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# Game fence presence and permeability influences the local movement and distribution of South African mammals

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**Abstract**

Fences are utilized throughout the world to restrict the movements of wildlife, protecting them from threats and reducing human-wildlife conflict. In South Africa the number of privately-owned fenced game reserves has greatly increased in recent years, but little is known about how fencing affects the distribution and movements of target and non-target mammals. We surveyed 2m either side of the complete fence line of a recently established commercial game reserve in South Africa, identifying signs of animal presence (spoor, scat, foraging or other field signs) while also recording damage (holes) to the fence. Every 250m we carried out 100m perpendicular transects either side of the fence, recording vegetation cover and height at 10m intervals along the transect. We found that livestock (largely cattle) were excluded from the reserve. However, 12% of records of large animal species were recorded outside of the fence line. These species had been introduced to the reserve, strongly suggesting that they had crossed the boundary into the surrounding farmland. Sixteen naturally present wild species were found on both sides of the fence, but we found more evidence of their presence inside the reserve. Observational evidence suggests that they were regularly crossing the boundary, particularly where the fence was damaged, with hole size affecting species recorded. We also found evidence that the construction of the fence had led to a difference in vegetation structure with plant richness and percentage of non-woody plant cover significantly higher inside the fence. While fencing was highly effective at preventing movement of livestock, introduced and wild animals were able to cross the boundary, via holes in the fence. This work shows that the efficacy of the most common approach to preventing animal movement around protected areas depends on the species being considered and fence condition.

**Key words:** fence characteristics, mammal community, permeability, populations, holes.

**Introduction**

Fences mark boundaries and act as barriers to the movement of people and wildlife (Hoare 1992; Boone and Hobbs 2004). In the context of wildlife management, fences can help protect wildlife from persecution (Hayward and Kerley 2009), predation (Lokemoen et al. 1982; Rimmer and Deblinger 1992), poaching, and can help reduce the spread of disease from wildlife or domestic animal reservoirs (Andrews 1990; Vanak et al. 2010). Fences have also been used to reduce the possibility of conflict with humans by inhibiting the access of larger wild mammals to crops (Thouless and Sakwa 1995) or livestock (Treves and Karanth 2003), reducing economic losses (Treves and Naughton-Treves 2005), or to prevent direct risks to humans, such as through colliding with vehicles on roads (Putman 1997; Woodroffe et al. 2014) or through attack (Sukumar 1991).

However, fences have resulted in large-scale negative effects. For example, the construction of dingo (*Canis lupus dingo* Meyer, 1793) exclusion fences in Australia led to mass mortality in kangaroos (Macropodidae Gray, 1821), and other native mammals, due to exclusion from seasonal resources (Caughley et al. 1987; Hayward and Kerley 2009), and from the increase in populations of mesopredators such as foxes (*Vulpes vulpes* Linnaeus, 1758) and domestic cats (*Felis catus* Linnaeus, 1758) (Dickman et al. 2009; Hayward and Kerley 2009). Similarly, the presence of veterinary fences in Botswana has led to considerable declines in migrating southern African ungulates (Mbaiwa and Mbaiwa 2006; Williamson and Williamson 2009; Hayward and Kerley 2009). Fencing can cause direct fatalities through electrocution, documented in small species including tortoises and pangolins (Beck 2010; Arnot and Molteno 2017) or from attempting to scale the fence (*Pers. obs*.). They can also alter dispersal routes (Boone and Hobbs 2004), indirectly disrupting gene flow, which in turn can increase the possibility of inbreeding and the risk of local extinctions (Hayward and Kerley 2009). Over-exploitation of resources may also occur as a consequence of restricting the movement of species that require large areas to forage (Vanak et al. 2010) which may also result in the local extinction of species (Ostfeld 1994; Bond and Loffell 2001; Boone and Hobbs 2004; Hayward and Kerley 2009). Thus fenced populations require effective management to reduce these risks (Hayward et al. 2009; Kettles and Slotow 2009).

Although fences are often considered to be impermeable this is rarely true for all species. Universal game fences usually consist of posts and steel wire strands and depending on the type of game or livestock enclosed they may be electrified (Hoare 1992). In South Africa, antelope species such as greater kudu (*Tragelaphus stepsiceros* Pallas, 1766) and common eland (*Taurotragus oryx* Pallas, 1766) are capable of clearing 2m fences; indeed, eland have been known to break some fences (Hoare 1992; Apps 2000). Other species, including warthog (*Phacochoerus aethiopicus* Pallas, 1766), bushbuck (*Tragelaphus scriptus* Pallas, 1766), and many mammalian carnivores can dig or crawl under fences, while leopard (*Panthera pardus* Linnaeus, 1758; Hayward et al. 2007) and arboreal species may simply jump over (Hoare 1992) if trees or rocks allow. Furthermore, all species can traverse a fence if any holes present are large enough to permit free passage. Together, these behaviours render many barriers semi-permeable (i.e. the fence does restrict or prevent the movement of some mammals, but not all), with permeability determined by fence construction and condition (Connolly et al. 2009). There has been a lack of research on the effect of semi-permeable barriers on mammal communities (Cozzi et al. 2013) which is surprising considering that the effects of other barriers, such as roads and railway lines, on animal movements have been widely studied (Adams and Geis 1983; Forman and Alexander 1998; Ng et al. 2004; Ito et al. 2005; Sheperd et al. 2008; Fahrig *and* Rytwinski 2009; Frantz et al. 2012). Although roads and railway lines could be viewed as permeable barriers, they are fundamentally different to fences. Barrier characteristics are an important factor in determining the movement of species (Cozzi et al. 2013; Forman and Alexander 1998) and each will differ in outcome.

In South Africa there is an estimated 9000 private game farms enclosing over 200,000 $km^2$ (Cousins et al. 2008; Lindsey et al. 2009; Taylor et al. 2016). Covering 16% of the country, this highlights how game reserve fencing could have a large-scale impact regarding increased habitat differentiation, and consequent changes in the distributions of larger (> 10kg) mammal species (Cozzi et al. 2013). However, little is known about how fencing affects the abundance and distribution of larger mammalian species, the consequences for plant community structure, and how fence condition (the presence of holes) can affect the passage of animals. Working at a small commercial game reserve in north eastern South Africa, we asked how a boundary fence: a) affects the distribution of larger mammals, both in terms of status (domestic, introduced wild species, or naturally occurring wild species that do and do not need to use holes to cross the fence); then, b) only considering species that require holes to cross the fence, we ask if feeding guilds (carnivore, grazer, browser) differ in their response to the presence of holes in the fence; and c) we consider what the consequences of fence presence have been for local plant communities.

