

Forage patch use by grazing herbivores in a South African grazing ecosystem

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Abstract Understanding how different herbivores make forage patch use choices explains how they maintain an adequate nutritional status, which is important for effective conservation management of grazing ecosystems. Using telemetry data, we investigated nonruminant zebra (*Equus burchelli*) and ruminant red hartebeest (*Alcelaphus buselaphus* subspecies *camaa*), use of burnt patches in a landscape mosaic of nutrient-poor, old grassland interspersed with young, recently burnt, nutrient-rich grass patches. The Mkambati Nature Reserve landscape on the east coast of South Africa provided large grazers with a challenge in finding and using appropriate patches in which to forage to meet their nutritional requirements. In Mkambati, grassland fires, mostly ignited by poachers, induce regrowth of young nutrient-rich grass, which subsequently attract grazers. We tested if the study animals

foraged more in burnt patches than in the unburned grassland and whether burnt patch use was related to the distance to the previously visited burnt patch, burnt patch size, burnt patch age, and distance to areas with high poaching risk using MANOVA. In general, zebra moved faster than red hartebeest, and both species moved faster in unburnt grassland than in burnt patches. Red hartebeest and zebra patch selection were influenced by interpatch distance, patch age, patch size, and poaching risk. A limited set of intrinsic traits, i.e., body mass, digestion strategy, and muzzle width, yielded different patch use rules for the two species. Large ungulates patch use behaviour varied among species and across conditions and was influenced by anthropogenic impacts such as poaching and changed fire regimes. This could potentially affect biodiversity negatively and needs to be factored into management of conservation areas.

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Introduction

Conservation managers attempt to simulate natural processes and maintain heterogeneity of ecosystems to promote conservation outcomes in protected areas (Grant et al. 2011). For large African ungulates whose populations have declined over the last three decades (Craigie et al. 2010), effective conservation management is crucial (Carbutt and Goodman 2013). Understanding how species in a system vary their behaviour to meet their biological needs and deal with anthropogenic impacts should underpin such conservation management strategies (Gibbs et al. 1999). This paper presents the results of a study that investigated the patch use behaviour of two different grazing ungulate species.

Large herbivores feed within forage patches and, in doing so, move through areas where no or little acceptable food is encountered (Bailey et al. 1996; Owen-Smith 2005; Prins 1996), and utilize high-value food by adjusting their movements to habitat structure (de Knegt et al. 2007; Fortin 2003). They accelerate when moving between food items (Shipley et al. 1996) and they spent more time in more rewarding patches (Courant and Fortin 2012; Distel et al. 1995). Normally, feeding is the dominant activity within a forage patch, although they engage in other activities such as walking, resting, and drinking (Green and Bear 1990; Ryan and Jordaan 2005; Shannon et al. 2008). Acceptable forage or habitat patches might not be discernible from a distance, and their location may shift continuously as the forage quality changes due to abiotic circumstances (e.g., fire, rainfall, or flood recession) (Archibald and Bond 2004; de Knegt et al. 2008; Olf et al. 2002; van Beest et al. 2010) or influences from other herbivores (Arsenault and Owen-Smith 2002; Kohi et al. 2011). Herbivores are therefore faced with the challenge of how to find and choose good quality forage patches in a landscape where the location of suitable patches is continuously changing (Bailey et al. 1996; Senft et al. 1987). Understanding how different herbivores make these choices explains how they maintain an adequate nutritional status, which is important for effective conservation management of grazing ecosystems.

Grazing ungulate food occurs in discrete patches (Bailey and Provenza 2008; Prins 1996; Prins and Van Langevelde 2008), and these patches are reasonably homogeneous with respect to some environmental feature(s) (Bailey et al. 1996; Bailey and Provenza 2008; Owen-Smith et al. 2010). Patch selection is scale dependent, and, although herbivores can often afford to be selective on a fine scale (plant part or species), this may not be the case at coarse scales (habitat patch) due to energetic constraints (van Beest et al. 2010). The quality of a patch, and the likelihood that it is selected by an animal, will be influenced by various factors, such as patch size and interpatch distance (Gross et al. 1995; Sibbald and Hooper 2003; Wallace 2008).

