

Poaching impedes the selection of optimal post-fire forage in three large grazing herbivores

Christopher F. Brooke^a, Daniel Fortin^b, Tineke Kraaij^a, Hervé Fritz^{a,c},

Margaret J. Kalule-Sabiti^d and Jan A. Venter^{a,c,e,*}

^aSchool of Natural Resource Management, Nelson Mandela University, George Campus, George, South Africa

^bCentre d'Étude de la Forêt and Département de Biologie, Université Laval, Québec City, Quebec G1V 0A6, Canada

^cREHABS International Research Laboratory, CNRS-Université Lyon 1-Nelson Mandela University, George Campus, Madiba drive 6531 George, South Africa

^dDepartment of Biological and Environmental Sciences, Walter Sisulu University, Mthatha, South Africa

^eEugène Marais Chair of Wildlife Management, Mammal Research Institute, University of Pretoria, Pretoria, South Africa

*Corresponding author at: School of Natural Resource Management – George Campus, Private Bag X 6531, Madiba Drive, George 6530, South Africa. jan.venter@mandela.ac.za

Highlights

- Optimal foraging reveals interplay between forages and resource distribution.
- Optimality models predict grazers can maximise their energy soon after fire.
- Herbivores generally avoided areas where likelihood of poaching was higher.
- Understanding how herbivores use resources is essential to manage populations.
- Allows managers to manipulate environments for resource facilitation of herbivores.

Abstract

Optimal foraging theory provides a powerful quantitative framework to reveal how foraging constraints and options define the interplay between forager and resource distributions. Although illegal hunting threatens wildlife worldwide, few studies have assessed the impact of poaching on the ability of animals to optimise their use of resources. We assessed how the risk of poaching hinders the ability of common reedbuck (*Redunca arundinum*), red hartebeest (*Alcelaphus buselaphus*), and plains zebra (*Equus quagga*) to maximise their daily intake of digestible energy in a complex mosaic of post-fire vegetation, in a small fenced nature reserve. Optimality models predict that all species can maximise their intake of digestible energy by feeding in young post-fire patches (29–37 days). We show that for all species, probability of finding and selectively using such high-value vegetation patches was higher at greater distance from points where poachers were likely to enter the reserve. For reedbuck, optimal patches were used only if they were >3.4 km from poacher entry-points. Red hartebeest became more likely to occur in optimal vegetation patches as the distance to likely poacher entry points increased. Only zebra maximized their daily intake of digestible energy regardless of the distance to poachers, but still selected areas where poaching was less likely. This study demonstrates how spatial patterns in poacher activities

and post-fire vegetation interact to shape herbivore distribution. Understanding how herbivores track and use this post fire green-up of vegetation is important for protected area managers to understand the trade-offs that herbivores make when foraging.

Keywords: Anthropogenic fire; Energy maximization; Green wave; Habitat selection; Optimal foraging, Protected areas

1. Introduction

Foraging behaviour is fundamental to multiple aspects of theoretical and applied ecology, from spatial and community ecology to ecological conservation and management. Optimal foraging theory provides a robust quantitative framework to understand dietary choice (MacArthur and Pianka, 1966), and the distribution of consumers (Babin et al., 2011). The theory, however, is most effective for immobile resources, such as dead mealworms consumed by birds or plants by herbivores (Sih and Christensen, 2001). This success is likely linked to the predictability of forage distribution, and thus to the ability of consumers to locate and consume optimal resources. In fact, consumers with imperfect information about resource distribution tend to have broader diets than expected for omniscient animals (Fortin, 2003), and to return to recently visited foraging patches (Merkle et al., 2017; Merkle et al., 2015; Piper, 2011).