## Methods

### *Study area*

The study took place during July and August 2015 and was conducted at Thaba Tholo wilderness reserve (TTWR), Mpumalanga, South Africa (Latitude: 24°57"404 S, Longitude: 30°21"105 E). The 1,500-ha privately owned game reserve was established in 2002, integrating smallholdings of land previously used for cattle; the surrounding land was still utilised as cattle and game farm. Evidence of cultivation such as human-constructed terraces from the Iron Age (Pistorius 2014) still remains on site; as well as remnants of the old cattle fencing. The perimeter was increased to incorporate an area of 5,400ha in 2009 (Figure 1), and is now a commercial reserve with a variety of game including giraffe (*Giraffa camelopardalis* Linnaeus, 1758), however, it excludes all but the leopard of the 'big five' (Pirie et al. 2016). The reserve boundary (apart from 3.3 km of boundary shared with a game farm stocking similar wild species; Figure 1) separates TTWR from areas of low intensity livestock farming. Naturally occurring species including greater kudu, bushbuck and common duiker (*Sylvicapra grimmia* Linnaeus, 1758), referred to as wild species here, occur either side of the fence. In addition TTWR also has populations (here referred to as introduced species) of extra-limital South African species (e.g. common eland; sable *Hippotragus niger* Harris, 1838; gemsbok, *Oryx gazelle* Linnaeus, 1758; plains zebra, *Equus quagga* Boddaert, 1785) which were introduced following the formation of the reserve. These species are either suited to more arid environments or had been historically present but were subsequently removed.

The site is located between the Steenkampsberg and Mauchsberg mountain ranges and altitudes range from 1100-2000m. The area receives an average annual rainfall of 700-900 mm mainly between October-February.

### *Fence characteristics*

The perimeter fence (29.3km, Figure 1) was erected in 2008/2009 to incorporate new property acquired and to confine species introduced into the reserve [plains zebra, blue wildebeest (*Connochaetes taurinus* Burchell, 1823), common eland, gemsbok, impala

(*Aepyceros melampus* Lichtenstein, 1812), nyala (*Tragelaphus angasii* Angas, 1849), sable, giraffe and waterbuck (*Kobus ellipsiprymnus* Ogilbyi, 1833)]. The fence is a standard game fence which follows the recommended criteria suggested by the Cape Nature Biodiversity Support Services and Scientific Services specifications (Brown et al. 2014), and are also used in other countries such as Botswana (Boast et al. 2016). The fence stands 2.2m high and consisted of 22 strands of galvanized steel wire, 2.5mm in diameter (Figure 2a, 2b). The bottom four strands were 5cm apart, the rest were separated by 10cm. The lowest wire was flush with the ground and the last wire flush with the top of the fence post. Each strand was attached by wire to a solid metal dropper located every meter along the fence and was threaded through a main fence post every ten metres. Corners and points over 200m from corners were strengthened by large metal posts (10cm in diameter), which were bolstered by thinner metal posts and guide wires. All metal posts were dropped 80cm into the ground. It is worth noting that there were two large gaps in the fence due to the presence of sheer rock faces; although difficult to traverse these could allow movement for agile species such as klipspringer (*Oreotragus oresotragus* Zimmermann, 1783), baboon (*Papio ursinus* Kerr, 1792), kudu and leopard, however, it was difficult to collect evidence from these areas. There was also damage to the fence which occurred during extreme weather conditions before the study commenced. Several eland escaped through the large hole in the fence before it was mended, of which some returned but a few remained outside the reserve. The fence line was routinely checked bi-monthly for snares, any damage to the fence or large holes that introduced species or livestock could traverse. If damage was found this would be repaired. However these checks were paused for the duration of this study as the research team were checking the fence line which allowed reserve workers to concentrate on other reserve maintenance tasks. If damage was found during the study it was reported.

Due to the length of the perimeter and ruggedness of the terrain, data were collected in subsections of the complete fence over the two month sampling period. Researchers walked along the perimeter fence collecting data, stopping every 250m to conduct transects, with the number of daily transects completed varying with terrain and weather conditions.

***Data collection***

*Mammal presence along the fence line*

Two teams of three observers simultaneously walked in single file along both sides of the entire fence line, with an experienced field guide at the rear to ensure data were not missed on either side of the fence. Evidence of terrestrial mammals (spoor, scat, foraging or other field signs) was recorded if within two metres of the fence line; GPS location (model; Garmin E-trex) and species found were noted. Most terrestrial and arboreal mammals present on TTWR were recorded. However, species smaller than lagomorphs (<40cm long; Stuart and Stuart 2001) were omitted from the study due to their ability to easily traverse the fence and difficulty in locating and differentiating their field signs. Additionally, it is difficult to distinguish genet species by field signs alone (Liebenberg 2005), therefore all genet signs were recorded as genet species.

Scat identification was based on size, shape and colour (following Murray 2011) and recorded when there were three or more pieces of scat to compare and the shape was intact. Isolated piles were classed as a single count. Herbivore scat was not recorded where only single pellets were found or squashed rendering them unidentifiable. Spoor was identified using Liebenberg (2005), and was only recorded if it was clear, entire and could be identified with certainty. Partial spoor was not recorded. Unless clear trails from different individuals were seen, spoor from a single species at a single location was recorded as one individual.