In addition, herbivores also need to avoid becoming prey to predators, and do so by responding to predation risk (Creel et al. 2005, 2008; Fortin et al. 2005; Kie 1999; Valeix et al. 2009b). Foragers may choose to ignore predator risk when deciding where to forage and focus on the quality of forage resources and/or other factors (Prins 1996). However, they may also respond by avoiding predators (Creel et al. 2005; Valeix et al. 2009a) or by moving out of harm's way when predators are encountered (Fischhoff et al. 2007; Winnie and Creel 2007). Human disturbance can cause large herbivores to respond in the same way as they do to natural predators (Blom et al. 2004; Manor and Saltz 2003; Morgantini and Hudson 1985; Proffitt et al. 2009), especially in areas with high

poaching incidence (Fischer and Eduard 2007; Hayward 2009).

An area where patch forage behaviour may be particularly important is the fire-prone, nutrient-poor grasslands on the east coast of South Africa. Here, grassland fires induce regrowth of young nutrient-rich grass (Shackleton and Mentis 1992), which may subsequently attract grazers (Allred et al. 2011; Parrini and Owen-Smith 2010). In these coastal grasslands, the biomass productivity is very high, and the grazing pressure is often too low to prevent the accumulation of moribund grass (Shackleton 1990). The moribund, low-nutrient grassland are interspersed with young, recently burned, nutrient-rich grass patches (Shackleton and Mentis 1992). Historically, these grasslands hosted a high diversity of large grazing herbivores (Venter et al. 2014). This landscape provides large grazers with a challenge in finding the appropriate forage patches, from which they can consume suitable food to maintain or surpass their nutritional requirements. The east coast grasslands of South Africa thus form a good model system to study grazer–forage interactions that are typical for the many undergrazed savanna grasslands.

Our study objective was to determine what factors influence forage patch use behaviour of large herbivores. We investigated how two species of large herbivores (zebra and red hartebeest) with contrasting intrinsic traits, used forage patches in a landscape of nutrient poor, moribund grassland, with a mosaic of higher-quality forage patches, under a gradient of higher and lower poaching risk. The differences in patch choice between the two species were investigated to establish any differences as a result of their intrinsic traits, i.e., their physiology and anatomy. This was done by assessing (1) whether burnt patches were selected as preferred forage habitat; (2) the confounding effects of poaching risk; (3) effects of distance from the previous patch, patch size, and patch age (time since burnt), on choice; and (4) contrasting patch choice between zebra and red hartebeest. In order to test for poaching and fire effects, we also tested whether there was a concordant danger and fire gradients within Mkambati, with risk decreasing from the boundary rivers.

Study area

The Mkambati Nature Reserve (Mkambati) is a 77-km² provincial nature reserve situated on the east coast of the Eastern Cape Province, South Africa (31°13'–31°20'S and 29°55'–30°04'E). The climate is mild subtropical with a relatively high humidity (de Villiers and Costello 2006). The high rainfall (1,200 mm annually), mild mean daily temperatures (18 °C winter and 22 °C summer), and presence of abundant streams and wetlands, results in a landscape that is not water limited in any season. Forests occur in small patches (mostly in fire refuge areas) and wetland habitats are abundant. More

than 80 % of Mkambati consists of Pondoland–Natal Sandstone Coastal Sourveld grassland (Mucina et al. 2006). The grassland communities are considered to be nutrient poor (Shackleton et al. 1991; Shackleton and Mentis 1992).

Grassland fire stimulates temporary regrowth high in crude protein (8.6 % compared to 4.6 % in older grassland), phosphorus concentrations (0.1 % compared to 0.05 % in older grassland), and dry matter digestibility (38.6 % compared to 27.1 % in older grassland) (Shackleton 1989). Nutrient concentrations remain elevated for up to 6 months postburn, by which time they are comparable to surrounding unburned grassland (Shackleton and Mentis 1992). Frequent fires cause a continuously changing landscape mosaic of nutrient-rich burnt patches within a matrix of older, moribund grassland and older burnt patches. Most fires are ignited by poachers with the aim to attract animals to certain areas. Poachers cross the two major rivers, i.e., the Mtentu river (on the northeastern boundary) and the Msikaba river (on the southwestern boundary), to poach wildlife in Mkambati. Security patrols and field ranger records show that poachers use rifles, dogs, and snares (Eastern Cape Parks and Tourism Agency, unpublished data). There are also prescribed management burns, but due to the high poacher fire incidence this rarely takes place. Lightning also causes fires, but only few have been recorded on Mkambati, and none during the study period (Eastern Cape Parks and Tourism Agency, unpublished data). Several large herbivore species are present in Mkambati but no large predators (Peinke et al. 2010).