Although most plants are immobile, their characteristics change over time, creating strong spatio-temporal structure in ecological stoichiometry (Ellis and Leroux, 2017). Herbivores impact plant availability, while plants can react to herbivory by changing their morphology and chemical composition (Karban and Myers, 1989). Abiotic factors (e.g., air temperature, sunlight, rain, fire) also create rapid changes in plant characteristics (e.g., biomass, nitrogen, carbon and fibre content, Augustine et al., 2018; Marshall et al., 2018). Still some herbivores can track those changes. For example, several species of North American large herbivore have been shown to 'surf' green-up waves of growing vegetation during spring (Raynor et al., 2015; Bischof et al., 2012). Admittedly green-up waves can be rather predictable over space (e.g. progressively occurring at increasing altitudes). By contrast, phenological changes in vegetation following rainfall can display strong stochastic patterns; yet, nomadic Thomson's gazelles (*Gazella thomsoni thomsoni* Günther) demonstrate an ability to make adaptive movement to match the spatial distribution of the most profitable vegetation patches (Fryxell et al., 2005; Fryxell et al., 2004). Likewise, fires can create 'ecological magnets' that result in the strong selection of post-fire regrowth in recently burned areas (Raynor et al., 2015). Foraging optimally may be particularly important in grassy areas where fires are frequent (Hopcraft et al., 2010). In grassland management fire is commonly used, as grazing pressure is often too low to prevent the build-up of moribund vegetation (Venter et al., 2014a). Furthermore, setting up multiple small fires at different times of the year can create a complex mosaic of grass patches at different phenological stages and thus nutrient availability (Brooke et al., 2018; Venter et al., 2014a, Venter et al., 2014b; Shackleton and Mentis, 1992). The ability of grazing herbivores to make timely adjustments to such fine-scale patterns of heterogeneity in dynamic landscapes remains poorly documented.

Energy-maximizing herbivores feeding on post-fire grass swards should avoid old patches because tall, mature plants are low in nitrogen and poorly digestible (Fryxell, 1991). They

should also avoid very young vegetation because the low biomass strongly constrains plant intake rate (Bergman et al., 2001). The synergistic impact of these digestive and availability constraints is such that maximum intake rate of digestible energy is achieved by consuming vegetation of intermediate maturation stages (Fryxell, 1991).

Foragers, however, may not always select plant types having the highest energy value (Sih and Christensen, 2001). Game theory demonstrates the fitness advantages of trading-off forage for safety (Vincent and Brown, 2005). At a broad scale, prey may simply avoid areas where they would be exposed to high risk. At a finer scale, fearful consumers may leave foraging patches relatively early (Jacob and Brown, 2000; Brown, 1999; Brown et al., 1999; Fraser and Huntingford, 1986), and they can become less selective for energy rewarding patches. For example, bison (*Bison bison* Linnaeus) are less selective for plants maximizing their energy intake rate where the risk of encountering a wolf (*Canis lupus* Linnaeus) is relatively high (Fortin and Fortin, 2009). Behavioural change to the risk of human encounters is often like that of predators (Lima and Dill, 1990). In many ecosystems humans have become the apex predator (Martin et al., 2013). Herbivore perception of predation risk is influenced by habitat characteristics, with many herbivores choosing to avoid risky areas (Krishna et al., 2016). Habitat selection decisions can become rather complex in human dominated systems (Krishna et al., 2016), as land-use change may result in habitat loss and the fear of humans may impact the use of some areas (Wilmers et al., 2013) or the time available for feeding (Ordiz et al., 2012). For example, in Murchison Falls National Park (unfenced at the time) in Uganda the effects of illegal hunting and associated fires set by the poachers attracted herbivores to forage outside the confines of the park where fires were set with the intention of attracting herbivores and thus increasing their risk of being poached (Oneka, 1990).

We tested whether multiple large herbivores could find and make selective use of post-fire grass sward ages that would maximise their daily energy intake, and we determined whether the risk of encounter with poachers impeded the selection of those patches. Specifically, we first identified the age of post-fire grass sward that maximized the daily intake of digestible energy for three sympatric large herbivores, namely, common reedbuck (*Redunca arundinum* Boddaert, hereafter reedbuck), red hartebeest (*Alcelaphus buselaphus* subsp. *Caama* Geoffroy Saint-Hilaire) and plains zebra (*Equus quagga* Boddaert, hereafter zebra) in Mkambati Nature Reserve (hereafter Mkambati). Second, we used GPS-collar information from each of the three herbivores to determine if they selected those patches optimally for energy maximization, and if they did, whether or not their selection varied with the distance to likely poacher entry points on the reserve (as identified by Venter et al., 2014a). On Mkambati poachers set fires (with the intention of attracting animals to hunt) further away from reserve infrastructure (Fig. 1) where the likelihood of getting caught is lower (Brooke et al., 2018). Here we assess the effect of illegal human activities on the ability/willingness of ungulates to make selective use of energy-rich forage and discuss the likely results for successful conservation of grazing herbivores.

