mesh: Rock apron	-1.560	1.479	-1.055	0.291
Vegetation height: Water presence	-0.449	0.569	-0.790	0.430
Vegetation height: Open ground (%)	-0.004	0.005	-0.896	0.371

Table 3: Estimate 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
No fence	0.095	209.0	0.04	9
Electric mesh	0.033	72.6	8.67	629
Electric Strand	0.010	22.0	4.74	104
Mesh	0.604	1328.8	0.33	445
Strand	0.258	567.6	0.20	112

Table 4: Estimate of the number of dead angulate tortoises for each fence type along 2200 km of road sampled in the southeastern Karoo.

Fence type	Proportion of fence type	Length of fence surveyed (km)	Dead angulate tortoises per km	Estimated number of dead angulate tortoises
No fence	0.095	209.0	0	0
Electric mesh	0.033	72.6	0.43	31
Electric Strand	0.010	22.0	0	0
Mesh	0.604	1328.8	0.42	557
Strand	0.258	567.6	0.08	44

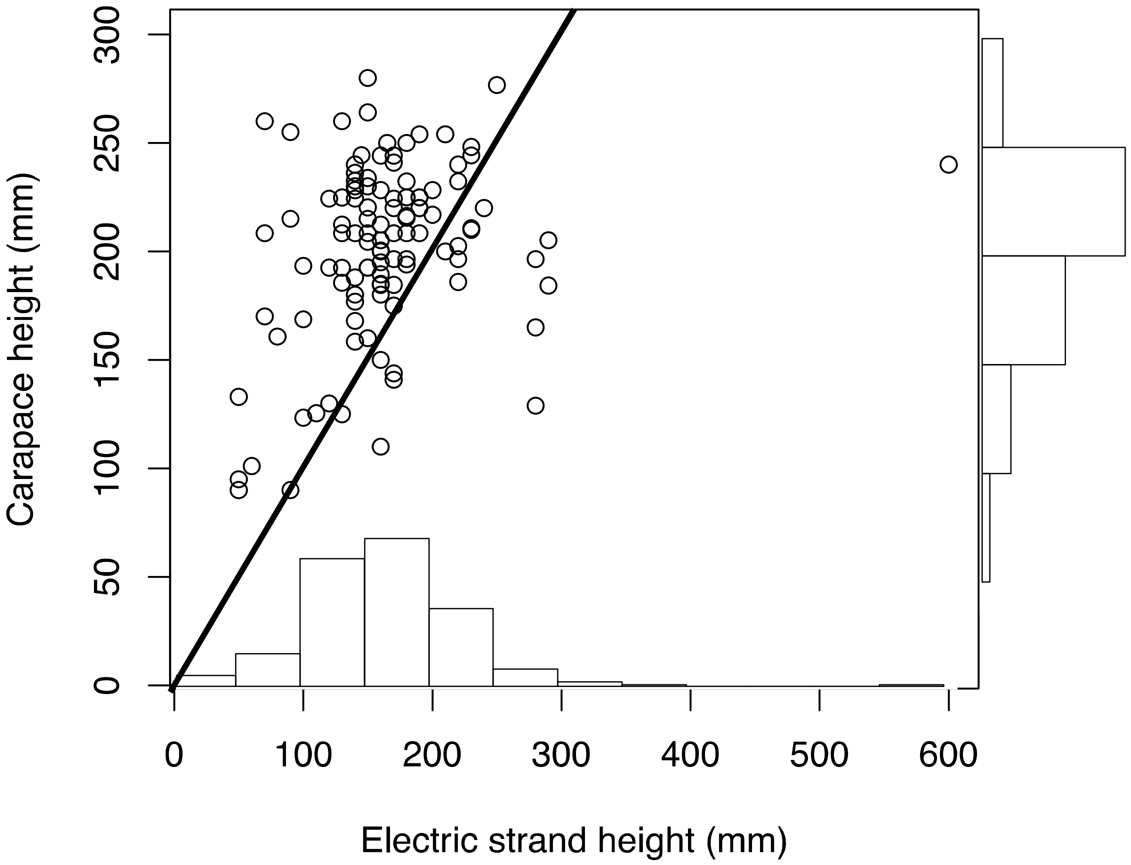


Figure 12: Plot showing carapace heights (circles) of dead leopard tortoises found alongside an electric fence with respective electric strand heights. Bars highlight distribution of points as data is heavily grouped. Line plotted is where carapace heights equals strand height ($x = y$).

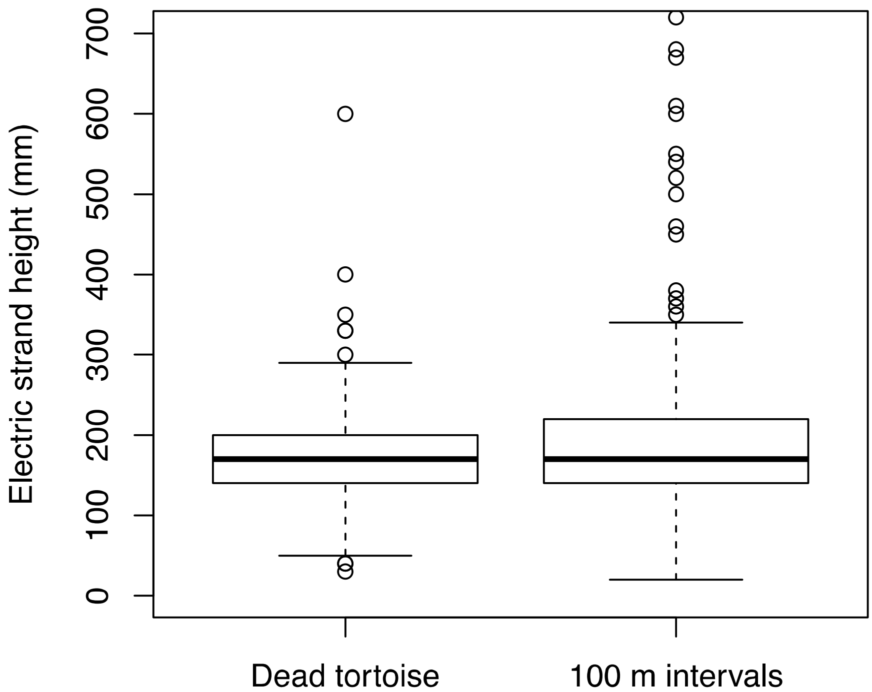


Figure 13: Boxplot of electric strand heights measured where dead leopard tortoises were found and at 100m intervals along transects. No significant difference exists when outliers above 400 mm are removed (W = 45298, p-value = 0.0842).

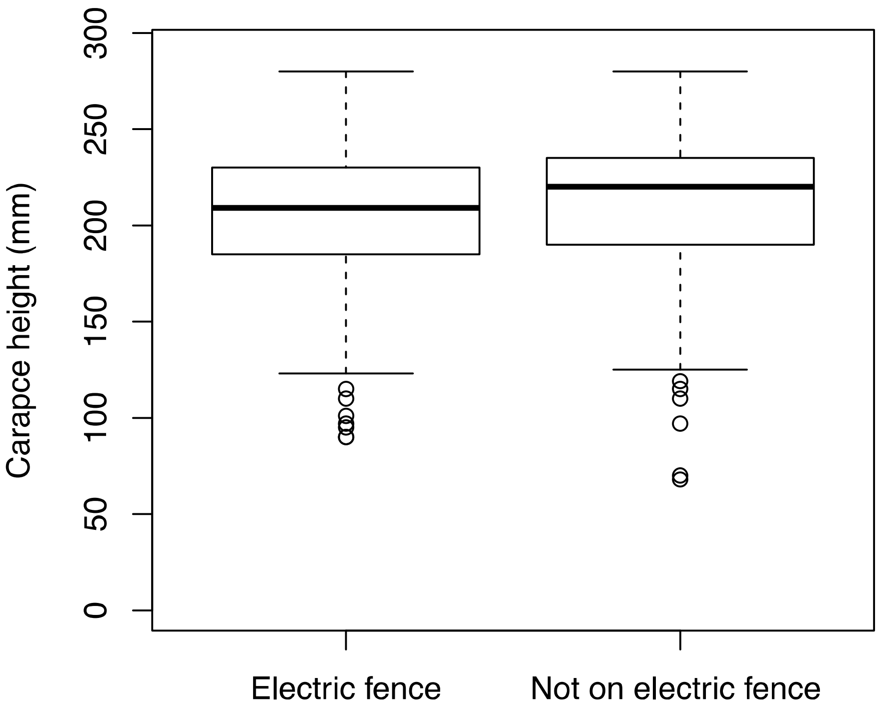


Figure 14: Boxplot of carapace heights of leopard tortoises found dead on electric fence transects and all other leopard tortoises recorded not on electric fence (incidental and transect data, dead and alive). No significant difference exists (W = 4930.5, p-value = 0.10).

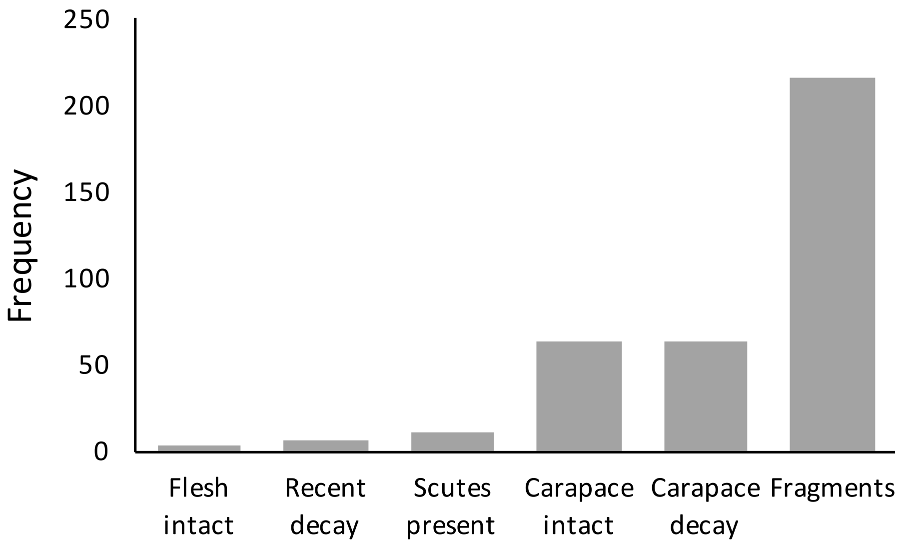


Figure 15: Frequency of various stages of decomposition for dead tortoises found during surveys.