In our study area, the two most dominant grazers are plains zebra (*Equus burchelli*) and red hartebeest (*Alcelaphus buselaphus camaa*). In areas with much moribund vegetation, grazing ruminants such as the red hartebeest face particular constraints because nearly all vegetation biomass has a low quality, which reduces food intake rates (Drescher et al. 2006a, b; van Langevelde et al. 2008). The hartebeest is an example of a concentrate selector; its skull morphology is specially adapted to be very selective at times when good forage is scarce (Schuette et al. 1998). The nonruminant zebra, in contrast, is much more tolerant to poor quality forage but must maintain a high rate of intake to be able to survive on this type of food (Okello et al. 2002; van Soest 1982). We therefore expected that zebra are better able to use more fibrous, older grassland patches than are red hartebeest (Sensenig et al. 2010).

Methods

All poaching incidents recorded by Mkambati field rangers between 2008 and 2010 were mapped and the distance to the nearest major river calculated in metres using ArcGIS (ArcGIS Desktop: Release 10, Environmental Systems Research Institute, Redlands, CA, USA).

Seven zebra (six female and one male) and nine red hartebeest (eight female and one male) were fitted with GPS-UHF collars (Africa Wildlife Tracking CK., RSA), active from September 2008 to August 2011. Ten eland (*Taurotragus oryx*) were also fitted with collars but their data was not used in this study. All animals were darted by an experienced wildlife veterinarian from a Robinson 44 helicopter. The work was approved by, and conducted in strict accordance with, the recommendations in the approved standard protocols of the Animal Ethics Sub-committee of the University of Kwazulu-Natal. All field work was conducted by, or under the supervision of the first author, a staff member of the Eastern Cape Parks and Tourism Agency, as part of the operational activities of the appointed management authority of Mkambati (Eastern Cape Parks and Tourism Agency Act no. 2 of 2010, Eastern Cape Province, South Africa). The animals were in separate harems or herds when they were collared. The collars were set to take a GPS reading every 30 min, and data were downloaded via UHF radio signal. The collars remained functional between 4 and 16 months depending on various factors, including loss of animals to poaching (11 % of $N=26$), lost collars (23 % of $N=26$) natural mortality (3 % of $N=26$), and malfunction (23 % of $N=26$). We suspected that the collars lost could also be attributed to poaching which would increase potential poaching effects to 34 %. Data downloaded from the collars were converted to geographical information system (GIS) format, after which it was manually screened for missing values. Sections of the data with missing values were removed and not used in the analysis.

All grassland fires in Mkambati from January 2007 (18 months before first collars were deployed) to August 2011 were mapped by Mkambati field rangers. Each burnt patch was given a unique ID number, and all unburnt patches (patches that have not burned post-2007) were given the same unique ID number. The patch ID number was linked to the collar data using ArcGIS (ArcGIS Desktop: Release 10). Patch visits were defined as the period from when an individual animal entered a burnt patch or unburnt grassland until it left again. Movement speed S (metre per hour) was calculated using the equation:

$$S = d / t \quad (1)$$

Where time spent t per visit was the sum of 30 min intervals (GPS-UHF data) per visit, and the cumulative distance d covered over that time was the total distance (m) travelled per patch visit.

To compare factors influencing the use of burnt patches, visits to these areas were identified from the GPS data. For this analysis, the location data in unburnt patches was not used. We measured (1) the distance (m) to the nearest major river

which served as a proxy for poaching risk, (2) the distances (m) between burnt patch centroids, (3) burnt patch sizes (ha), and (4) time (days) since burn. A control was established by also measuring the four different factors for all the available burnt patches not visited at the time of each choice. The distance from previous patch (m) was calculated by measuring the distance between the centroid of the burnt patch that the animal had departed to the centroid of the new burnt patch entered. The percentage frequency of use of burnt patches entered to the time since burn was also determined for both hartebeest and zebra. Due to the nature of the data used in the analysis, i.e., burnt patch visits rather than consecutive 30 min GPS points there was no risk of autocorrelation (Dray et al. 2010).