Legend

- ☆ Infrastructure
- Roads
- ➡ Likely poacher entry points

Vegetation type

- ☐ Merged grasslands
- ☐ Forests
- ☐ Rocky outcrops
- ☐ *Themeda* grasslands
- ☐ Wetlands



Fig. 1. Reserve map of Mkambati Nature Reserve including vegetation types (Adapted from Shackleton, 1989), likely poacher entry points and reserve infrastructure (buildings on Mkambati).

2. Methods

2.1. Study site

Mkambati Nature Reserve (31.26°S and 29.99°E) is a small (9200 ha) fenced nature reserve situated on the south-east coast of South Africa within the Pondoland Centre for Plant Endemism (De Villiers and Castello, 2013). Mkambati is managed by Eastern Cape Parks and Tourism Agency under a land claim settlement agreement with the local Mkambati community being the land owners (Kepe, 2004). Mkambati is bounded on two sides by major natural rivers (Mtentu River to the north and the Msikaba River to the south) with the only manmade boundary being a fence inland to the west (Shackleton, 1989). High annual rainfall (1200 mm with a minimum of 50 mm expected monthly) and mild temperatures (average of 18 °C in winter and 22 °C in summer) give rise to a mild subtropical climate with relatively high humidity (Shackleton et al., 1991). The vegetation is dominated by Pondoland-Ugu Sandstone Coastal Sourveld interspersed with patches of indigenous forest (scarp and southern coastal forest), wetlands and rocky outcrops (Mucina et al., 2006). The vegetation is nutrient poor resulting from the underlying geology and high levels of leaching (Venter and Kalule-Sabiti, 2016; Mucina et al., 2006). Frequent fires result in a dynamic mosaic of recently burnt, nutrient rich grasses and older, more moribund grasses (Brooke et al., 2018; Venter et al., 2014b). The peak fire season on Mkambati is during winter and the mean fire return interval of approximately three years (Brooke et al., 2018). These fires

create a short-term spike in nutrients (within the first six months after fire) in vegetation (Shackleton, 1989). Most of the fires are ignited by poachers near to the likely poacher entry points (Fig. 1) with the intention of attracting herbivores to areas where they are easier to hunt (Brooke et al., 2018; Van Wilgen and Forsyth, 2010; Shackleton, 1989). Mkambati management undertakes limited prescribed burning due to the high incidence of fires associated with poaching (Venter et al., 2014b). Aside from poaching the only other predation of herbivores comes from a small population of black-backed jackal (*Canis mesomelas*, Schreber), however few mortalities have been attributed to them (Peinke and Gerber, 2016).

2.2. Study species

GPS/VHF satellite collars (manufactured by African Wildlife Tracking) were fitted to three large herbivore species on Mkambati. NAN collars (Appendix S1) were satellite (Iridium) collars, whereas AU collars (Appendix S1) were GPS/UHF collars. All collars included a VHF transmitter (148/152 MHz). These species were reedbuck (small bodied ruminant with a narrow muzzle), red hartebeest (medium bodied ruminant with a narrow muzzle enabling them to selectively crop short grasses) and zebra (medium bodied non-ruminant with a broad muzzle preventing them from selectively cropping short grass) (Appendix S1). Collars were fitted at varying times throughout the study period (2008–2016) and recorded GPS positions at fixed time intervals of 30 min for red hartebeest and zebra 60 min for reedbuck over varied time periods (Appendix S1). Variation on recording intervals resulted from the expected lifespan of the collar and when the collars were fitted (Appendix S1). All animals were darted by an experienced veterinarian from a Robinson 44 helicopter. Work on red hartebeest and zebra began in 2008 and was approved by and carried out in accordance with the recommendations in the standard protocols of the animal ethics sub-committee of the University of KwaZulu-Natal (Approval number 012/09/Animal). Field work was conducted by or under the direct supervision of author JAV while he was a staff member of 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). Work on reedbuck began in October 2015 and was approved by and carried out in accordance with the protocols set out by the animal ethics research committee at the Nelson Mandela University (Approval number RA 0214) and with a government issued permit (Threatened or protected species permit number O 02263).