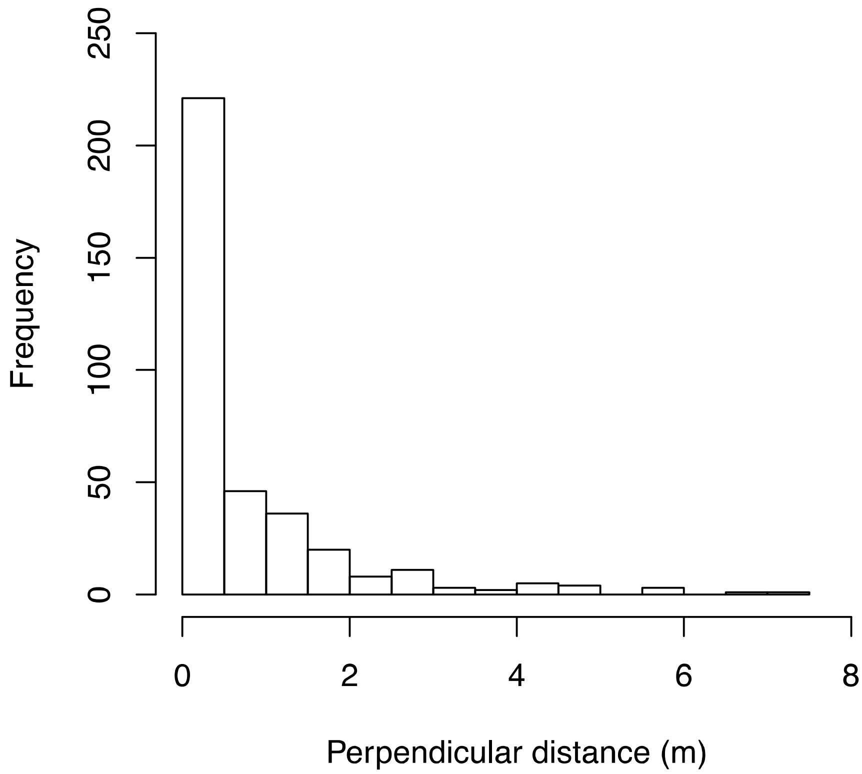


Figure 16: Histogram of tortoise carcass distances to fence, for data used in GLMs analyses.

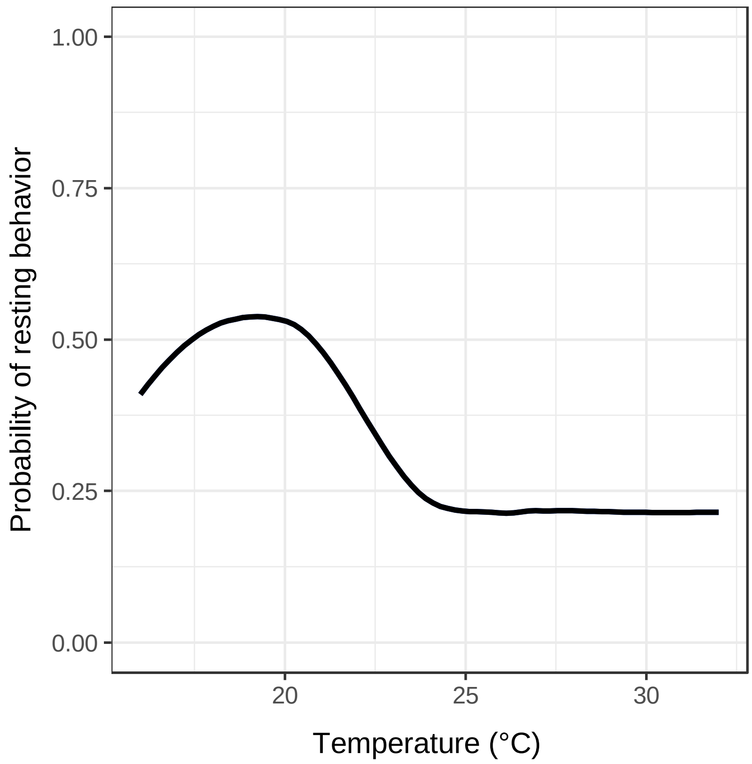


Figure 17: Probability of tortoises resting behavior in relation to temperature. Black line indicates calculated probability using loess regression and grey area highlights 95% confidence intervals.

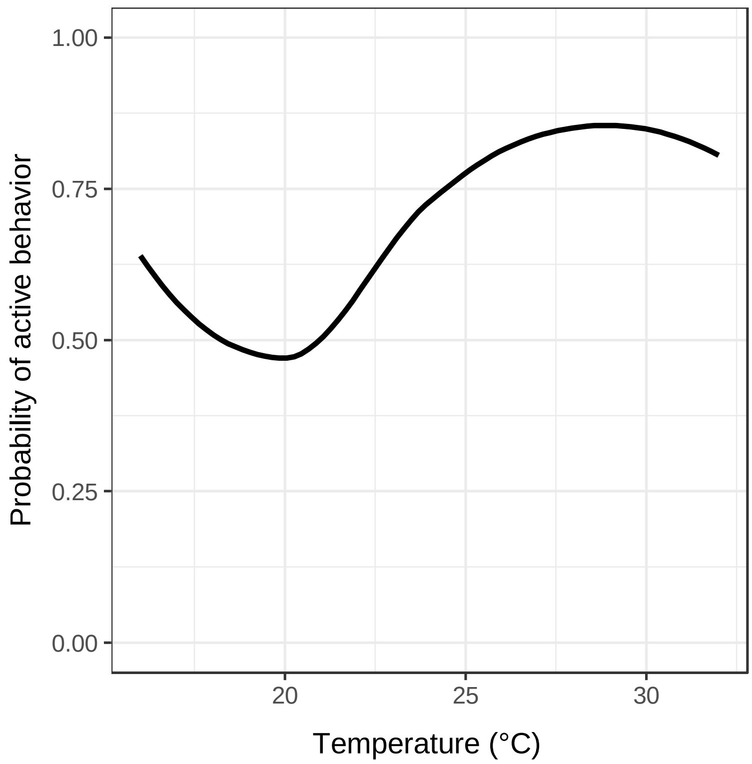


Figure 18: Probability of tortoise active behavior in relation to temperature. Black line indicates calculated probability using loess regression and grey area highlights 95% confidence intervals.

Discussion

Tortoise mortalities along fences

Mortality along electric fences was the highest of the different categories, as hypothesized in the introduction given findings of Burger & Branch (1994) and Beck (2010). However, this is the first time that tortoise mortalities have been reported along non-electric fences. Fence structure also is important because mesh fences cause more tortoise mortalities than strand fences, regardless of whether the fence was electrified or not. With significantly more dead tortoises being found along all fence types than open veld transects, it highlights the potential danger that fences present to tortoises. However, different tortoise species were affected differently by fence types.

<u>Leopard tortoises</u>

My findings support those of previous studies (Burger & Branch 1994; Beck 2010) that leopard tortoises are more heavily impacted by electric fencing than are other species and underline the danger of increased electric fencing to leopard tortoises. Mortality along electric mesh fencing was higher than along electric strand fences, possibly because the mesh is more of a barrier to the tortoise, making it harder to escape. In addition, this study highlighted the threat posed to large tortoises and hence the importance of the height of the lowest electric strand. A tortoise's carapace height needs to match or be taller than the height of the electric strand to remain part of the circuit once it retracts its legs, thus larger tortoises are more prone to electrocution (it is important to note that not all deaths are caused by electrocution). However, the size distribution of tortoises found along electric fences were not significantly different to all other leopard tortoises found. This results from electric strands being lower than the carapace heights, thus placing the majority of leopard tortoises in this study area at risk of electrocution. It is important to note a potential survey bias towards larger tortoises as they are easier to detect.

As tortoise shells are rounded, any shell, irrespective of its size, typically would make contact before the maximum height of the carapace. If they dropped immediately, they would not remain part of the circuit. This implies that tortoises either continue to walk after the initial shock, or their momentum carries them forward to where they become part of the circuit. If the tortoise's carapace height is taller than the height of the strand, it could scoot forward and become part of the circuit. If lower than the electric strand height, it could be safe from electrocution if it scooted forwards. However, it may also become trapped between the fence and the electric strand, and be shocked somewhere else along the fence as it tries to find a way through.

The two transects with the highest number of mortalities were outliers when compared to the average number of dead tortoises predicted (Fig. 6B), but highlight the danger electric fences can pose to leopard tortoises in small areas. In one instance, I recorded the electric strand caused an open bleeding wound in the carapace, where the electric pulses would sputter the blood (Fig. 19). This observation was not reported by Burger & Branch (1994) who described in detail the effects of electric fences on the tortoise's body.

Leopard tortoise mortality rates along non-electric fences were higher than natural mortality rates estimated from open veld transects. However, the cause of death of these large leopard tortoises along non-electric fences could not be determined (Fig. 20). These previously unaccounted leopard tortoise mortalities along non-electric fencing should be recognized as an additional threat to leopard tortoises. These tortoise mortalities along non-electric fences may also explain the dead tortoises on electric fences where carapace height was shorter than the electric strand (Fig. 12). However, these tortoises may have been shocked when they stood to walk, unable to escape and may have been compromised by heat exposure.

Despite forming only approximately 4 % of all roadside fencing, electric fences account for 56 % of leopard tortoise mortalities in this study. This validates the concern for increased electric fence use in the future and the potential impacts on leopard tortoises (Beck 2010; Farber 2016). Although non-electric fences had significantly fewer leopard tortoise mortalities per km, the predominance of non-electric fencing (specifically mesh fencing) makes them a comparable threat (43 % of mortalities) to electric fencing considering current fence distribution.

Although the population was not sampled sufficiently for reliable population demographics, the skews found in dead tortoises (towards larger sizes and more females) have also been reported in other leopard tortoise population studies (Grobler 1982; Mason et al. 2000) including in the Nama-Karoo Biome (McMaster & Downs 2009). Although this may be due to differential longevity of carcasses or larger carcasses being easier to find, only 12 leopard tortoises were comparable in size to angulate tortoises (Appendix Figs S1 and S2). With fences killing larger reproductive individuals, there is concern that additional fence mortalities may reduce recruitment and threaten future populations as suggested by Beck (2010).