Data analysis

First, we used a linear regression analysis to test whether there was a relationship between number of poaching incidents and distance from the major rivers. The linear regression analysis was performed using IBM SPSS Statistics for Windows, Version 19.0 (IBM Corp., Armonk, NY, USA). We tested whether animals preferred foraging in burnt patches than in the unburned grassland by assessing time spent per visit and speed travelled per visit using a multivariate analysis of variance (MANOVA). To separate species effects from random variations among individuals, the independent variables included both a species identifier and a habitat variable describing whether the animal was in a burnt patch or in unburnt grassland and adding an individual animal identifier as a covariate. Both the time spent and speed travelled variables were log transformed and a total of 11 extreme outliers identified through box plots were removed from the dataset. We tested whether the animals' burnt patch use was related to the distance to the previously visited burnt patch, burnt patch size, burnt patch age (i.e., time since burn in days), and distance to areas with high poaching risk (near the major rivers) using MANOVA. The dependent variables were distance to the previously visited burnt patch, burnt patch size, time since burn, and distance to the nearest major river. The independent variables was whether the patch was visited or not and species, and the covariate was an individual animal identifier. The MANOVA's was performed using IBM SPSS Statistics for Windows, Version 19.0 (IBM Corp.). The MANOVA was complemented with a logistic regression analysis to assess if the probability that a patch was entered depended on the distance to the patch from the previous patch, the size of the patch, the days since it burned, and distance to major river. The logistic regression analysis were done using the R-Statistics package version 2.11 (R-Development-Core-Team 2011).

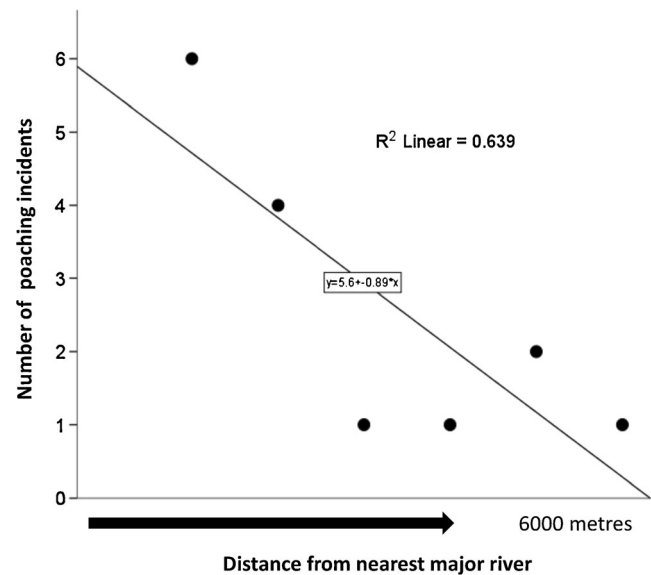


Fig. 1 The relationship between number of poaching incidents (as recorded by field rangers on Mkambati from 2008 to 2010) and distance from the nearest major river

Results

The linear regression established that distance from a major river could statistically significantly predict number of poaching incidents ($F(1, 4)=7.066$, $P=0.05$), and it accounted for 55 % of the explained variability in poaching incidents (Fig. 1). The time animals spent in a patch depended on the habitat type, animal species, and individual animal (Table 1). The species–habitat type interaction was statistically significant (Table 1). Both zebra and red hartebeest spent more time

Table 1 The results of the MANOVA test, testing for the difference between mean time spent within the unburnt grassland and the burnt patches and the difference between mean speed travelled within the unburnt grassland and the fire-patch mosaic

| Source | <i>df</i> ^a | <i>F</i> | <i>P</i> value |
|-------------------|------------------------|----------|-------------------|
| Time spent | | | |
| Individual | 1 | 1.672 | 0.196 |
| Habitat | 1 | 304.486 | <0.0001 |
| Species | 1 | 8.338 | 0.004 |
| Habitat × species | 1 | 7.292 | 0.007 |
| Residuals | 8,523 | | |
| Speed travelled | | | |
| Individual | 1 | 113.463 | <0.0001 |
| Habitat | 1 | 13.401 | <0.0001 |
| Species | 1 | 1,122.71 | <0.0001 |
| Habitat × species | 1 | 5.182 | 0.023 |
| Residuals | 8,523 | | |

Bold data are <0.05

^a Residual degrees of freedom in the model represent visits to forage patches

during visits to burnt patches than to the unburned grassland (Fig. 2). Red hartebeest generally spend more time in both burnt patches and old grassland compared to zebra (Fig. 2). The speed animals moved at while in a patch depended on the habitat type, animal species, and individual animal (Table 1). For speed in a patch, the species–habitat interaction was significant (Table 1). Both red hartebeest and zebra moved equally fast in both habitats, but zebra moved faster than red hartebeest (Fig. 2). Compared to other available patches, both zebra and red hartebeest chose to enter patches closer to the one they last vacated, and there was no difference between the two species in this regard (Table 2 and Fig. 3). Both species entered younger burnt patches more frequently, but zebra were less likely to visit older burnt patches than red hartebeest