2.3. Vegetation types and distance to poachers

Mkambati's original vegetation classification was recognised into six distinct grassland vegetation types (Shackleton, 1989). For the purposes of this study we consolidated these into two grassland types (after Brooke et al., 2018), namely those affected by fire (merged grasslands; combining *Aristida junciformis-Helichrysum mixtum*, *Cymbopogon validus-Digitaria natalensis*, *Festuca costata-Albuca setosa*, *Stoebe vulgaris-Athanasia calva* and *Tristachya leucothrix-Loudetia simplex* communities) and those not affected by fire (coastal *Themeda* grasslands, *Themeda triandra-Centella asiatica* community). Our assessments of daily intake of digestible energy only pertained to the merged grasslands that are affected by fires and burnt frequently. Indigenous forests, rocky outcrops and wetlands also occur

interspersed throughout the grasslands (Shackleton, 1989). We only looked at the short-term response of herbivores to recently burnt vegetation and thus did not consider temporal and seasonal variability in climate. To assess the influence of poaching, the main form of predation on the reserve (Venter et al., 2014a), we calculated the distance from each point (both random and observed; see statistical analysis of animal movement for detailed description) to the nearest likely poacher entry point (personal communication: V. Mapiya, Mkambati Nature reserve Manager, Eastern Cape, South Africa). The calculation was performed using the 'near tool' GIS using ArcGIS version 10.1 (ESRI, 2013).

2.4. Daily intake of digestible energy

For the merged grasslands we used the post fire field data provided by Shackleton (1989) to calculate the biomass (B) and digestibility (D) based on the two grassland communities (*T. leucothrix* – *L. simplex* and *C. validus* – *D. natalensis* communities) that predominate in Mkambati. Biomass increased with the number of days since the last fire ($days_{post\ fire}$) ($R^2 = 0.67$, $n = 42$) following: $B = 570.10 \exp(-115.83/(days_{post\ fire}))$, where the proportion of digestibility for ruminants feeding merged grasslands decreased with $days_{post\ fire}$ ($R^2 = 0.78$, $n = 41$) following: $D = -9.675 \log(days_{post\ fire}) + 84.184$. Because equids generally digest a smaller portion of the vegetation than ruminants, we used Eq. (5) of Vermorel and Martin-Rosset (1997) to transform plant digestibility for ruminants to expected digestibility for horses and used the values in subsequent analysis for zebra.

Instantaneous intake rate (I , g/min) of vegetation for ruminants was based on a type II functional response (Wilmshurst et al., 2000): $I = R_{max} B / (b + B)$, where R_{max} (g/min) is the maximum instantaneous cropping rate and b (g/m²) is the vegetation biomass at which intake is half of the maximum for a given herbivore species, and V is the biomass of vegetation (g/m²). To determine R_{max} and b for the ruminant species, we developed a relationship based on Table 1 of Wilmshurst et al. (2000). We found that R_{max} and b covaried with body mass (M) following $R_{max} = 0.1617 \times M + 1.9771$ ($R^2 = 0.94$, $n = 15$) and $b = 0.5768 \times M$ ($R^2 = 0.60$, $n = 15$). These allometric relationships were then applied to estimate vegetation intake rate for the ruminant species assuming a body mass of 38 kg for reedbeek and 120 kg for red hartebeest.

Instantaneous rate of vegetation intake (I) for zebra (non-ruminant) was taken from Okello et al. (2002) who provided relationships between I and bite size and cropping time, together with the relationship between bite size and V . On this basis, we were thus able determine the relationship between I and V .

To estimate the I_{DDE} (MJ/day), we consider two additional constraints, a time constraint:

where the maximum daily intake is constrained by T_{max} , the maximum time that can be spent foraging in a day (780 min / day, Wilmshurst et al. (2000); and a digestive constraint:

where the constant 18.41 kJ/g corresponds to the gross energy content of vegetation (National Research Council, 1996), and V_i , is the daily voluntary intake (kg/day) of vegetation given ad libitum forage availability. Meissner and Paulsmeier (1995) showed that V_i (range: 16 and 62 g/M^{0.9}/day) varied linearly with ratio between D and neutral detergent fibre

Table 1

Step selection model (SSF) of GPS satellite collared herbivore species on Mkambati Nature Reserve throughout the study period (2008–2016).