The threat posed by fencing may extend to the ecosystem as the ecological role these tortoises play is reduced or lost. Milton (1991) found that leopard tortoises eat 75 species of grasses, succulents and forbs belonging to 26 plant families. Germination trials suggest that leopard tortoises disperse seeds of Aizoaceae, Chenopodiaceae, Crassulaceae, Cyperaceae, Fabaceae, Poaceae and Scrophulariaceae and could thus play an important role in shaping the unique flora found in the Karoo (Milton 1991). In addition, many of the succulents that leopard tortoises eat are avoided by sheep, goats and indigenous antelope that are unable to metabolize the toxins in these plants (Milton 1991, Milton et al. 1999).

<u>Angulate tortoises</u>

Although it is possible for angulate tortoises to be electrocuted, they are generally small enough to pass under the lowest electric strand. The largest angulate tortoise heights (100 mm) are well below the interquartile range of the electric strand heights measured (140 – 210 mm) making electrocution a rare occurrence. Angulate tortoises are also less likely to be affected by strand fences as their smaller size allows them to pass through easier than large leopard tortoises. Angulate tortoises found in this study were smaller than the largest SCLs for the species stated by Alexander and Marais (2007). However, angulate tortoises in the eastern areas of their distribution (including the study area) are small, rarely exceeding 220 mm in length (Branch 1998).

Angulate tortoises apparently are more affected by mesh structure of fences than by the electrified strand. When an angulate tortoise tries to pass through the mesh, it becomes trapped if the mesh size is slightly smaller than the tortoise's body height (Fig. 21). Once wedged in the mesh, they lack the strength to escape. The same issue likely affects other small tortoise species and young leopard tortoises. For example, all but one dead tent tortoise was found along mesh fences.

Approximately 64 % of all roadside fences have mesh structures and account for 93 % of angulate tortoise mortalities. This high risk of mesh fences should be considered for angulate tortoise populations. Perhaps mortality rates are genuinely low along some fence types as none were found, but the need for future studies to build on this dataset is vital to fully understand the impact of fencing. This is even more relevant when considering the rarer tortoise species.

Although the estimated number of dead angulate tortoises likely to be found along the 2200 km of roads sampled is considerably less than leopard tortoises (Tables 4 and 5), it does not mean that these deaths can be disregarded. Furthermore, this may be an underestimate, as smaller tortoises are not as easily found compared to large leopard tortoises, so the relative threat of mesh fencing on angulate tortoise may be underrepresented.

Although patterns in angulate tortoises could not be identified, the same population skews as those for leopard tortoises (more adults and more females) have been reported (Mason et al. 2000). Small angulate tortoises would be difficult to locate and are unlikely to be affected by any fence, explaining why none were found. Angulate tortoises found in this study were smaller than expected, which raises concern as to why no larger tortoises were found alive, on non-mesh fence types or by chance. Considering mesh fences are so predominant, mesh fences may be removing reproductive angulate tortoises and prevent them from growing larger, which may threaten populations. However, this may be a result of regional differences in size.

Other tortoise species

Only five tent tortoises and no padloper tortoises were found. Although these tortoises are known to be rare and occur in low abundances (Alexander & Marais 2007), it was expected that a few would be encountered. However, concern has been raised about increased avian predation on these smaller tortoises and the resulting impacts on their populations (Fincham & Lamberts 2014; Loehr 2017). The roles these tortoises play in the ecosystem is not fully understood, but may be similar to leopard tortoises.

Causes of mortality

This study investigated the probability of finding tortoises along fences, but the causes of mortalities could not be determined. It is likely that some mortalities were not caused by fences (e.g. natural deaths, vehicle accidents, predation). Considering that most tortoise carcasses were found on or within 0.5 m of the fence and given potential disturbance by scavengers or people, it is likely that the fence had an impact whether it be direct (previously discussed) or indirect.

One potential indirect reason for mortalities clustering along fences could simply be a result of increased tortoise presence along fences. This is supported as all fence types had higher probabilities of live tortoises than open-veld transects, with only non-electric mesh fences being significantly higher. If non-electric mesh fences are barriers to tortoises, it can be expected that they would spend longer along a fence than in open veld. Perhaps with a larger dataset, other fence types may tend towards significance. Grobler (1982) describes how some tortoises will move more than 5 km, thus will likely come into contact with a fence. Milton (1992) reported that leopard tortoises feed on vegetation types that occur along areas of disturbance in the Karoo, such as road verges or water points used by livestock. Although all fences in this study were along roads, fences are also points of disturbance with fence installation and maintenance. Road verges may also be preferred habitat as they are free from grazing pressure. In addition, tortoises like many animals prefer to walk along paths of least resistance (e.g. where vegetation has been cleared), which is often seen along fences as game trails, roads or maintenance paths (Figure 22) (Burger & Branch 1994).

Farber (2016) reported concern for tortoises unable to cross fences to access resources. Fences separate different land practices, which may differ in vegetation (Figure 23) creating incentive for tortoises to attempt to cross fences. Other incentives include access to water (Milton 1991; Milton et al. 1999; Farber 2016), which is important to consider given recent drought in the area. Tortoises may also have been trying to gain access to mates as it was breeding season. Tortoises will walk along fences (Figure 22) where they are likely to be killed by the fence or by another cause (Burger & Branch 1994; Ruby et al. 1994, Milton et al. 1999; Beck 2010), until they find a way through. This raises questions of a fence's permeability. Leopard tortoises were observed to squeeze between strands of some fences or make use of holes in fencing caused by problem animals (Figure 24).

Another potential indirect impact of fences could be increased avian predation on tortoises. Fences may provide look-out posts for crows and other predatory birds, increasing hunting pressure (Chavez-Ramirez et al. 1994). However, the carapaces of small predated tortoises would not be represented in this study as pied crows carry small prey back to their nests or suitable pecking substrates. This primarily affects small tortoises which may further explain the low frequencies of smaller rare tortoise species and the demographic skews towards larger tortoises.

Dead tortoises appeared to be grouped, as several tortoises were often found in less than 15 m of each other (Figure 25), which may indicate local factors in determining tortoise presence. Grobler (1982) states that tortoises take refuge under vegetation as most were found in a valley with green foliage and water. Many tortoises were observed frequenting man-made sources of water and were often found along dry river valleys with tall or thick vegetation. However, vegetation height was only significantly positive in describing the presence of dead tortoises. Considering that the carcasses in Fig. 25 are at different stages of decomposition, a suggested theory that requires further investigation is tortoises are attracted to the smell of dead tortoises.

All fences walked in this study were along roads, so mortality rates as a consequence of road accidents, which are common in the Karoo (Milton et al. 1999), needs to be considered. However, road type was not significant in describing presence of tortoises. Road verges were often large, with distances between fence and road often exceeding 2 m. Most carcasses found were closer to the fence and carcasses were readily found on both sides of fences, but this may be partly due to greater observer vigilance along the fence line. In addition, road collisions often occur at high speed resulting in the tortoise carapace being broken apart. The clustering of carcass fragments and intact carcasses recorded indicate that road collisions were unlikely cause of death for majority of carcasses found. However, we should account for these variables in future studies.

Another possibility of tortoise mortality may be human-induced mortalities. Although no carcasses could be conclusively identified as human related, some carcasses had questionable punctures in the carapace (Figure 26). These holes were not a result of decomposition as the carapaces were otherwise intact, scutes were still attached and were not warped by sun damage. These holes also did not occur along carapace bone sutures. Human-induced mortalities have been reported in several studies and with varying rationale. Boycott & Bourquin (2000) report that some farmers believe leopard tortoises compete for grazing against domestic animals. Milton et al. (1992) reports that tortoises urinate and drown in drinking troughs, spoiling water sources meant for livestock. Personal communications with landowners suggest that large leopard tortoises may enlarge and round holes fences caused by other animals when trying to pass through a fence (Figure 24), although no reports exist of tortoises making the initial holes (Kesch et al. 2014). Other reports suggest that farmers are concerned that tortoises spread ticks, potentially carrying diseases to livestock and game (Boycott & Bourquin 2000; Milton et al. 1999). All these motives relate to losses of livestock and other economic costs. Not all farmers hold such negative attitudes towards tortoises many landowners have an affinity for tortoises and go to great lengths and personal cost to prevent tortoise mortalities (discussed in mitigation strategies). In addition, I spoke to several landowners that mark tortoises to keep a record of populations and individual tortoises on their properties.

Suggested mitigation strategies

Electric strand height

By raising the minimum height of the electrified strands to 200 – 250 mm, unintentional animal mortalities including those of tortoises may be reduced (Burger & Branch 1994; Beck 2010). Although this would not prevent all mortalities, significantly fewer leopard tortoises were found killed by higher strands (Beck 2010). All other South African chelonian shell heights are lower than 200 mm (Burger & Branch, Alexander & Marais 2007), thus would be safe from electrocution. However, raising electrical strand height is impractical from the perspective of problem animal control as the low-lying electric strand is what prevents animals from digging under the fence. Burger & Branch (1994) describe the effectiveness of their strand height suggestion at deterring porcupines and bushpig, but do not mention jackal, which are renowned for digging under barriers (Kesch et al. 2014). Thus, this suggestion is poorly implemented (median strand height 170 mm) and has created tension between farmers and conservationists (Pietersen et al. 2014; Woodroffe et al. 2014).

Rock aprons

Rock aprons are used to prevent animals digging under fences as rocks will fall in place of dispersed soil (Beck 2010). It is also thought that they may prevent tortoises from coming into contact with electrified strands as tortoises are unable to climb over rocks (Beck 2010). Although Beck (2010) did not directly investigate the effectiveness of rock aprons in preventing tortoise and other animal mortalities, he did note that only a single chelonian mortality was recorded at Pilanesberg National Park. He attributed this low mortality rate to the rock-packed apron and concluded that rock-packed aprons may be a viable and more eco-friendly mitigation strategy than electric strands. However, rock aprons were poorly implemented in the southeastern Karoo as they were only present on 7 % of fences.

In this study rock aprons did not have a significant affect in describing the presence or absence of a dead tortoise, and individual observations contradicted Beck's (2010) conclusions. Tortoises are able to climb over rock aprons or find a way around them. In cases where tortoises climb rock aprons, the effective electric strand height is lowered, effectively placing smaller tortoises at risk of electrocution (Figure 27A). If a tortoise does manage to pass the rock apron, there is a risk of the tortoise becoming trapped between the fence and the rock apron (Figure 27B). A rock apron may also hinder an angulate tortoise's ability to escape a mesh fence (Figure 21B). Additionally, rock aprons are openly accessible for crows to drop juvenile tortoises as they attempt to break their carapace (Branch 1998). I thus find no evidence that rock aprons are an effective mitigation strategy.