(Table 2 and Fig. 3). Although both species selected relatively large patches, zebra mostly used larger patches (Table 2 and Fig. 3). Both species were more likely to enter patches further from the major rivers, but zebra were more likely to do so (Table 2 and Fig. 3). The probability that a new patch was entered depended on the distance to the patch the animal previously visited, the size of the new patch, time since it burned, and the distance to the major river (Table 3).

Discussion

Red hartebeest moved slower and spend more time in patches compared to zebra. This was expected because being

Fig. 2 Time spent and movement speeds per visit to burnt patches and old grassland for zebra and red hartebeest. *Error bars* indicate upper and lower 95 % CI. *Silhouettes* indicate species

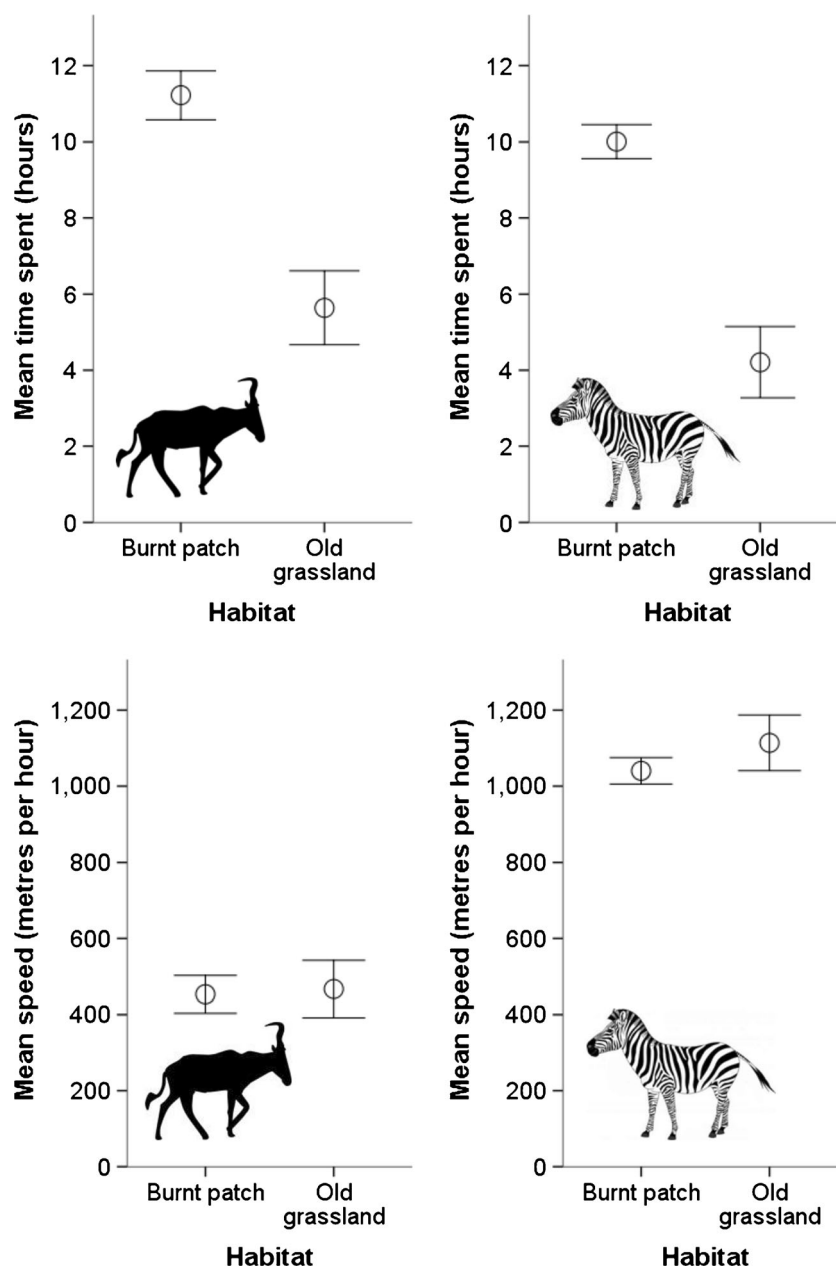


Table 2 The results of the MANOVA test, testing for the distance between the fire patch that the animal left and the new fire patch an animal entered in comparison to the other patches it did not enter; the size of the patch of the new fire patch an animal entered in comparison to the other fire patches it did not enter; the time (days) since burning of the new patch an animal entered in comparison to the other fire patches it did not enter; and the distance from the nearest major river to the new fire patch an animal entered in comparison to the fire patches it did not enter