*Hole utilisation*

Holes were identified based on disturbance of the substrate caused by animal digging or erosion, or damage to the wire. The latter was largely seen on the bottom strands and resulted from falling rocks, growing tree roots or the force of animal movement through the fence. Occasionally strands higher up were cut by poachers, but these were not treated as holes as they were in a difficult position for animals to utilise and showed no sign of exploitation. The size of hole was categorised based on permeability to key species: a) lagomorphs or smaller <10cm (small), b) too small for an adult leopard or brown hyena to easily utilize, but could allow mesopredators, dwarf antelope, grey duiker (*Sylvicapra grimmia* Linnaeus, 1758) and klipspringer through >10cm - <25cm (medium), c) large enough for a bushbuck or large predator which could influence herbivore movement e.g. an adult leopard or hyena head and body without much struggle, >25cm (large; mean zygomatic width for adult leopards in Namibia: male, 15.6cm, female 11.3cm [Stein and Hayssen (2013); while hip or shoulder widths are more likely to be the restrictive factor in ability to traverse a fence (Stullken and Kirkpatrick 1953), no such measurements were available]. Holes were categorised visually and by using foot pressure to test the freedom of movement of the bottom wires and substrate to assess the potential full size of the hole. Where it was difficult to visually categorize hole size, it was measured. Utilisation was assessed based on the absence of debris or presence of flattened vegetation, both indicators of very recent use (Liebenberg 2005). The presence of a game trail passing through the hole was also recorded which served as an indication of the hole being present before the study commenced and its utilization over a longer period. Therefore if there was no game trail but there was evidence of recent use, the hole was considered to be relatively new. A hole with a game trail which was recently used could be considered a main entrance/exit point for the time of year the study took place. When a vegetation transect (see below) location landed within 3m of a medium or large hole it was adjusted to be taken at the hole as this would fall within the error associated with the GPS.

*Vegetation comparisons from transects*

Transects were taken every 250m along the boundary fence line commencing from the main access point onto the reserve (unless within 3m of a hole; see above). A point 100m away from the fence was marked either side, perpendicular to the fence. Vegetation cover, height and species were recorded at each ten metre point along the transect using a tape measure. Vegetation cover was recorded as bare ground (BG), non-woody plants including grasses / sedges / flowers / *Lampranthus* spp. (O) and woody plants such as trees and bushes (T). If the point crossed the canopy of the bush / tree it was recorded as T. The height of the vegetation was categorized as 1: 0-20cm; 2: 20cm-1m; 3: 1-2m; 4: 2-3m; 5: 3-4m and 6: > 4m. Altitude was recorded at the fence and at the ends of each transect. Vegetation was identified to species where possible following Schmidt et al. (2002), Van Oudtshoorn (2012) and Manning (2009). Where this was not possible taxa were recorded to morphospecies. If a transect location was found to be too dangerous to sample, a replacement was located at the closest possible point to the original and the distance subtracted from the next 250m point.

***Statistical Analysis***

Inspection showed that the data were unsuitable for parametric analyses. Where multiple tests were conducted P-values were adjusted using sequential Holm-Bonferroni calculations to avoid errors associated with multiple tests (Holm 1979). All analyses were conducted using R (R Core Development Team 2012). Data collected from the 3.3km section of the boundary that bordered the adjacent game reserve were omitted from analysis.

*Mammal presence along the fence line*

The Morisita-Horn index (Magurran 2004) calculates the proportion of similarity in species richness and abundance between two communities. If identical species occur in the same proportions in both samples the index will be 1. The index can be sensitive to the most abundant species (Magurran 2004) therefore it has been recommended the data are $\log_{10}(x+1)$ transformed prior to analysis (Clarke and Warwick 2001). Here it was used to calculate large and meso-mammal community similarity either side of the fence based on the presence of pooled scat and spoor evidence recorded either side of the fence line.

G-tests (log-likelihood tests; Sokal and Rohlff 1995) were used to test if species were more likely to be recorded (pool evidence) on one side of the fence line (inside the reserve against outside). We compared records based on; a) animal origin (introduced wild species, naturally occurring wild species that needed holes to cross the fence and species which did not need holes to cross the fence, livestock), b) only species that needed to use holes to cross the fence were compared focusing on diet guild (carnivores, herbivores, grazers, browsers), and c) for all recorded species. Species that could fit between the bottom fence strands, climb over or through the fence easily or dig tunnels independent of the fence were classed as “facultative hole-users”. Included in this category were baboon, galago, aardvark, genet species, mongoose species and lagomorphs. The rest of the species were classified as “obligate hole-users”. Although leopard may jump over a fence (Hoare 1992), we decided to classify it as the later due to the lack of suitable vegetation close to the fence and difficulty of climbing the fence.

*Hole utilization*

The distribution of holes (clumped, random, or even) was explored using nearest neighbour analysis (QGIS version 2.18) which compares the nearest neighbour index based on observed distances between holes with an expected Poisson distribution (Sadar and Rodier 2012). A Z-score of between -1.96 and 1.96 indicates a random distribution, >2 has an even distribution and <-2 shows clustering at a significance level of 5% (Rifaie et al. 2015). This was repeated for each hole size category. We then examined if there was an association between hole size and a) rate of utilization, and b) the presence of game trails, using G-tests.

*Vegetation comparisons from transects*

The Morisita-Horn index was used to calculate the similarity in plant species found either side of the fence. Paired Wilcoxon tests were used to compare vegetation traits (maximum and median vegetation height, plant richness, proportion of bare ground, and proportion of woody and non-woody plant cover) recorded on transects either side of the fence for a) all complete transects, b) transects without holes and c) transects with holes.

## Results

### ***Mammal presence along the fence line***

The Morisita-Horn index of 0.84 suggests a moderately high degree of overlap between the two sides in terms of species richness and abundance. Thirty-two mammal species were identified along the fence line, with evidence more likely to be located inside the fence for introduced animals, wild species that needed holes to cross the fence and wild species that did not need holes to cross the fence ($G_1 = 284.00$, adjusted $p < 0.001$, $G_1 = 28.27$, adjusted $p < 0.001$, $G_1 = 37.95$, adjusted $p < 0.001$ respectively; Figure 3). When livestock were considered, significantly more evidence was located outside the fence ($G_1 = 385$, adjusted $p < 0.001$; Figure 3). There was significantly more evidence found inside the reserve for the obligate hole-using browsers and grazers ($G_1 = 51.6$, adjusted $p < 0.001$, $G_1$ 207.28, adjusted $p < 0.001$ respectively; Figure 4). When only obligate hole-using wild herbivores were considered, there was significantly more evidence found inside ($G_1 = 39.47$, adjusted $p < 0.001$, Figure 4) the fence line, which was also true for wild browsers ($G_1 = 37.30$, adjusted $p < 0.001$). However when only obligate hole-using wild grazers or carnivores were considered the difference in evidence between locations was not significant (Figure 4).