Electric fence switches

The use of switches on electric fences can control intervals when the electric fence is on and off. These can be programmed to specific times, set to randomizers or use regulated cut-off controls (e.g. solar or thermostatic switches). The rationale for the use of these is that it may provide an opportunity for tortoises to recover and escape from electric fences (Burger & Branch 1994; Beck 2010). Field ranger anecdotes from Burger and Branch (1994) say that tortoises may survive up to an hour or longer once caught on an electric fence. Some land owners suggested that tortoises may survive longer than 24 hours. This has not been quantified due to ethical issues with specific trials, but is likely to vary on many factors (voltage, temperature, sun exposure, etc.).

However, farmers expressed concern that switching fences off periodically causes them to lose their effectiveness at deterring predators and other problem animals because the animals learn when the fence is on or off. However, most problem animals are nocturnal and pose minimal threat to livestock or game during the day. One landowner using a solar switch reported a reduction in tortoise mortalities and experienced no increased predation on his livestock. On the kilometre-long transect walked on his property, only three tortoises were found, all of which were old carcasses (fragment stage) where only a few fragments no longer white in color were found.

The behavioral change of tortoises in relation to temperature found in this study may highlight how effective thermostatic switches on electric fences could be implemented without compromising effectiveness. Below 20 °C, tortoises remain inactive and would unlikely move away from the electric fence when it is off (Figure 17). Conversely, the probability of active behavior increases above 20 °C thus increasing the chance of a tortoise escaping the strand (Figure 18). If an electric fence is set to switch off at temperatures above 20 °C, it would maximize time the electric fence stays on, whilst giving tortoises the best opportunity to escape. Average night temperatures are well below 20 °C in the hottest months, thus the electric fences will remain effective against nocturnal problem animals. Tortoises would not be at risk of electrocution in winter when average midday temperatures are below 20 °C because they would be inactive. This is supported by Beck (2010) who found no tortoise mortalities along electric fences between May and August in a four-year period.

Barriers in front of fence

Burger and Branch (1994) suggest barriers in front of a fence may reduce tortoise mortalities as they won't be able to reach the fence. However, they also state it may decrease the effectiveness of the fence as animals would dig before the fence and not make contact with the electric strands. It may also be impractical and expensive to set up and maintain (Burger
& Branch 1994). Personal observations found that *Vachellia* branches were often laid down along a fence and compacted, which may act as barriers, but no data or reports were collected to measure the effectiveness of this measure.

Voltage control

By lowering the voltage of electric fences, it is thought that the lethality of such fences would decrease (Burger & Branch 1994). However, electric fences are used to control animals larger than tortoises, so lowering the voltage is impractical. Cape Nature (2014) suggests a minimum of 6000 V for electric fences. However, fence designs implementing a gradual voltage increase could prove useful if there was a wire apron extending from the base of the fence outward with voltages increasing closest to fence (Burger & Branch 1994). Animals would turn away when voltages become uncomfortable (Burger & Branch 1994). Unfortunately, these designs are expensive to install and maintain, and are thus generally impractical.

Physical checking of fences

One landowner who was fond of tortoises, and was aware of the impact of his electric fencing, took the initiative to employ staff to remove tortoises from his electric fence. They patrol the electric fences surrounding the property and remove any tortoises trapped by the electric fence. This comes at great economic cost with no inherent benefit to the farm. In the first two weeks of October 2016, 22 tortoises were saved. Unfortunately, the length of fencing was not reported. In this case, installing a switch for the electric fence (such as a thermostatic switch), could be beneficial to the farm and tortoises. Staff who patrol fences when the fence is on would be available for other jobs when the fence is off.

Fence design

My results indicate that strand fences have fewer tortoise mortalities than mesh fences. However, strand fences are more permeable than mesh fences, not only for tortoises, but also predators and problem animals, which may explain why mesh fences are more widely employed, despite their greater input costs. A study investigating desert tortoise responses to barriers found that the most effective was a screen mesh with opening small enough to exclude a tortoise's head (Ruby et al. 1994). The same mitigation strategy could be applied to South African fences, which would prevent angulate and similar tortoises becoming trapped in mesh fences. However, the extra metal in the fence may prove costly. Conversely, a fence with larger openings such as 150 mm tall would allow angulate tortoises (maximum height found 100 mm, but angulates found in this study were smaller than expected) and other small tortoises to pass through freely whilst still being small enough to prevent problem animals from squeezing through.

Underway tunnels

Underway tunnels and eco-passages that reduce mortalities along roads (Ruby et al. 1994; Baxter-Gilbert et al. 2015) could be used to reduce mortalities along other barriers. Ruby et al. (1994) found that desert tortoises easily passed through fences when openings of an appropriate size were available. However, Baxter-Gilbert et al. 2015 found that eco-passages were ineffective when alternative crossing options are available (such as holes in a fence). No such experiments have been attempted in South Africa. Due to the large size of leopard tortoises, it may be impractical to construct large tunnels under fences, which would also be used by problem animals. Smaller tunnels may prove useful for smaller tortoise species if built from strong material (e.g. concrete) to prevent other animals from damaging or enlarging it. They would have to be large enough to prevent angulate tortoises becoming trapped, as they did in mesh fencing. If such eco-passages are used in conjunction with suggested improvements to fence design, it could negate many of the negative impacts of fencing described in the introduction for small tortoises. Such materials may be expensive but it may be beneficial for protected areas focused on conservation to implement such measures where threatened tortoise species are found, not only in the southeastern Karoo but globally.

Removal of fencing

Removal of fences is the most effective way to reduce tortoise mortalities associated with fences. 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 (such as in Ithala and Pilanesberg) has helped to restore large mammal populations (Woodroffe et al. 2014). Fence removal could have the same effect for tortoise populations and is a worthwhile avenue for further studies.

Farmland is being converted to wildlife habitats and conservation in the Karoo due to social and economic drivers (Brandt & Spierenburg 2014). In addition to the social and economic drivers, other incentives such as the Cape Stewardship Programme further promote land conversion and restoration. This opens opportunities to study any impacts of fence removal on tortoise populations. Instead of fencing large areas, fencing could be used to enclose only small areas of human-wildlife conflict such as livestock paddocks, settlements and grain stores (Woodroffe et al. 2014). Other alternative approaches to fencing include traditional farming practices such as crop guarding, livestock heading and planned grazing (Woodroffe et al. 2014).

Problem animal control

Electric fences are primarily used to control predators and many farmers also actively control predator populations through culling or hunting (Watson et al. 2008; Todd et al. 2009). The effectiveness of culling is debated as jackal may have larger litters and more female pups in response to lower population sizes (Conradie 2015). However, non-lethal methods such as stock collars, use of guard dogs or shepherds may be implemented (Todd et al. 2009) and have been shown to be economically advantageous compared to lethal methods of predator control (McManus et al. 2015). The use of virtual fences has proven successful for some species such as scent marks for wild dogs (Jackson et al. 2012) and could be applied to other predators. If predators can be successfully managed it may reduce the need for fencing. Salomon (2013) suggests that herding could be preferred over fencing for several reasons, including the possibility of advertising predator-friendly livestock products.

Collaboration

Conflict and tension between landowners and conservationists need to be resolved in order to promote collaboration in solving issues. Conservationists need to understand and account for landowner's values and goals, so that wildlife sensitive land-use planning can be formulated, taught and implemented by landowners. The Karoo Predator Project is an example of how predator conflict research is expanding into a multi-disciplinary to involve biological, economic and social sciences to further understand issues landowners face (Karoo Predator Project 2017). However, working together may be challenging as livestock farmers in the study area showed a dislike towards conservation groups because they see conservationists to be a threat to their livelihood as they protect problem animals and try to dictate how farm land should be managed. Some livestock farmers were angered by the news article (Farber 2016) as the mitigation strategies suggested were impractical and could come as a personal cost. There is a strong feeling amongst farmers that they are unfairly labeled as the "bad guys", which further hinders their willingness to work in conjunction with conservation efforts. Farmers move dead tortoises off electric fencing to prevent the circuit from being interrupted, so are aware of the number of dead tortoises seen along their fence.

Recommendations

Conservation efforts

When designing a code of best practice, conservationists, landowners and other stakeholders need to work together. If suggestions are impractical, they will not be implemented and may create tension. Perhaps multiple codes of best practice could be created for specific land practices. More research is needed on the effectiveness and applicability of some of the suggested mitigation strategies in this study. Successful mitigation strategies that meet conservation and landowner's needs should then be advertised to increase their adoption across the Karoo or South Africa.

If the diverse tortoise populations in the Karoo or South Africa are recognized as a primary conservation concern, funding generated for conservation could be used to provide and implement mitigation strategies to landowners to alleviate personal costs to the landowner. Public awareness of these issues need to raise to generate support for tortoise conservation. The possibility of increased use of electric fencing in the future may further threaten leopard tortoise populations, so efforts should be made to prevent more electric fences being erected, or mitigate their impacts. Mesh fences also pose problems for smaller tortoises. Electric and mesh fences should be removed when possible such as on land that has been converted to conservation or wildlife practices.

Future studies

This study could be improved by controlling for the effect of roads as all fence transects were adjacent to roads. Although road type was not significant and observations indicate few road mortalities occurred, fence of all types that are not adjacent to roads should be included. This may be difficult as permission is needed for internal fencing. Additionally, transects along roads without fences should be walked. Other variables could also be collected such as land-use practice, width of road verges, cause of death, clustering of fragments, and which side of the fence tortoises were found. An additional decomposition classification should be included in future studies that have a similar design. This study did not distinguish between stages once the carcass was in fragments. Carapace fragments from older carcasses were no longer white as they were stained from moss and soil. Currently the stages of decomposition are purely descriptive and reflect uneven time steps between stages. If the stages of tortoise carcass decomposition could be related to time since death in the Karoo habitat and climate (similar to Bourn and Coe's 1979 study on Aldabra tortoises), estimations of a mortality rate (individuals/km/yr) could be calculated using data collected in this study.

A larger dataset would strengthen models and allow a better understanding of the impacts of fencing on rarer tortoise species, thus there is reason for studies to build on this dataset. Variables that were not significant in this study may tend towards significance (such as rock aprons). It would also allow further variables to be investigated, such as presence of electric strands (or rock aprons) on one or both sides of the fence or any if there is any interaction between rock aprons and electric strands. The fence type on the opposite side of the road could also have an impact. Thus, the data collected in this study could act as a foundational dataset that can be built on and adapted in future studies. Future studies could be expanded to include mortalities of other taxa along fences.

Information on all the fences present in an area (including internal fences on properties) would allow mortalities (or mortality rates) to be scaled to better understand the impact of fences. Although total fence lengths could be calculated from satellite images, there is no way of knowing the fence type. Currently, no census of fences exists to provide the total lengths of each fence type in the Karoo. Fence mortalities could be compared to detailed tortoise population studies to investigate whether fence mortalities are selective or just representative of the population.