| Source | <i>df</i> ^a | <i>F</i> | <i>P</i> value |
|-------------------------------|------------------------|-----------|-------------------|
| Distance to previous patch | | | |
| Individual animal | 1.000 | 0.029 | 0.864 |
| Patch being entered | 1.000 | 4,170.870 | <0.0001 |
| Species | 1.000 | 0.212 | 0.645 |
| Patch being entered × species | 1 | 7.016 | 0.008 |
| Residuals | 138,409 | | |
| Patch size | | | |
| Individual animal | 1.000 | 4.322 | 0.038 |
| Patch being entered | 1.000 | 4,459.201 | <0.0001 |
| Species | 1.000 | 58.413 | <0.0001 |
| Patch being entered × species | 1.000 | 42.48 | <0.0001 |
| Residuals | 138,409 | | |
| Days since burn | | | |
| Individual animal | 1.000 | 205.699 | <0.0001 |
| Patch being entered | 1.000 | 244.943 | <0.0001 |
| Species | 1.000 | 317.149 | <0.0001 |
| Patch being entered × species | 1.000 | 0.641 | 0.423 |
| Residuals | 138,409 | | |
| Distance to river | | | |
| Individual animal | 1.000 | 6.013 | 0.014 |
| Patch being entered | 1.000 | 3,426.923 | <0.0001 |
| Species | 1.000 | 7.461 | 0.006 |
| Patch being entered × species | 1.000 | 38.11 | <0.0001 |
| Residuals | 138,409 | | |

Bold data are <0.05

^a Residual degrees of freedom in the model represent visits to forage patches

ruminants they have to spend more time resting while ruminating (Bell 1971). By having a more efficient digestive system red hartebeest thus moved slower through patches in the landscape compared to zebra. Contrary to expectations, red hartebeest used older burnt patches more than zebra. In east Africa, ruminants selected recently burnt patches more compared to nonruminants (Sensenig et al. 2010). The east African grassland biomass is depleted seasonally at the onset of the dry season by high grazing pressure (McNaughton 1976). At Mkambati, grazing pressure is so low that significant accumulation of grass biomass occurs (Shackleton 1990), which, after a few months of growth, results in large quantities of moribund grass. Hartebeest have a specially adapted “long faced” skull morphology that enables them to graze scarce regrowth from between this moribund material when good forage is scarce (Schuette et al. 1998). This was evidenced by

the abundant presence of “feeding holes” in moribund grass patches at Mkambati, made by the muzzle of red hartebeest (Jan A. Venter, personal observation). Although the patches lost their elevated nutritional value due to aging and the build-up of moribund material, this adaptation probably enabled red hartebeest to use older burnt patches more even though there were younger burned patches of better quality available elsewhere.

In contrast to red hartebeest, zebra should be more tolerant of fibrous food, but would have to sustain a much higher intake rate to maintain energy levels when feeding on low-quality forage (Bell 1971; Okello et al. 2002). Zebra moved faster and further than red hartebeest which is consistent with their higher food intake requirements associated with their digestive system. Higher movement rates by zebra compared to ruminants have also been observed in other recent studies (Owen-Smith and Goodall 2014). In hindgut fermenters (nonruminants), faster throughput is an advantage that outweighs their lower digestive efficiency, particularly when feeding on poor-quality foods (Illius and Gordon 1992). When other species of equids were faced with similar trade-offs, their decisions depended on forage quality (Edouard et al. 2010). Unlike red hartebeest, zebra are not able to be highly selective within older burned grasslands, and were therefore dependent on the more nutritious recently burnt patches to maintain their energy levels. In addition, it is probable that zebra with their wider muzzle, are better able to exploit very short grass sprouting on recently burnt patches, and thus maximize bite size and intake rate on these swards (Gordon and Illius 1988) compared to red hartebeest which are not able to do so with equal efficiency. We thus showed that intrinsic traits, such as muzzle width, could possibly carry over into patch use rules in an unexpected way. As muzzle width can evolve relatively independently of body mass, our results show how a very limited set of intrinsic traits (i.e., body mass, digestion strategy, and muzzle width) may yield very different patch use rules for animals that rely on the same resource.