Parameter	β value	Robust SE	SE ratio	CI	X^2	P
Reedbuck						
Log step length (m)	-4.692	0.273	2.761	0.535	294.621	< 0.0001
Step length (m)	1.056	0.401	2.997	0.786	6.943	0.008
Cos(θ) (degree)	0.548	0.069	2.122	0.135	63.049	< 0.0001
F_{IDDE}	-0.286	0.204	0.531	0.4	1.968	0.16
Distance to poachers (km)	0.052	0.086	1.738	0.169	0.365	0.56
$F_{IDDE} \times$ distance to poachers	0.089	0.035	0.482	0.069	6.062	0.01
k-fold: \hat{r}_S global 0.74 (range: 0.46–0.98) $n = 100$						
Red Hartebeest						
Log step length	-3.792	0.376	17.439	0.737	101.689	< 0.0001
Step length	0.760	0.173	15.403	0.339	19.350	< 0.0001
Cos(θ)	-0.736	0.250	21.893	0.49	8.639	0.003
F_{IDDE}	0.294	0.535	3.509	1.049	0.301	0.58
Distance to poachers	0.052	0.105	14.236	0.206	0.241	0.62
$F_{IDDE} \times$ distance to poachers	0.376	0.109	2.802	0.214	0.001	0.001
k-fold: \hat{r}_S global 0.50 (range: 0.10–0.83) $n = 100$						
Zebra						
Log step length	-4.186	0.096	1.384	0.188	1890.306	< 0.0001
Step Length	-0.205	0.095	1.266	0.186	4.710	0.03
Cos(θ)	1.154	0.041	1.447	0.08	793.490	< 0.0001
F_{IDDE}	0.498	0.146	0.815	0.286	11.638	0.0006
Distance to poachers	0.097	0.041	1.205	0.08	0.570	0.02
$F_{IDDE} \times$ distance to poachers	0.038	0.039	0.717	0.076	0.946	0.33
k-fold: \hat{r}_S global 0.85 (range: 0.32–0.97) $n = 100$						

($NDF;vD:NDF$) in Africa. Given that NDF varies linearly with both D and V_i (Wilmshurst et al., 2000) and that Meissner and Paulsmeier (1995) analysis is based on D with a similar range (0.24–0.83) than the one we studied (0.16–0.61), we assumed that the ratio $D:NDF$ took its lowest of 0.3 when $D = 0.16$, and its highest value of 2.4 for $D = 0.61$, and increased linearly within that range ($D:NDF = 0.0467D - 0.447$). On this basis, we converted our estimates of D into $D:NDF$ ratios, and then used the relationship between V_i and $D:NDF$ for grass provided in Table 3 of Meissner and Paulsmeier (1995) to estimate the voluntary intake of vegetation by our two ruminant species (reedbuck and red hartebeest). For zebra, we estimated V_i for our estimates of D based on the relationship between NDF and D and between V_i and NDF (Edouard et al., 2008). Our estimation of V_i were estimated assuming of body mass of 38 kg for reedbuck, 120 kg for hartebeest, and 300 kg for zebra.

The daily intake of digestible energy (MJ/day) was then estimated from:

2.5. Statistical analysis of herbivore movement

We used step selection functions (SSFs) to determine how foragers selectively adjust their movements to habitat features (I_{DDE} , distance to poachers and the interaction therein). Specifically, we tested if the relative probability of occurrence in optimal vegetation patches varies with the distance to poachers. SSFs are based on a comparison between observed (i.e. recorded by GPS collars) and random steps, with a step being the straight line linking two successive locations (Turchin, 1998). For all individuals, each observed step was paired with 10 random steps sharing the same starting location but differing in length and direction. We used the ‘create random points’ tool of ArcGIS version 10.1 (ESRI, 2013) to draw the endpoint locations of random steps within predetermined buffers for each species (2.5 km for reedbuck, 5.4 km for red hartebeest and 6.2 km for zebra). The buffers encompassed the 99 percentile of step lengths for each species. The lengths of random steps were thus drawn uniformly within these buffers, while turning angles were drawn uniformly over 360° (see Nicosia et al., 2017 for details) and encompassed varying forage quality and distance to the likely poacher entry points.