Species with <10 samples recorded on both sides of the fence were omitted from further analysis. Evidence for six of the 16 species was significantly more likely to found inside the reserve (Figure 4), five which were introduced native species (blue wildebeest: $G_1 = 28.09$, adjusted $p < 0.001$; plains zebra: $G_1 = 70.19$, adjusted $p < 0.001$; common eland: $G_1 = 97.35$, adjusted $p < 0.001$; gemsbok: $G_1 = 51.45$, adjusted $p < 0.001$; nyala: $G_1 = 2814$, adjusted $p < 0.001$), and one locally occurring species (greater kudu: $G_1 = 24.80$, adjusted $p < 0.001$).

***Hole utilization***

A total of 1697 holes were recorded along the reserve fence line (735 small; 444 medium; 518 large; mean of 32.8 holes > 10cm in size per 1km of fence). Of the large holes, 77 were large enough to allow leopard/dwarf antelope very easy access (2.6 holes per 1km), six of which were large enough to allow medium sized antelope very easy access (1 hole per 5km). Small holes were more likely to be present than medium or large ($G_1 = 72.6$, adjusted $p < 0.001$; $G_1 = 37.8$, adjusted $p < 0.001$, respectively), with large holes more likely to be present than medium ($G_1 = 5.7$, adjusted $p = 0.017$). Large holes were more likely to be recently used and contain a game trail than either medium ($G_1 = 17.86$, adjusted $p < 0.001$) or small holes ($G_1 = 24.84$, adjusted $p < 0.001$). Small holes were more likely to be unused, compared to medium and large holes ($G_1 = 183.89$, adjusted $p < 0.001$, $G_1 = 150.7$, adjusted $p < 0.001$ respectively; Figure 5). Game trails were more likely to be present where evidence of use was found at a hole ($G_1 = 8.62$, $p = 0.003$; Figure 5) suggesting animals were utilizing long term routes. Hole location along the fence line was found to be highly clumped (Z-score -70.5). When the hole categories were examined separately, small holes were found to be more highly clumped (Z-score -45.1) compared to large (Z-score -36.3) and medium holes (Z-score -33.8). Sixteen mammal species were identified from scat or spoor located in the hole, utilizing 36 holes in total (Table 1).

During the survey a female kudu was found to have perished on the fence, the position of the body suggested that she had attempted to jump the fence.

***Vegetation comparisons from transects***

One hundred and sixteen transects were completed; 15 were incomplete due to cliff edges and were omitted from further analyses. Eighty-eight plant species were identified; ten woody plants and fewer than twelve non-woody plants were not identified to species. The Morisita-Horn index of 0.91 suggests a relatively high similarity between the two sides in terms of relative species richness and abundance (unknown plants were grouped according to plant type). This may reflect the dominance of a few species. Plant richness along transects and percentage of non-woody plant cover was significantly higher inside the reserve for all transects and for transects without holes, however there was no significant difference in vegetation height, percentage of bare ground or woody plant cover (Table 2). There was no significant difference between transects with holes inside and outside of the reserve for any vegetation traits.

**Discussion**

Fences are ubiquitous, playing a central role in isolating larger species of conservation or economic concern from threats (Thouless and Sakwa 1995; Hayward and Kerley 2009; Packer et al. 2013), to ease management and to reduce the spread of disease between domestic and wild species (Andrews 1990; Vanak et al. 2010). The recent, rapid growth in numbers of small commercial game reserves in countries such as South Africa (Cousins et al. 2008; Taylor et al. 2016) has resulted in a substantial increase in the number of pockets of populations of wild and introduced animals often surrounded by agricultural land maintained for crops and livestock (Lindsey et al. 2009). Here, we report the results of a study investigating how the erection of a fence around a relatively new small commercial game reserve affected the distribution of larger naturally occurring wild animals, introduced native species, and domestic mammals. While domestic animals were restricted to agricultural land, there was an indication of some movement across the boundary of introduced species with the exception of eland. However, there was evidence suggesting sizeable movement of meso and large wild mammals, mainly kudu and brown hyena, across the fence line, evidenced by use of holes. We found direct support for the hypothesis that fence condition (measured by the presence of holes in the fence) affects movement, with larger holes being associated with more evidence of recent (scat, spoor) and long term (game trails) use. From this we can infer that animals were able to utilise known breaks in the fence to pass between habitats. Although vegetation structure was not studied prior to the erection of the fence, and there were no notable differences before construction (*pers. comm*. Alan Watson, reserve owner), it is difficult to definitively say if the vegetation has changed since the fence was erected. However, fence presence is likely to have brought about changes in rates of herbivory (notably through the exclusion of domestic livestock), which in turn can alter vegetation structure, and consequentially is likely to alter the distribution and abundance of a wider range of species.

We inferred the effect of the fence on the distribution and behaviour of animals by searching for evidence of their presence along the fence line itself. There was significantly more animal evidence (a proxy for abundance) inside the fence line of the game reserve for all wild species. However, when we consider the nature of the animals, whether through the perspective of their relationships with humans (domestic, introduced or naturally occurring wild mammals) or their feeding guild, differing patterns emerge.

We found no evidence of movement of domestic animals (almost all cattle) across the fence. In contrast, Chigwenhese et al. (2016) found that cattle would utilise holes in fences at Gonarezhou National Park, Zimbabwe, while buffalo only crossed where the fence was completely removed as a result of elephant damage. However, with introduced animals there is evidence for limited movement across the fence line, with 12% of records (70% of which were eland, which is likely to be due to individuals that escaped through a large breach in the fence when damaged during a storm) for introduced species found outside of the game reserve; these are not naturally present in the local mammal community. Records of wild species were more even (61% of wild animal records were collected inside the reserve), but these could be the result of the formation of two populations, isolated by the introduction of the fence. Nevertheless, when we consider individual species, it is noteworthy that the greatest differences in evidence along the fence line are for introduced animal species (wildebeest, zebra, eland, gemsbok, nyala) and domestic animals. The only 'wild' animal species to show a significant difference in evidence across the fence line was greater kudu, which was more abundant inside the reserve.