Conclusions

Fencing of all types have associated tortoise mortalities, with leopard and angulate tortoises being affected differently. Until now, the impact of non-electric fencing has been largely overlooked, despite the estimate of numbers of tortoises killed being comparable to electric fencing (given the relatively small proportion of electrified fences). Previously suggested mitigation strategies may not be practical for landowners and have thus been poorly implemented. Mitigation strategies should be developed in conjunction with landowners to be successful. The effectiveness of suggested mitigation strategies needs to be investigated. 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). With global fence use increasing around the world (Sudip 2016) and tortoises being so widespread (Alexander & Marais 2007; van Dijk et al. 2014), the suggestions from this study extend beyond the Karoo.

Figure 19: A live tortoise where the electric strand has caused an open bleeding wound in the carapace, where the electric pulses splatter the blood by boiling.

Figure 20: A large dead leopard tortoise against a mesh fence with no obvious cause of death.


(A)
(B)

Figure 21: Angulate tortoise which trapped in a mesh fence (A) and mesh fence which with a rock apron (B).

Figure 22: Three leopard tortoises walking along a fence where vegetation has been cleared.

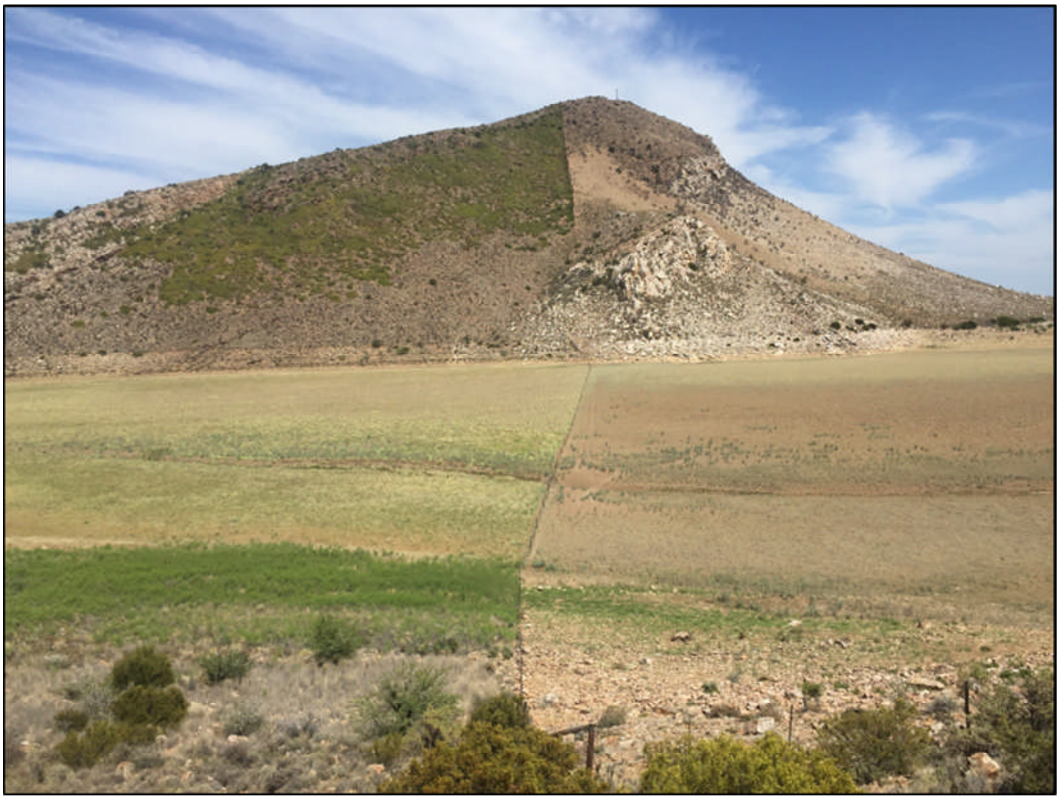


Figure 23: Fence-line contrast showing how vegetation can differ with different land-use practices.

Figure 24: A hole in fence caused by problem animals that tortoises can use to cross the fence.

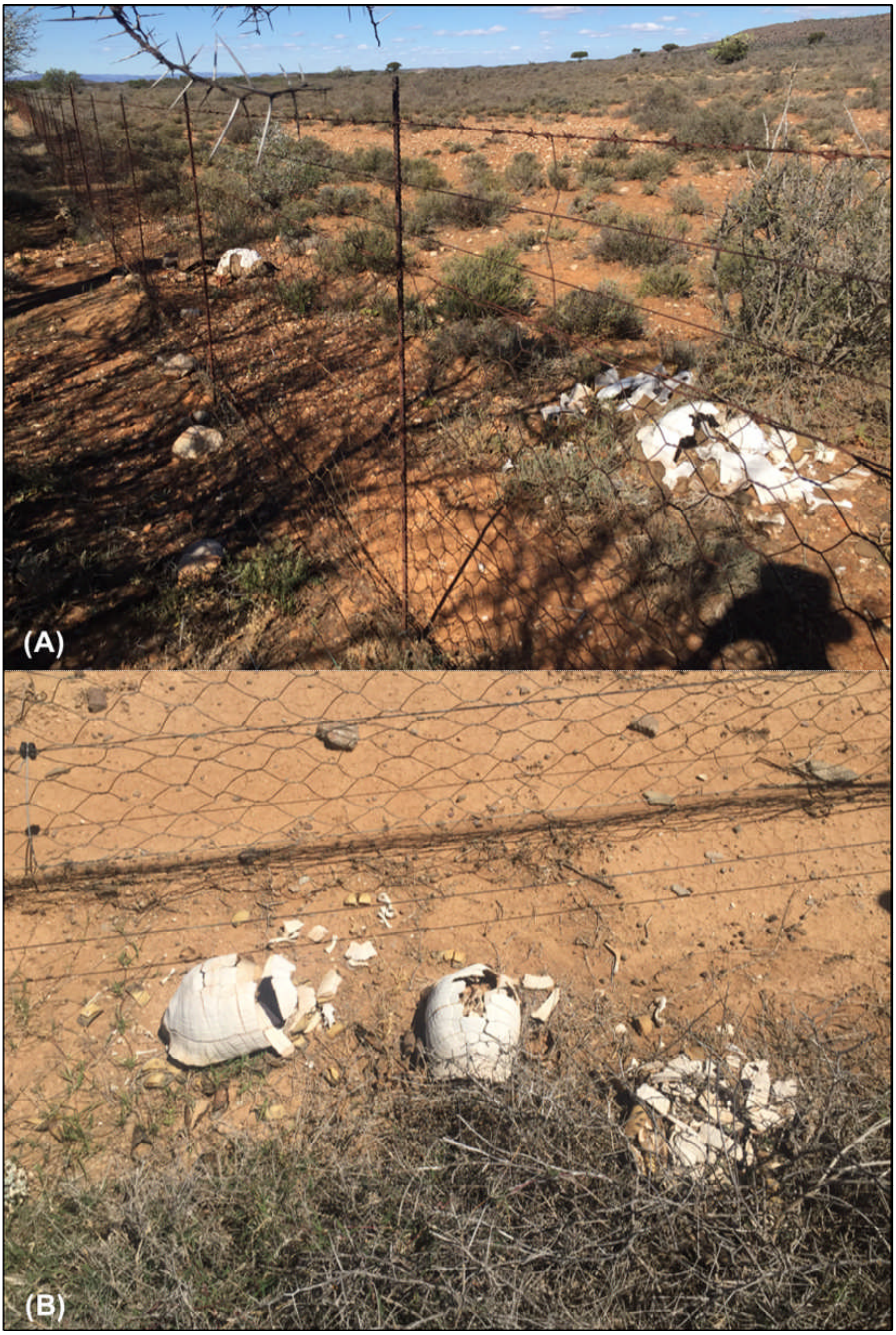


Figure 25: Dead tortoises are often clustered together in a small area along a fence: (A) four large dead leopard tortoises, (B) three small dead leopard tortoises.

Figure 26: Dead leopard tortoises with punctures in carapace: (A) and (B).

Figure 27: Rock aprons may cause additional tortoise mortalities by (A) effectively lowering the electric strand height as tortoises climb the rocks (B) by trapping smaller tortoises between rock and the fence (arrow indicates tortoise position).

References

Alexander G. Marais J. 2007. A guide to the reptiles of southern Africa. Struik, Cape Town, South Africa.

Bates MF, Branch WR, Bauer AM, Burger M, Marais J, Alexander GJ, De Villeiers MS. 2014. Atlas and Red List of the Reptiles of South Africa, Lesotho and Swaziland. *Suricata* 1. South African National Biodiversity Institute, Pretoria, South Africa.

Bates D, Maechler M, Bolker B, Walker S. 2015. Fitting Linear Mixed-Effects Models using lme4. Computation: 1–51.

Baxter-Gilbert JH, Riley JL, Lesbarrères D, Litzgus JD. 2015. Mitigating reptile road mortality: fence failures compromise ecopassage effectiveness. PLos one **10**: 1–15.

Beck A. 2010. Electric fence induced mortality in South Africa. MSc thesis. University of the Witwatersrand, Johannesburg, South Africa.

Ben-Shahar R. 1993. Does fencing reduce the carrying capacity for populations of large herbivores? Journal of Tropical Ecology **9**:249–253.

Bjornstad ON. 2016. ncf: Spatial Nonparametric Covariance Functions. R package version **1**: 1–7.

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

Boone RB, Hobbs NT. 2004. Lines around fragments: effects of fencing on large herbivores. African Journal of Range & Forage Science **21**: 147–158.

Bourn D, Coe MJ. 1979. Features of tortoise mortality and decomposition on Aldabra. Philosophical Transactions of the Royal Society of London: Biological Sciences **286**:

189–193.

Boycott RC, Bourquin O. 1988. The South African tortoise book: a guide to South African tortoises, terrapins and turtles. Southern Book, Gauteng, South Africa.

Branch, WR, Benn GA, Lombard AT. 1995. The tortoises (Testudinidae) and terrapins (Pelomedusidae) of southern Africa: their diversity, distribution and conservation. South African Journal of Zoology **30**: 91–102.

Branch WR. 1998. Field guide to snakes and other reptiles of southern Africa. Struik, Cape Town, South Africa.

Branch WR. 2012. Tortoises, terrapins & turtles of Africa. Struik, Cape Town, South Africa.