We estimated SSFs from the observed and associated random steps using conditional logistic regression (Fortin et al., 2005), and SSFs were structured as follows:

where $Step_{Length}$ is step length, and the SSF includes both $Step_{Length}$ and $\log(Step_{Length})$ together with $\cos(\vartheta)$ is the cosine of the tuning angle between successive steps as suggest by Nicosia et al. (2017). F_{IDDE} is a dichotomic variable representing the optimal maturation stage (i.e. number of days after a fire) for the maximization of I_{DDE} (i.e. the F_{IDDE} coefficient indicates that occurrence in optimal patches occurs more frequently than can be expected randomly). F_{IDDE} took a value of 1 when the vegetation patch was within 10 days of the maturation stage; otherwise, F_{IDDE} was set to 0. $D_{Poacher}$ was the distance (km) to the nearest likely poacher entry point. The steps with a higher SSF score ($w[x]$) are those more likely to be chosen by the animal.

GPS locations were recorded for animals at frequent time intervals, and because of this successive steps were not independent of one another; such autocorrelation does not affect β values but may bias their standard errors (Craiu et al., 2008). By dividing observations into

independent clusters (Fortin et al., 2005; Ling and Wei, 1989; Wei et al., 1989) the approach allowed us to calculate robust standard errors of SSF parameters through the use of robust sandwich estimation of the covariance matrix. Analysis of autocorrelation of the deviance residuals for each species showed that autocorrelation disappeared after a lag of 19 fixes (19 h) in reedbuck, 16 (8 h) in red hartebeest and 25 (12.5 h) in zebra. On this basis we created 25–30 clusters for each species, which should be sufficient to provide robust variance for regression coefficients (Prima et al., 2017).

A k -fold cross validation was run to determine the model robustness following Fortin and Fortin (2009), an SSF was built using 80% randomly selected strata. The SSF was then used to estimate the $w[x]$ scores for the observed and random locations of the 20% withheld strata. The observed and random strata were ranked against each other from 1 to 11 (potential ranks given that each stratum included one observed and 10 random locations) based on their $w[x]$ scores where 1 was the lowest and 11 was the highest possible rank. Ranks of these observations were then tallied into 11 potential bins and Spearman rank correlation (r_s) was performed between the bins ranking and its associated frequency. For each of the three study species the process was done 100 times and the mean and range of r_s was reported.

3. Results

Studied grassland patches were available at a broad range of post fire ages, ranging from 1 to 2949 days after fire. Within this range, we found that grazers should maximise their I_{DDE} by feeding on relatively young vegetation patches (Fig. 2). Specifically, patches that have burned 29 days ago would be optimal for both reedbuck and zebra, whereas 37 days old patches would be optimal for hartebeest.

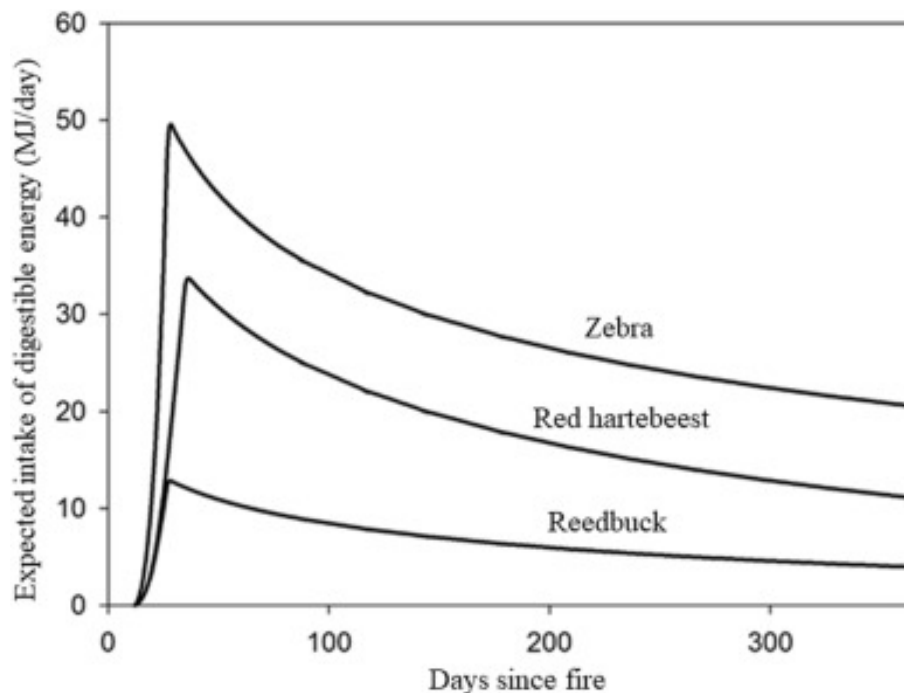


Fig. 2. Expected intake rate of digestible energy for red hartebeest, zebra and common reedbuck on Mkambati Nature Reserve.