It is evident that the TTWR fence line is not an impermeable barrier. We present data showing that some animals can directly cross through or over the fence, but it is the presence of damage which is most likely to increase the opportunity for movement across the boundary line. We found 962 holes larger than 10 cm along the boundary; these were not random, but instead holes showed a clumped distribution. While fewer than half of small holes showed evidence of use (presence of a game trail and/or animal signs), over 70% of medium and large holes were used. As expected, smaller species (rock hyrax *Procavia capensis* Pallas, 1766, Smith's rock rabbit *Pronolagus rupestris* A. Smith, 1834) used small holes, while larger holes were used by a wide range of species, including brown hyena *Parahyaena brunnea* Thunberg, 1820, grey duiker, klipspringer and kudu. Large, medium and small holes were clumped in areas along the fence line, suggesting there is a pattern of movement which may be driven by something other than physical attributes (Connolly et al. 2009).

Nevertheless, evidence suggests that despite the opportunity for movement across the fence line, the reserve may well be acting as a preferred habitat for these species or that the presence of the fence is a deterrent to movement even when damage renders transit possible. The presence of livestock could affect the habitat preferences of wild species through direct (Madhusudan 2004) or indirect (Adams 1975) competition for food, with wild species avoiding areas of high livestock density. The presence of livestock will also result in changes in vegetation structure and there will also be differences in approaches to land management between the properties.

While fences can protect wildlife and humans (Sukumar 1991, Hayward and Kerley 2009) as well as lead to rapid population growth for species of conservation concern (e.g. a brown hyena population increased by almost four-fold in 10 years at Kwandwe Private Game Reserve in the Eastern Cape, South Africa following fencing; Welch and Parker 2016), their use is controversial among conservation biologists (Creel et al. 2013, Woodroffe et al. 2014). Fences can result in fragmented landscapes, and where habitat fragments are small, predators and large mammal populations can rapidly decline (Woodroffe et al. 2014). Fences can act as attractants for species (e.g. rodents, Connolly et al. 2009), and predators can use them to trap prey (Van Dyk and Slotow 2003; Davies-Mostert et al. 2013). Fences prevent herbivores from tracking changes in vegetation availability over a landscape scale (Caughley et al. 1987), and where water is seasonal, reduce access to this resource (Williamson and Williamson 2009). Such constraints can lower the carrying capacity of the fenced area, as well as resulting in habitat degradation through over-grazing. For example, Cassidy et al. (2013) found significantly reduced vegetation inside a fence surrounding a wildlife management area in Botswana. Notably, woody cover and tree richness was half that outside the fence, an area used for tribal grazing.

It is unsurprising that such patterns are evident, and to a large extent these will depend on stocking density and management. While the TTWR fence has only been fully in position for six years and it is not certain if vegetation differed before the fence, we found a slight difference in richness either side of the fence line, and an increase in the contribution of smaller (non-woody) plants to ground cover, suggesting that grazing intensity is much higher in the surrounding farmland. However, woody cover was not different, suggesting the distribution of browsers either side of the fence was potentially equalizing the effect on woody plants, reflecting similar findings by Augustine et al. (2011), who found that wild browsers mixed with livestock reduced bush encroachment. We acknowledge that our analysis of plant community structure is relatively simple, and fails to capture the complexity of patterns seen on the ground. Nevertheless, there are clear differences in plant community structure, which are likely to reflect grazing pressure (notably by cattle and introduced species), leading to rapid change in plant communities and hence wild herbivore communities either side of the fence line (cf. Todd and Hoffman 1999).

***Management implications***

Fences are ubiquitous and their use in conservation is controversial (e.g. Caughley et al. 1987; Mbaiwa and Mbaiwa 2006; Williamson and Williamson 2009; Dickman et al. 2009; Hayward and Kerley 2009). In some circumstances, fences can be beneficial, yet we have surprisingly little understanding of how effective they can be. Here we show that fences can be effective barriers against the incursion of domestic animals into protected areas, but less so in terms of introduced game animals. The fence was much less effective at limiting the movement of other wild large mammals, the latter in part associated with damage to fences and the variation in the agility of some species (e.g. greater kudu). The erection of a standard game fence may have resulted in differences observed in vegetation structure, differences that are likely to be caused by the differing herbivore pressures found either side of the fence (Todd and Hoffman 1999). However, it is plausible these effects may be limited by allowing the movement of wild fauna (Augustine et al. 2011) through specific sized holes in a fence (Dupuis-Désormeaux et al. 2016). In addition this could also potentially reduce the risk of genetic isolation of highly mobile and endangered species in areas where alternate barriers or conservancies are not feasible, while still restricting the movement of more valuable introduced species and livestock.

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Figure 1: Perimeter fence of Thaba Tholo Wilderness Reserve showing the shared boundary with cattle farms (black) and game only farms (white dash) and location within South Africa (produced in Quantum GIS 2.8 2, using Bing maps downloaded 17 March 2015).