Red hartebeest and zebra in Mkambati selected patches closer to the one they came from, supporting other studies on patch selection (Gross et al. 1995; Sibbald and Hooper 2003). The red hartebeest and zebra in Mkambati chose to use larger burnt patches compared to other available burnt patches. Smaller burnt patches could have higher quality grass compared to larger burns, due to being maintained as closely cropped grazing lawns (Sensenig et al. 2010). In addition, smaller-bodied animals prefer smaller burns (Sensenig et al. 2010). Intensive grazing by smaller herbivores could change grazing conditions and potentially displace other large herbivores (Illius and Gordon 1992). Red hartebeest and zebra chose to visit larger habitat patches, which may be related to interspecific competition. If smaller patches are preferred by smaller grazers (Cromsigt et al. 2009; Sensenig et al. 2010), species such as blesbok (*Damaliscus pygargus phillipsi*)

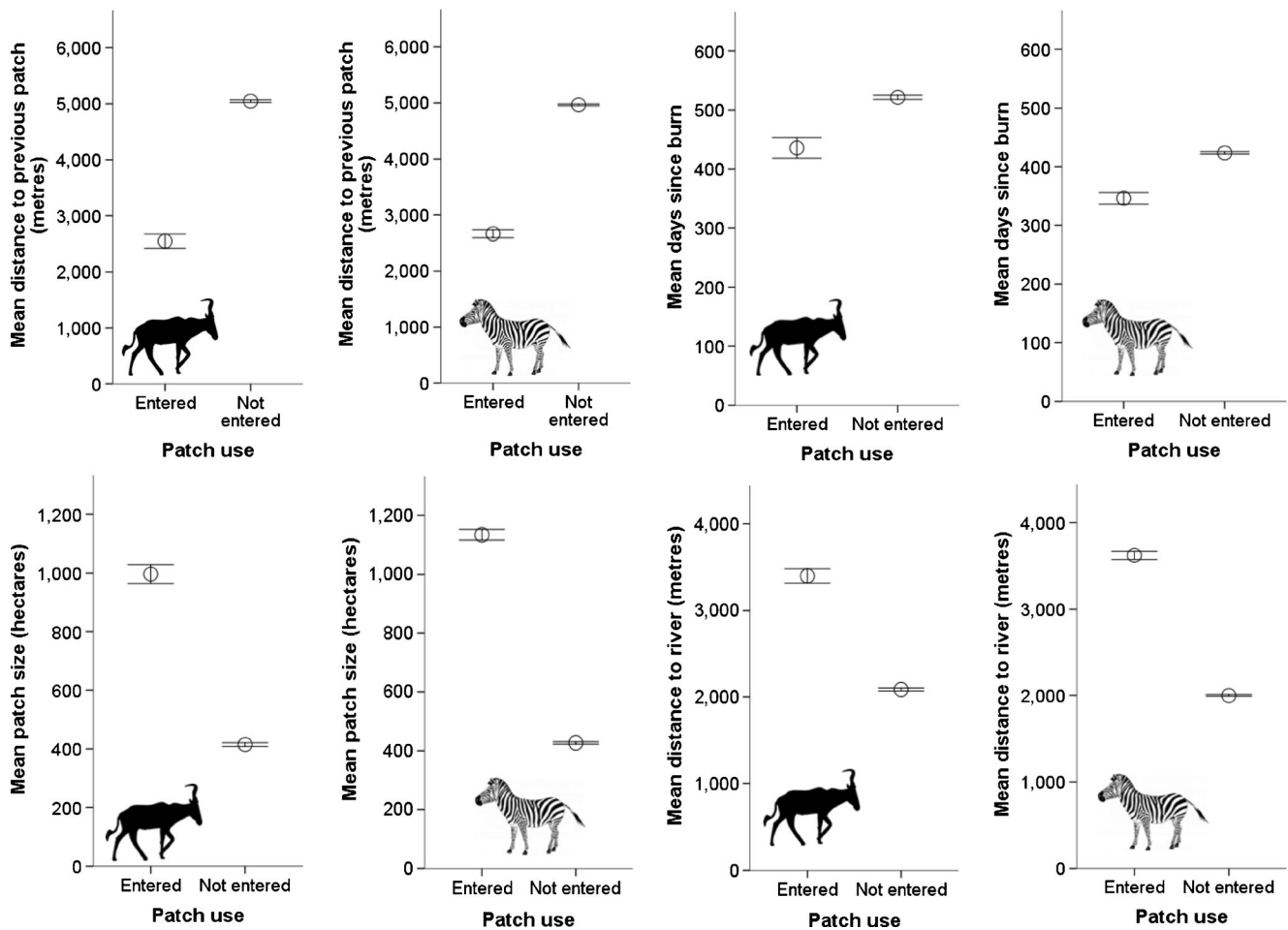


Fig. 3 The effect of interpatch distance, time since burn, patch size, and distance to major river of fire patches entered compared to fire patches not entered by red hartebeest and zebra. Error bars indicate upper and lower 95 % CI. Silhouettes indicate species

(61 kg as compared to 140 kg for red hartebeest and 210 kg for zebra), which were present in large numbers in Mkambati, would have the competitive advantage. By altering the vegetation state (being able to temporarily maintain very small burned patches as closely cropped grazing lawns) (Sensenig et al. 2010), we would predict blesbok to be able to

competitively exclude the larger grazers like red hartebeest and zebra (Illius and Gordon 1992; Prins and Olf 1998).

Both red hartebeest and zebra reduced the probability of encountering poachers by choosing to visit patches further away from major rivers. By focussing on suitable patches within areas of lower 'predation' (or poaching) risk (Gude

Table 3 The results of the logistic regression analysis to assess whether the probability that a new patch is entered depends on the distance from the burnt patch, the patch size, days since burn, and the distance to a major river

| Interaction | Estimate | Std. error | z value | P value |
|--------------------------------------|------------------------|-----------------------|---------|---------|