The movements of the study species were influenced by some level of directional persistence (represented by $\cos[\vartheta]$), together with the spatial distribution of patches maximizing their I_{DDE} and the distance to the nearest likely poacher entry point (Table 1). The distances to the nearest likely poacher entry point were 4.1 ± 0.8 km (average \pm standard deviation) for reedbuck ($n = 23,216$ observation; $N = 5$ individuals), 4.6 ± 1.2 km for red hartebeest ($n = 95,338$, $N = 9$), and 4.9 ± 1.3 km for zebra ($n = 96,302$; $N = 7$). Among the three species, only zebra selected optimal vegetation patches near the poacher entry points (i.e. zebra were not influenced by the interaction between F_{IDDE} and the distance to poachers, $P = 0.33$) as they were strongly driven by F_{IDDE} ($P = 0.0006$). Furthermore, zebra selected optimal vegetation patches throughout the rest of the reserve (occurrence in optimal patches was higher than could be expected randomly), irrespective of the distance to the nearest likely poacher entry point. This suggests that zebra was the only species to maximise their energy regardless of the distance to the nearest likely poacher entry point, however the probability of occurrence increases in both optimal and suboptimal vegetation as the distance to likely poacher entry points increases (Fig. 3). By contrast, red hartebeest and reedbuck were both influenced by the interaction between F_{IDDE} and the distance to likely poacher entry points and selected optimal patches only when away from poacher entry points ($P = 0.01$ and $P = 0.001$ respectively; Table 1). Red hartebeest quickly became much more likely to occur in optimal rather than non-optimal vegetation patches as the distance to likely poacher entry points increased (Fig. 3). The SSF predicted a higher probability of occurrence of reedbuck in optimal (i.e. where they could maximise their energy) than non-optimal patches only when distances exceeded 3.4 km from the likely poacher entry points (Fig. 3). To verify this relationship, we re-ran the analysis based on subsets of all observations. Consistently with the analysis of all observations (Table 1, Fig. 3), we found an avoidance of optimal patches (F_{IDDE} coefficient: -0.21 ± 0.11 , $p = 0.05$) when restricting the analysis to the observed steps occurring within 3.4 km from potential entry points, whereas we observed a strong selection for optimal patches (F_{IDDE} coefficient: 0.35 ± 0.07 , $p < 0.001$) when restricting the analysis to further locations.