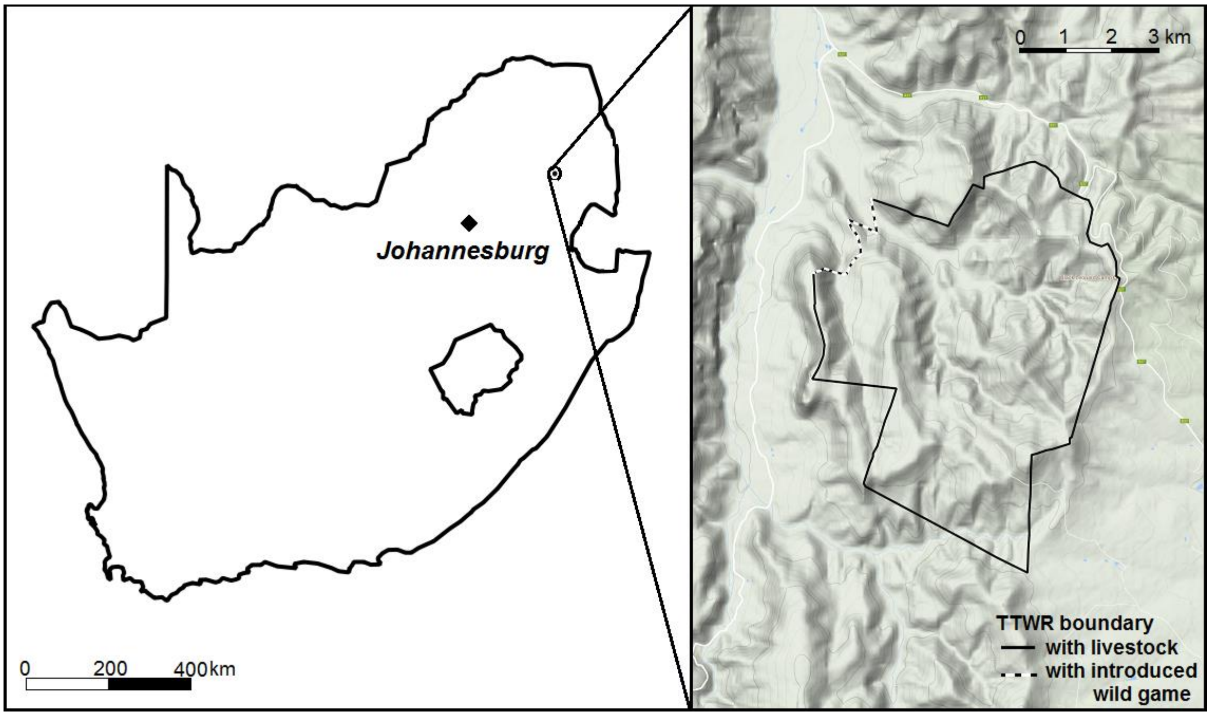

Figure 2: Thaba Tholo Wilderness Reserve game fence a) the full height of the fence, and b) the four strands at the bottom of the fence and ground conditions at a hole viewed from above.

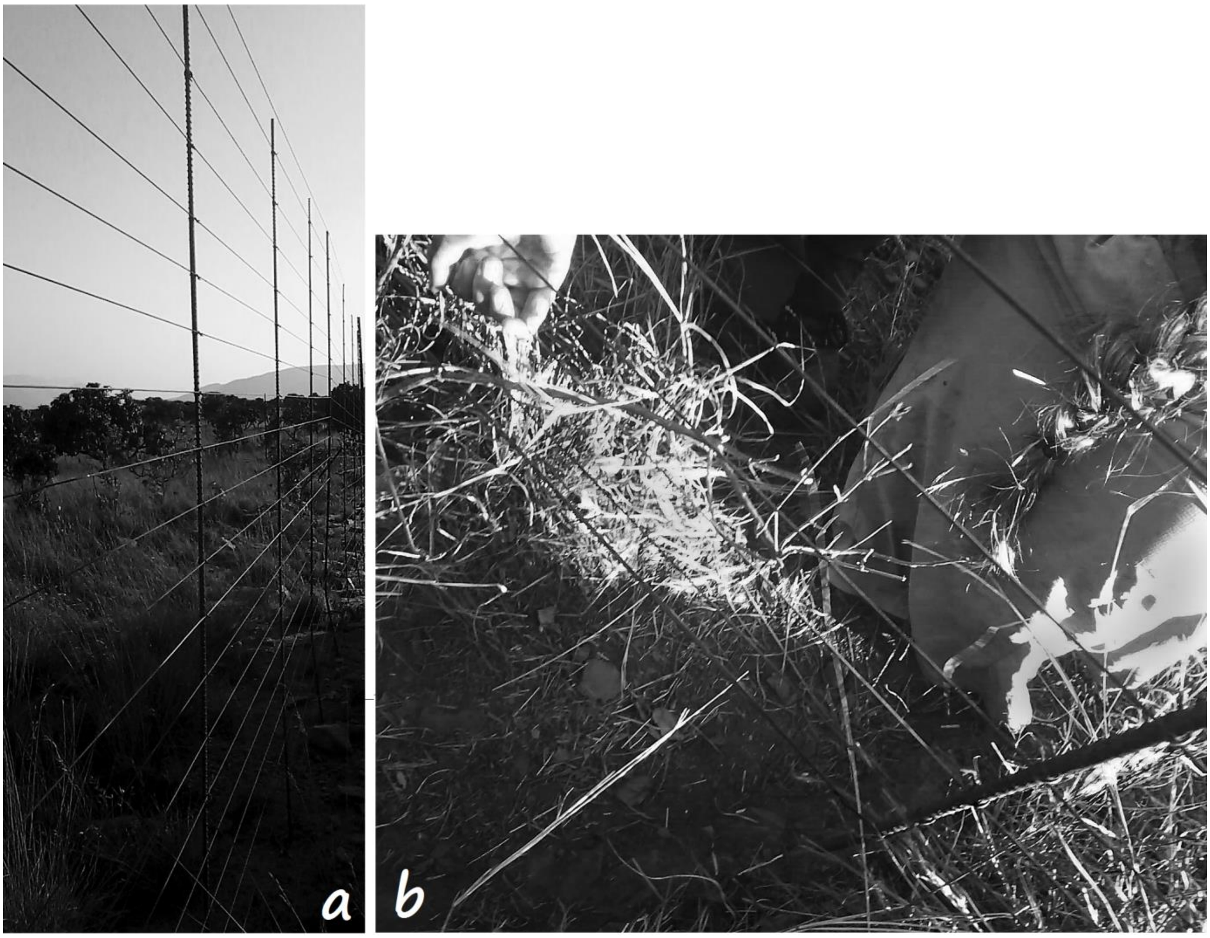

Figure 3: Total counts for each species recorded immediately inside and outside of the fence categorized by status, with data from the 3.3km boundary with the neighbouring game farm removed. Species names appear in ascending order matching placement on the chart.