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

Branch, WR, Benn GA, Lombard AT. 1995. The tortoises (Testudinidae) and terrapins (Pelomedusidae) of southern Africa: their diversity, distribution and conservation. South African Journal of Zoology **30**: 91-102.

Branch WR. 1998. Field guide to snakes and other reptiles of southern Africa. Struik, Cape Town, South Africa.

Burger M, Branch WR. 1994. Tortoises mortality caused by electrified fences in the Thomas Baines Nature Reserve. South African Journal of Wildlife Research **24**: 32–37.

Cape Nature. 2014. Policy on fencing and enclosure of game, predators and dangerous animals in the Western Cape Province. Page Cape Nature Biodiversity Support Services: 1–26. Cape Town, South Africa.

Cape Nature. 2017. Conservation stewardship. Available from http://www.capenature.co.za/carefor-nature/stewardship (accessed 5 March 2017).

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**: 513–527.

Catano CP, Stout IJ. 2015. Functional relationships reveal keystone effects of the gopher tortoise on vertebrate diversity in a longleaf pine savanna. Biodiversity and Conservation **24**: 1957–1974.

Chavez-Ramirez, Gawlik DE, Prieto FG, Slack RD. 1994. Effects of habitat structure on patch use by loggerhead shrikes wintering in a natural grassland. Condor **96**: 228–231.

CITES. 2017. Available from http://checklist.cites.org (accessed on 5 March 2017).

Conradie B. 2015. Effective predator control?: management-predation. Wolboer/Wool Farmer **3**: 48–51.

Cumming DHM, Osofsky SA, Atkinson SJ, Atkinson MW. 2015. Beyond Fences : Wildlife , Livestock and Land Use in Southern Africa. One health: The theory and practice of integrated health approaches:243–257. Zinsstag J, Schelling E, Waltner-Toews D, Whittaker M, Tanner M. CABI. Oxfordshire, UK.

Cunningham SJ, Madden CF, Barnard P, Amar A. 2016. Electric crows: powerlines, climate change and the emergence of a native invader. Diversity and Distributions **22**: 17–29.

Davies-Mostert HT, Mills MGL, Macdonald DW. 2013. Hard boundaries influence African wild dogs' diet and prey selection. Journal of Applied Ecology **50**: 1358–1366.

Day T, Macgibbon R. 2007. Multiple-species exclusion fencing and technology for mainland sites. Managing Vertebrate Invasive Species: Proceedings of an International Symposium: 418–433. Pitt WC, Fagerstone KA. University of Nebraska, USA.

Department of Labour. 2011. Government Notices. Government Notices **34154**: 3–33.

ESRI. 2016. Available from https://www.arcgis.com (accessed 25 January 2017).

Ewen JG, Parker KA, Richardson K, Armstrong D, Smuts-Kennedy C. 2011. Translocation of hihi *Notiomystis cincta* to Maungatautari, a mainland reserve protected by a predator-exclusion fence, Waikato, New Zealand. Conservation Evidence **8**: 58–65.

Farber T. 2016. Shell-Shocked: A tortoise massacre. The Sunday Times: 8. (30 October 2016).

Fincham J, Lambrechts N. 2014. How many tortoises do a pair of pied crows *Corvus alba* need to kill to feed their chicks? Ornithological Observations **5**: 135–138.

Galileo. 2016. Available from https://galileo-app.com (accessed 20 August 2016).

Grobler JJ. 1982. The leopard tortoise in the Mountain Zebra National Park. Koedoe **25**: 49–53.

Hansen DM, Donlan CJ, Griffiths CJ, Campbell KJ. 2010. Ecological history and latent conservation potential: Large and giant tortoises as a model for taxon substitutions. Ecography **33**: 272–284.

Hoare RE. 1992. Present and Future Use of Fencing in the Management of Larger African Mammals. Environmental Conservation **19**: 160–164.

Hoffman MT, Cousins B, Meyer T, Petersen A, Hendricks H. 1999. Historical and contemporary land use and the desertification of the Karoo. The Karoo: ecological patterns and processes: 257–273. Dean RJ, Milton SJ. Cambridge University Press. Cambridge, UK.

Hothorn T, Hornik K. 2017. exactRankTests: Exact Distributions for Rank and Permutation Tests. R package version 0.8–29.

IUCN. 2017. Available from www.iucnredlist.org (accessed on 5 March 2017).

Jackson CR, McNutt JW, Apps PJ. 2012. Managing the ranging behaviour of African wild dogs

(*Lycaon pictus*) using translocated scent marks. Wildlife Research **39**: 31–34.

Joseph GS, Seymour CL, Foord SH. 2016. 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.

Karoo Predator Project. 2017. Available from https://karoopredatorproject.wordpress.com (accessed on 3 March 2017).

Kesch KM. 2014. Game fencing as a human-wildlife conflict mitigation strategy and its implications for conservation. PhD thesis, University of Hamburg, Hamburg, Germany.

Kesch KM, Bauer DT, Loveridge AJ. 2014. Undermining game fences: Who is digging holes in Kalahari sands? African Journal of Ecology **52**: 144–150.

Lau M. and Shi HT. 2000. Conservation and trade of terrestrial and freshwater turtles and tortoises in the People's Republic of China. Chelonian Research Monographs **2**: 30–38.

Lenth RV. 2016. Least-Squares Means: The R Package lsmeans. Journal of Statistical Software **69**: 1–33.

Loehr, V.J., Henen, B.T. and Hofmeyr, M.D., 2004. Reproduction of the smallest tortoise, the Namaqualand speckled padloper, Homopus signatus signatus. Herpetologica. **60**(4): 444–454.

Loehr VJT. 2012. Road mortality in the greater padloper, *Homopus femoralis* (Testudinidae). Chelonian Conservation and Biology **11**: 226–229.

Loehr VJT. 2017. Unexpected decline in a population of speckled tortoises. Journal of Wildlife Management: 1–7.

Lotter M. 2014. River map layer. NFEPA. Available from https://www.arcgis.com/home/item.html?id=757f119cc15841e382fd8194bd646b4 (accessed

27 January 2017).

Mason MC, Kerley GIH, Weatherby CA, Branch WR. 2000. Angulate and leopard tortoises in the Thicket Biome, Eastern Cape, South Africa: Populations and biomass estimates. African Journal of Ecology **38**: 147–153.

Macdonald, I. 2005. Use of electrical fencing in Agriculture. Department of Agriculture and Environmental Affairs, Pietermaritzburg, South Africa.

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).

McManus JS, Dickman AJ, Gaynor D, Smuts BH, Macdonald DW. 2015. Dead or alive? Comparing costs and benefits of lethal and non-lethal human–wildlife conflict mitigation on livestock farms. Oryx, **49**: 687–695.

McMaster MK, Downs CT. 2009. Home Range and Daily Movement of Leopard Tortoises (*Stigmochelys pardalis*) in the Nama-Karoo, South Africa **43**: 561–569.

Milton SJ. 1991. Plants eaten and dispersed by adult leopard tortoises *Geochelone pardalis* (Reptilia: Chelonii) in the southern Karoo. African Zoology **27**: 45–49.

Milton SJ, Davies RAG, Kerley GIH. 1999. Population level dynamics. The Karoo: Ecological patterns and processes, pp.183-207. Dean RJ, Milton SJ. Cambridge University Press. Cambridge, UK.

Ndlovu Fencing. 2012. The Law and electric fencing. Available from http://www.techno-group.co.za/legalbooklet.pdf (accessed on 27 January 2017).

Pietersen DW, McKechnie AE, Jansen R. 2014. A review of the anthropogenic threats faced by Temminck's ground pangolin, *Smutsia temminckii*, in southern Africa. South African Journal of

Wildlife Research **44**: 167–178.

Ruby DE, Spotila JR, Martin SK, Kemp SJ. 1994. Behavioral responses to barriers by desert tortoises: Implications for wildlife management. Herpetological Monographs: 144–160.

Reptile database. 2017. Available from http://www.reptile-database.com (accessed on 5 March 2017).

Salomon M, Cupido C, Samuels I. 2013. The good shepherd: remedying the fencing syndrome. African Journal of Range & Forage Science **30**: 71–75.

Scofield RP, 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.

Steventon J, Liebenberg L, Derbecker M, Bapat V, Miles DG. 2011. CyberTracker. Available from http://cybertracker.org/ (accessed 24 August 2016).

Sudip S, 2016. Global fencing market to expand from 4.40 % CAGR from 2012 to 2018 owing to rising safety concerns. Available from http://www.transparencymarketresearch.com/pressrelease/fencing-market.htm (accessed March 5 2017).

Taylor WA, van Rooyen C. 2015. The role of the wildlife ranching industry in South Africa's green economy. Endangered Wildlife Trust, Johannesburg, South Africa.

Taylor WA, Lindsey PA, Davies-Mostert H. 2015. An assessment of the economic, social and conservation value of the wildlife ranching industry and its potential to support the green economy in South Africa. Endangered Wildlife Trust, Johannesburg, South Africa.

Todd S, Milton S, Dean R, Carrick P, Meyer A. 2009. Ecological best-practice livestock production guidelines for the Namakwa District. Karoo Consortium.

Turtle Conservation Fund 2002. A Global Action Plan for Conservation of Tortoises and Freshwater Turtles. Strategy and Funding Prospectus 2002–2007. Conservation International and Chelonian Research Foundation Washington, DC, USA.

UNEP-WCMC. 2014. Review of three South African tortoise species. UNEP-WCMC, Cambridge, UK.

van Dijk PP, Iverson JB, Rhodin AGJ, Shaffer HB, Bour R. 2014. Turtles of the World, 7th Edition: Annotated Checklist of Taxonomy, Synonymy, Distribution with Maps, and Conservation Status. Conservation Biology of Freshwater Turtles and Tortoises **5**: 243–328.

van Niekerk HN. 2010. The cost of predation on small livestock in South Africa by medium-sized predators. MSc thesis. University of the Free State, Bloemfontein, South Africa.

Vanak AT, Thaker M, Slotow R. 2010. Do fences create an edge-effect on the movement patterns of a highly mobile mega-herbivore? Biological Conservation **143**: 2631–2637.

Watson L, Loehr VJT, Milton S. 2008. Karoo Landowner Conservation Guidelines. Nama Karoo Foundation, Graaff-Reinet, South Africa.

Wickham H. 2009. ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag, New York, USA.

Wickham H and Romain Francois. 2016. dplyr: A Grammar of Data Manipulation. R package version 0.5.0.

Woodroffe R, Hedges S, Durant SM. 2014. Ecology. To fence or not to fence. Science **344**: 46–48.