| Intercept | -1.960 | 0.077 | -25.518 | <0.0001 |
| Distance to previous patch | -5.71×10^{-4} | 1.2×10^{-5} | -47.278 | <0.0001 |
| Patch size | 8.79×10^{-4} | 1.9×10^{-5} | 45.321 | <0.0001 |
| Time since burn (days) | -1.67×10^{-3} | 6.1×10^{-5} | -27.518 | <0.0001 |
| Distance to major river | 3.67×10^{-4} | 1.4×10^{-5} | 26.183 | <0.0001 |
| Species | 1.03 | 0.3 | 3.433 | 0.0005 |
| Distance to previous patch × species | 0.02×10^{-4} | 2.2×10^{-5} | 0.073 | 0.9418 |
| Patch size × species | -2.44×10^{-4} | 3.7×10^{-5} | -6.636 | <0.0001 |
| Time since burn × species | 8.32×10^{-4} | 1.05×10^{-4} | 7.902 | <0.0001 |
| Distance to major river × species | -0.88×10^{-4} | 0.25×10^{-4} | -3.471 | 0.0005 |

Bold data are <0.05

et al. 2006; Thaker et al. 2010), rather than only reacting when ‘predators’ (or poachers) are encountered (Creel et al. 2005; Fortin et al. 2005; Kittle et al. 2008), hartebeest and zebra appear to have a cognitive approach to patch use at a landscape scale by actively avoiding high poaching-risk areas. With ever-increasing poaching in Africa (Craigie et al. 2010; Hayward 2009; Waltert et al. 2009), this is a result with significant implications for protected area management. The consistent unnatural selection of forage areas by ungulates due to poaching impact could have negative impacts on forage resources (Ruggiero 1992), ecosystem services (Brodie et al. 2009; Wright and Duber 2001), and biodiversity through cascading effects (Eisenberg et al. 2013; Ripple and Beschta 2007). This effect could be worse in small- to medium-sized protected areas.

Conclusion

In conservation areas, where managers attempt to simulate the natural processes and heterogeneity of ecosystems (Grant et al. 2011), patch use dynamics of large herbivores is a critical aspect to consider. In this study, we demonstrated how red hartebeest and zebra actively use particular types of burnt patches with suitable forage, and that their choice of foraging patches was influenced by direct and secondary poaching effects. This illustrates that both fire management and anti-poaching action could potentially impact ecosystem resilience (Eisenberg et al. 2013; Ripple and Beschta 2007). This is especially the case for more intensively managed small- to medium-sized conservation areas like Mkambati Nature Reserve.

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