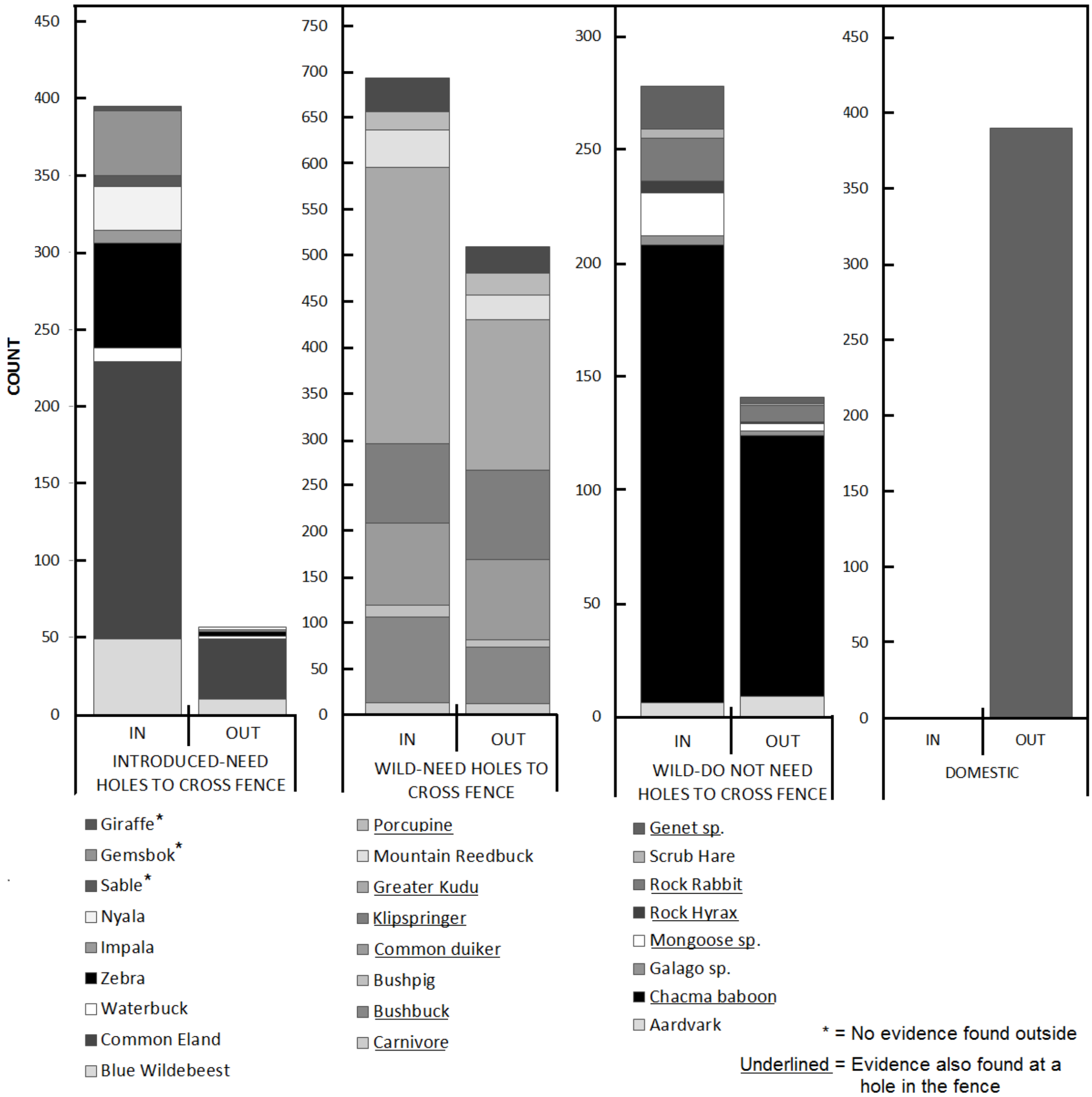

Figure 4: Total counts for each species recorded immediately inside and outside of the fence categorized by diet, with data from the 3.3km boundary with the neighbouring game farm removed. Species names appear in ascending order matching placement on the chart.