Appendices

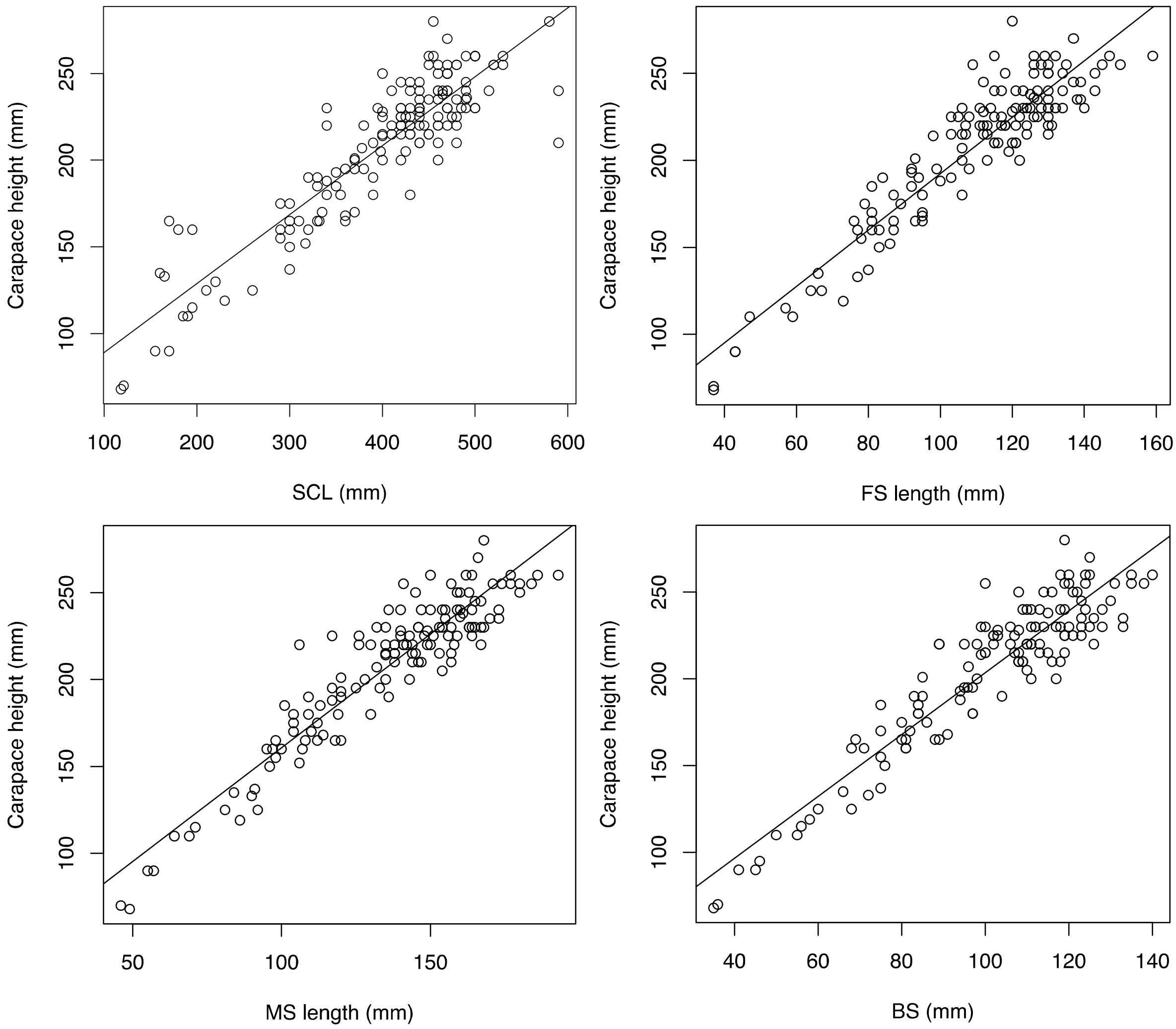


Figure S1: Leopard tortoise scute lengths and SCL regressions against carapace height

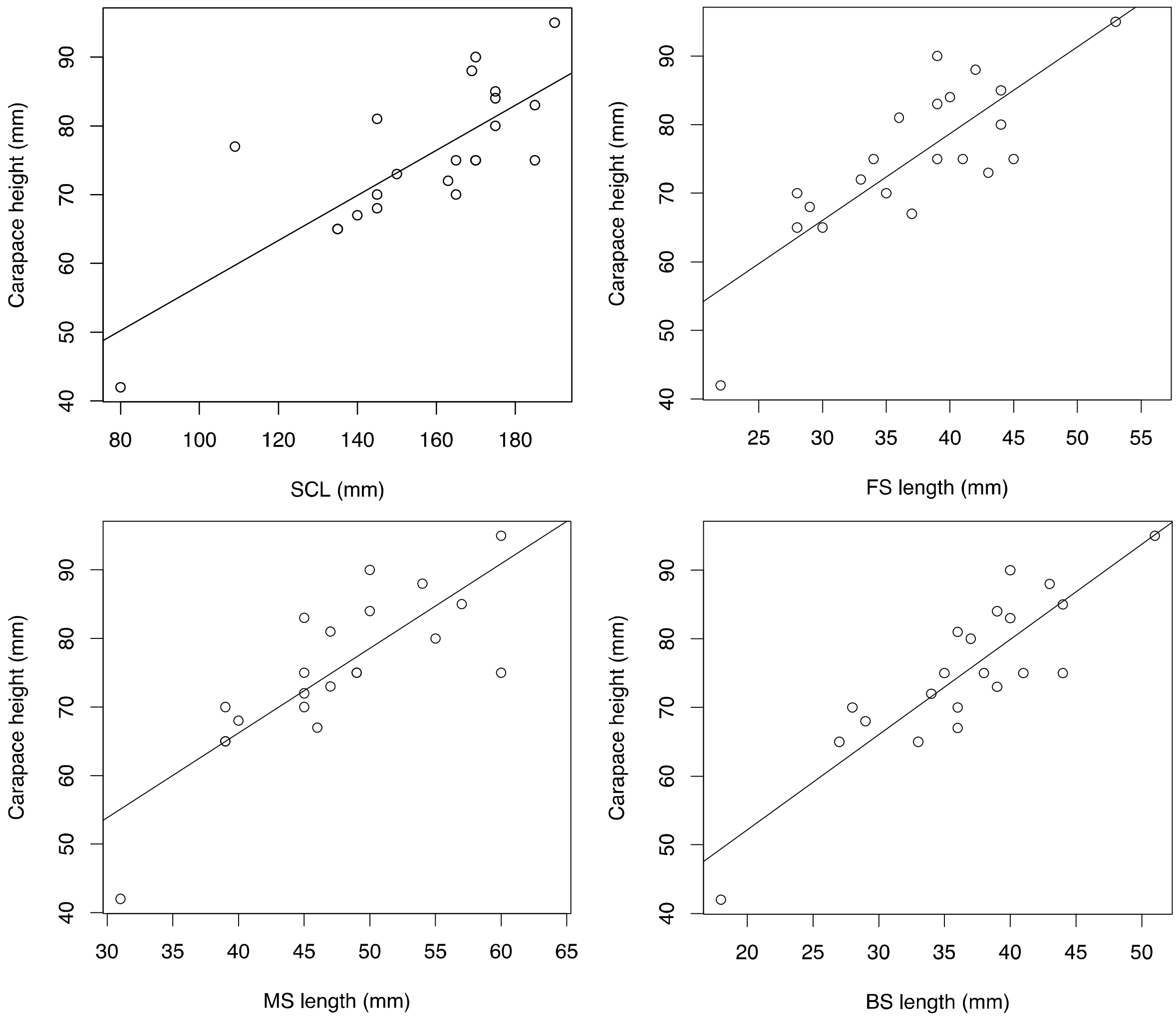


Figure S2: Angulate tortoise scute lengths and SCL regressions against carapace height

Table S1: Scute lengths and SCL regression equations used to predict height of tortoise carapaces.

Measurement	Equation	SE	R^2	Adjusted R^2	F	df	p
Leopard SCL	y = 0.397*x* + 49.42	0.016	0.808	0.807	636.70	151	<0.001
Leopard FS	y = 1.620*x* + 30.34	0.057	0.854	0.853	794.80	136	<0.001
Leopard MS	y = 1.306*x* + 30.04	0.044	0.867	0.866	877.60	135	<0.001
Leopard BS	y = 1.781*x* + 25.38	0.063	0.858	0.857	804.00	133	<0.001
Angulate SCL	y = 0.327*x* + 23.99	0.060	0.602	0.582	30.24	20	<0.001
Angulate FS	y = 1.265*x* + 28.09	0.212	0.652	0.634	35.66	19	<0.001
Angulate MS	y = 1.236*x* + 16.74	0.208	0.650	0.631	35.20	19	<0.001
Angulate BS	y = 1.386*x* + 24.44	0.181	0.755	0.742	58.49	19	<0.001

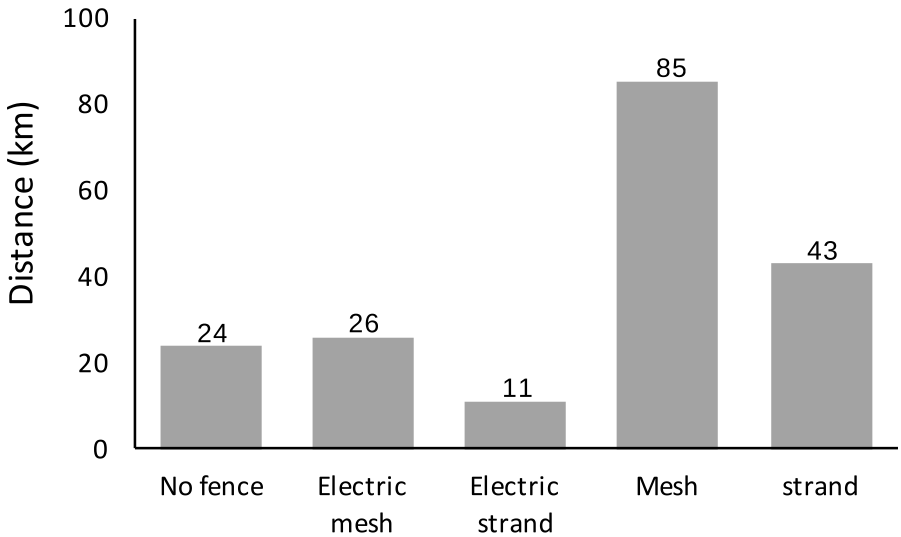


Figure S3: Distances of fence types used in analyses. Numbers of above bars indicate the number of transects.