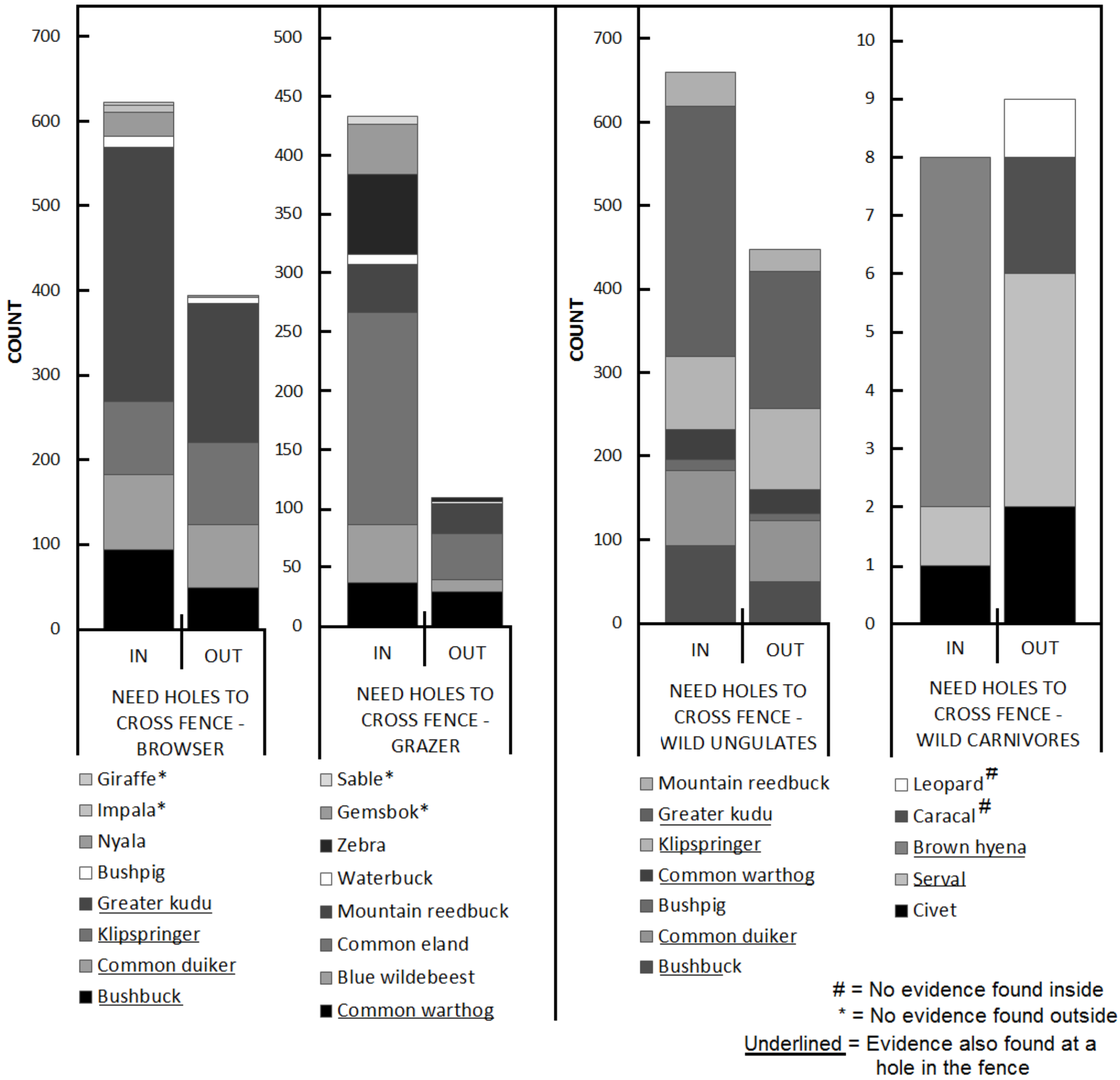

Figure 5: Percentage of unused and used holes for each size category; large (>25cm), medium (>10cm - <25cm ) and small (<10cm) holes found along the TTWR fence line, divided into non-used, used, game trail present and used with a game trail present.

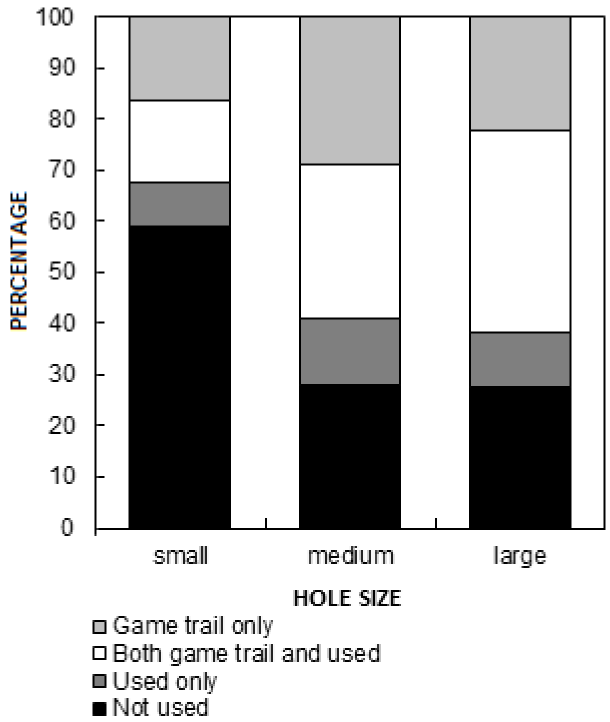

Table 1: Number of records for each species documented utilizing a hole, the size of hole and whether there was a presence of a game trail.

| Hole | Species present | Binomial name | Taxonomic authority | Count | Game trail presence |
|---|---|---|---|---|---|
| **Small** | Rock hyrax | *Procavia capensis* | Pallas, 1766 | 1 | 1 |
| | Smith's rock rabbit | *Pronolagus rupestris* | A. Smith, 1834 | 1 | 1 |
| **Medium** | Baboon | *Papio ursinus* | Kerr, 1792 | 4 | 4 |
| | Meller's mongoose | *Rhynchogale melleri* | Gray, 1865 | 1 | 1 |
| | Vervet monkey | *Chlorocebus pygerythrus* | F. Cuvier, 1821 | 1 | 1 |
| **Large** | Bushbuck | *Tragelaphus scriptus* | Pallas, 1766 | 1 | 1 |
| | Samango monkey | *Cercopithecus mitis* | Wolf, 1822 | 1 | 1 |
| | Serval | *Leptailurus serva* | Schreber, 1776 | 1 | 0 |
| | Greater kudu | *Tragelaphus strepsiceros* | Pallas, 1766 | 3 | 2 |
| **Small and medium** | | | | 0 | |
| **Medium and large** | Aardvark | *Orycteropus afer* | Pallas, 1766 | 2 | 2 |
| | Brown hyena | *Parahyaena brunnea* | Thunberg, 1820 | 6 | 3 |
| | Grey duiker | *Sylvicapra grimmia* | Linnaeus, 1758 | 3 | 3 |
| | Warthog | *Potamochoerus porcus* | Linnaeus, 1758 | 2 | 2 |
| | Cape porcupine | *Hystrix africaeaustralis* | Peters, 1852 | 2 | 2 |
| | *Genet species | *Genetta spp.* | | 4 | 3 |
| | Klipspringer | *Oreotragus oreotragus* | Zimmermann, 1783 | 3 | 2 |
| **All three** | | | | 0 | |
| **Total** | | | | 36 | 29 |

*Genet species are difficult to distinguish separately by field signs.

Table 2: Effect of the fence on vegetation attributes for all transects and transects without holes, with p-values adjusted following sequential Holm-Bonferroni correction. (Height categories were as follows: 1: 0-20cm; 2: 20cm-1m; 3: 1-2m; 4: 2-3m; 5: 3-4m and 6: > 4m. Plant cover percentages were taken along each transect).

| **Transect data** | **Attribute** | **Median inside** | **Median outside** | ***Z*** | **n** | **Adjusted *P*** |
|---|---|---|---|---|---|---|
| **All excluding incomplete** | Vegetation richness | 6 | 5 | 3559 | 101 | <0.001 |
| | Max. vegetation height category | 2 | 2 | 1187 | 101 | NS |
| | Median vegetation height category | 2 | 2 | 1247 | 101 | NS |
| | Percentage of bare ground | 9 | 9 | 1616 | 101 | NS |
| | Percentage of non-woody plant cover | 73 | 64 | 3470.5 | 101 | 0.019 |
| | Percentage of woody plant cover | 18 | 18 | 2008.5 | 101 | NS |
| **Without holes** | Vegetation richness | 6 | 5 | 534.5 | 81 | <0.001 |
| | Percentage of non-woody plant cover | 73 | 65.7 | 738 | 81 | 0.004 |