Table S2: Statistical results for GLM that investigated the probability of a live tortoise occurrence per kilometer for each fence type (df = 184).

Fence type	Estimate	SE	Z	P
No fence	-3.110	0.389	-7.998	<0.001
Electric mesh	0.574	0.486	1.181	0.238
Electric Strand	-14.639	512.308	-0.029	<0.001
Mesh	1.313	0.407	3.226	<0.001
Strand	0.894	0.440	2.033	0.042

Table S3: Statistical results of fence type comparisons for GLM that investigated the probability of a live tortoise occurrence per kilometer for each fence type (df = 184).

Contrast	Estimate	SE	Z	P value
No fence - Electric mesh	-0.574	0.486	-1.181	0.762
No fence - Electric strand	14.639	512.308	0.029	1.000
No fence - Mesh	-1.313	0.407	-3.226	0.011
No fence - Strand	-0.894	0.440	-2.033	0.250
Electric mesh - Electric strand	15.213	512.308	0.030	1.000
Electric mesh - Mesh	-0.739	0.315	-2.341	0.132
Electric mesh - Strand	-0.320	0.357	-0.896	0.898
Electric strand - Mesh	-15.952	512.308	-0.031	1.000
Electric strand - Strand	-15.533	512.308	-0.030	1.000
Mesh -Strand	0.419	0.238	1.764	0.395

Table S4: Statistical results for GLM that investigated the probability of a dead tortoise occurrence per kilometer for each fence type (df = 184).

Fence type	Estimate	SE	Z	P
No fence	-2.371	0.281	-8.431	<0.001
Electric mesh	5.550	0.480	11.575	<0.001
Electric Strand	2.963	0.374	7.920	<0.001
Mesh	1.992	0.294	6.779	<0.001
Strand	1.138	0.317	3.590	<0.001

Table S5: Statistical results of fence type comparisons for GLM that investigated the probability of a dead tortoise occurrence per kilometer for each fence type (df = 184).

Contrast	Estimate	SE	Z	P value
No fence - Electric mesh	-5.550	0.479	-11.575	<0.001
No fence - Electric strand	-2.963	0.374	-7.920	<0.001
No fence - Mesh	-1.992	0.294	-6.779	<0.001
No fence - Strand	-1.138	0.317	-3.590	0.003
Electric mesh - Electric strand	2.587	0.460	5.622	<0.001
Electric mesh - Mesh	3.558	0.398	8.948	<0.001
Electric mesh - Strand	4.412	0.415	10.635	<0.001
Electric strand - Mesh	0.971	0.261	3.719	0.002
Electric strand - Strand	1.826	0.287	6.367	<0.001
Mesh -Strand	0.855	0.169	5.054	<0.001

Table S6: Statistical results for GLM that investigated the average number of live tortoises per kilometer of fence type (df = 184).

Fence type	Estimate	SE	Z	P
No fence	-3.154	0.442	-7.130	<0.001
Electric mesh	0.542	0.568	0.954	0.340
Electric Strand	-17.149	1836.489	-0.009	0.993
Mesh	1.751	0.466	3.757	<0.001
Strand	1.967	0.488	4.027	<0.001

Table S7: Statistical results of fence type comparisons for GLM that investigated the average number of live tortoises per kilometer for among different fence types (df = 184).

Contrast	Estimate	SE	Z	P value
No fence - Electric mesh	-0.542	0.568	-0.954	0.876
No fence - Electric strand	17.149	1836.489	0.009	1.000
No fence - Mesh	-1.751	0.466	-3.757	0.002
No fence - Strand	-1.967	0.488	-4.027	0.001
Electric mesh - Electric strand	17.690	1836.489	0.010	1.000
Electric mesh - Mesh	-1.209	0.385	-3.142	0.015
Electric mesh - Strand	-1.425	0.412	-3.463	0.005
Electric strand - Mesh	-18.900	1836.489	-0.010	1.000
Electric strand - Strand	-19.116	1836.489	-0.010	1.000
Mesh -Strand	-0.216	0.254	-0.850	0.915

Table S8: Statistical results for GLM that investigated the average number of dead tortoises per kilometer of fence type (df = 184).

Fence type	Estimate	SE	Z	P
No fence	-2.461	0.282	-8.716	<0.001
Electric mesh	4.668	0.295	15.810	<0.001
Electric Strand	4.016	0.315	12.754	<0.001
Mesh	2.241	0.290	7.732	<0.001
Strand	1.164	0.313	3.725	<0.001

Table S9: Statistical results of fence type comparisons for GLM that investigated the average number of dead tortoises per kilometer for among different fence types (df = 184).

Contrast	Estimate	SE	Z	P value
No fence - Electric mesh	-4.668	0.295	-15.810	<0.001
No fence - Electric strand	-4.016	0.315	-12.754	<0.001
No fence - Mesh	-2.241	0.290	-7.732	<0.001
No fence - Strand	-1.164	0.313	-3.725	0.002
Electric mesh - Electric strand	0.652	0.164	3.969	0.001
Electric mesh - Mesh	2.428	0.108	22.396	<0.001
Electric mesh - Strand	3.504	0.160	21.937	<0.001
Electric strand - Mesh	1.776	0.154	11.528	<0.001
Electric strand - Strand	2.852	0.194	14.729	<0.001
Mesh -Strand	1.076	0.149	7.208	<0.001

Table S10: Statistical results for GLM that investigated the probability of a dead leopard tortoise occurrence per kilometer for each fence type (df = 184).

Fence type	Estimate	SE	Z	P
No fence	-3.110	0.389	-7.998	<0.001
Electric mesh	5.553	0.480	11.581	<0.001
Electric Strand	3.702	0.461	8.038	<0.001
Mesh	1.674	0.403	4.153	<0.001
Strand	1.366	0.425	3.213	0.001

Table S11: Statistical results of fence type comparisons for GLM that investigated the probability of a dead leopard tortoise occurrence per kilometer for each fence type (df = 184).

Contrast	Estimate	SE	Z	P value
No fence - Electric mesh	-5.553	0.479	-11.581	<.001
No fence - Electric strand	-3.702	0.461	-8.038	<.001
No fence - Mesh	-1.674	0.403	-4.153	<.001
No fence - Strand	-1.366	0.425	-3.213	0.012
Electric mesh - Electric strand	1.851	0.374	4.955	<.001
Electric mesh - Mesh	3.879	0.300	12.931	<.001
Electric mesh - Strand	4.187	0.329	12.737	<.001
Electric strand - Mesh	2.028	0.269	7.547	<.001
Electric strand - Strand	2.336	0.301	7.775	<.001
Mesh -Strand	0.309	0.202	1.529	0.543

Table S12: Statistical results for GLM that investigated the probability of a dead angulate occurrence per kilometer for each fence type (df = 184).

Fence type	Estimate	SE	Z	P
No fence	-18.779	570.330	-0.033	0.974
Electric mesh	17.783	570.331	0.031	0.975
Electric Strand	0.030	1019.174	0.000	1
Mesh	17.550	570.331	0.031	0.975
Strand	16.292	570.331	0.029	0.977

Table S13: Statistical results of fence type comparisons for GLM that investigated the probability of a dead angulate tortoise occurrence per kilometer for each fence type (df = 184).

Contrast	Estimate	SE	Z	P value
No fence - Electric mesh	-17.783	570.331	-0.031	1.000
No fence - Electric strand	-0.030	1019.174	0.000	1.000
No fence - Mesh	-17.549	570.331	-0.031	1.000
No fence - Strand	-16.292	570.331	-0.029	1.000
Electric mesh - Electric strand	17.753	844.653	0.021	1.000
Electric mesh - Mesh	0.234	0.199	1.177	0.765
Electric mesh - Strand	1.491	0.286	5.209	<0.001
Electric strand - Mesh	-17.520	844.653	-0.021	1.000
Electric strand - Strand	-16.262	844.653	-0.019	1.000
Mesh -Strand	1.257	0.250	5.027	<0.001

Table S14: Statistical results for GLM that investigated the average number of dead leopard tortoises per kilometer of fence type (df = 184).

Fence type	Estimate	SE	Z	P
No fence	-3.154	0.393	-8.017	<0.001
Electric mesh	5.313	0.406	13.089	<0.001
Electric Strand	4.710	0.425	11.092	<0.001
Mesh	2.060	0.404	5.105	<0.001
Strand	1.528	0.424	3.605	<0.001

Table S15: Statistical results of fence type comparisons for GLM that investigated the average number of dead leopard tortoises per kilometer for among different fence types (df = 184).

Contrast	Estimate	SE	Z	P value
No fence - Electric mesh	-21.449	3321.204	-0.006	1.000
No fence - Electric strand	0.000	5995.949	0.000	1.000
No fence - Mesh	-21.433	3321.204	-0.006	1.000
No fence - Strand	-19.736	3321.204	-0.006	1.000
Electric mesh - Electric strand	21.449	4992.094	0.004	1.000
Electric mesh - Mesh	0.016	0.197	0.080	1.000
Electric mesh - Strand	1.713	0.298	5.755	<0.001
Electric strand - Mesh	-21.433	4992.094	-0.004	1.000
Electric strand - Strand	-19.736	4992.094	-0.004	1.000
Mesh -Strand	1.697	0.261	6.511	<0.001

Table S16: Statistical results for GLM that investigated the average number of dead angulate tortoises per kilometer of fence type (df = 184).

Fence type	Estimate	SE	Z	P
No fence	-22.300	3321.000	-0.007	0.995
Electric mesh	21.450	3321.000	0.006	0.995
Electric Strand	0.000	5996.000	0.000	1.000
Mesh	21.430	3321.000	0.006	0.995
Strand	19.740	3321.000	0.006	0.995

Table S17: Statistical results of fence type comparisons for GLM that investigated the average number of dead angulate tortoises per kilometer for among different fence types (df = 184).

Contrast	Estimate	SE	Z	P value
No fence - Electric mesh	-21.449	3321.204	-0.006	1.000
No fence - Electric strand	0.000	5995.949	0.000	1.000
No fence - Mesh	-21.433	3321.204	-0.006	1.000
No fence - Strand	-19.736	3321.204	-0.006	1.000
Electric mesh - Electric strand	21.449	4992.094	0.004	1.000
Electric mesh - Mesh	0.016	0.197	0.080	1.000
Electric mesh - Strand	1.713	0.298	5.755	<0.001
Electric strand - Mesh	-21.433	4992.094	-0.004	1.000
Electric strand - Strand	-19.736	4992.094	-0.004	1.000
Mesh -Strand	1.697	0.261	6.511	<0.001