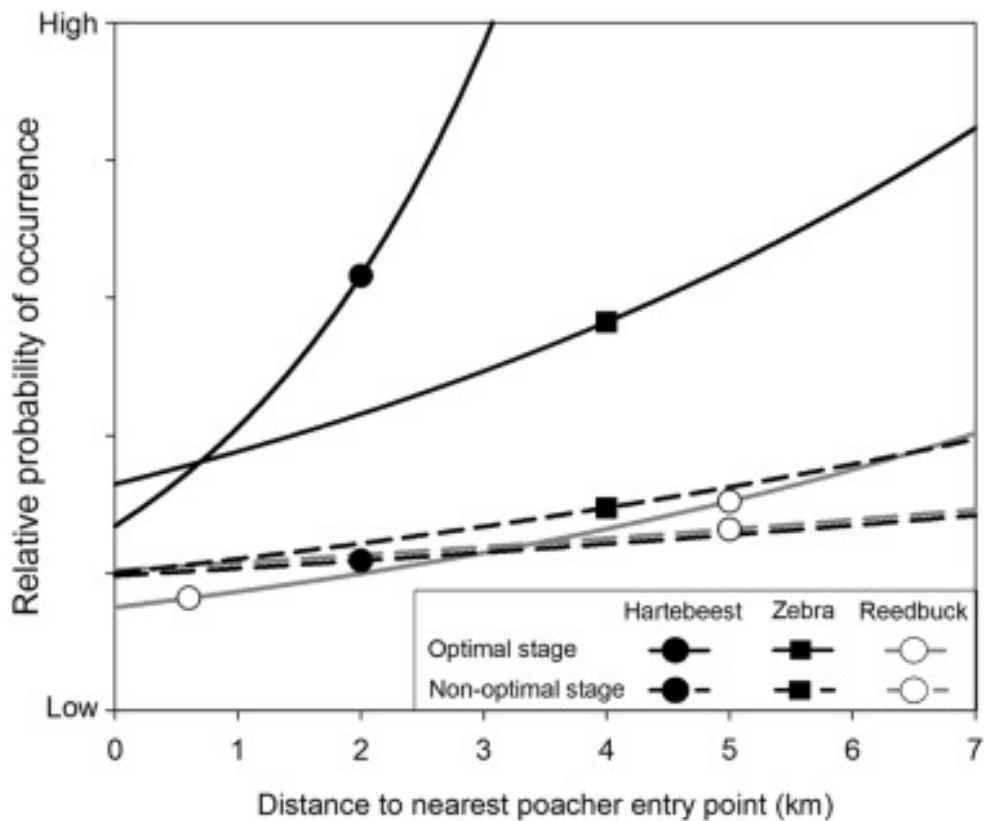


Fig. 3. Relative probability of occurrence of three herbivores (red hartebeest, zebra and common reedbuck) on Mkambati Nature Reserve in relation to the nearest likely poacher entry point in optimal and non-optimal vegetation. Optimal vegetation was within 10 days of the optimal vegetation stage for herbivores to maximise their instantaneous intake of digestible vegetation.

4. Discussion

We demonstrated that three contrasting large grazing herbivores were able to find and make selective use of post-fire patches at a maturation stage that maximized their daily energy intake. Importantly, the movements of these herbivores were further driven by an apprehension of poachers; all species were most likely to occur in optimal vegetation patches located far from poaching activities, and most species even adjusted forage selection to poaching risk (feeding in areas further away from the likely poacher entry points). Our study demonstrates how the optimal decisions of herbivores for energy maximization can be impeded by poaching activities.

We showed that all three herbivore species (two ruminants and a non-ruminant) can maximise their daily intake of digestible energy at a relatively early maturation stage of post-fire vegetation. Hack et al. (2002) pointed out that, as a non-ruminant, zebra can exploit coarse vegetation of low nutrient value; we showed that although they can tolerate low nutrient vegetation, that is not necessarily what they do. Zebra selected vegetation patches maximizing their daily energy intake throughout the reserve, irrelevant of the distance to poachers as they are driven more by the quality of vegetation than the risk of poaching. The occurrence of zebra in optimal patches was higher than could be expected randomly throughout the reserve (Table 1), even though their relative probability of occurrence increased further away from poachers. The selection of zebra for young

vegetation is well documented. In Botswana, zebra adjusted their movements to match low to intermediate vegetation green-ups (Bartlam-Brooks et al., 2013). In South Africa, both zebra and red hartebeest spend more time during visits to the burnt rather than unburnt vegetation (Venter et al., 2014a), and particularly younger vegetation (less than four years in fynbos) (Kraaij and Novellie, 2010). Interestingly, this appears to be one of the first studies linking reedbeest's use to relatively young vegetation. Previous studies into reedbeest have all made the link between reedbeest's need for dense vegetation and wetlands that offer adequate cover (du Plessis et al., 2016; Skinner and Chimimba, 2005; Howard, 1986). Here we used optimal foraging theory to demonstrate that not only did all three herbivores forage in recently burned grassland patches, but they located and selectively exploited the optimal patches where they could maximise I_{DDE} within a complex patch mosaic of burnt and unburnt vegetation.

Testing predictions of energy maximization principles for several grazers explains how adaptive evolution has shaped the foraging decisions of sympatric species, how current foraging constraints control diet choices, and the extent to which specific habitat attributes (e.g. spatial pattern of risk) can hamper the rate of energy acquisition. Nonetheless such tests remain rare. Optimal diet has been identified for multiple large herbivores, without being tested (Wilmshurst et al., 2000), while many field studies have outlined the preference of large grazers for recently burnt vegetation without assessing the optimal choices or by studying a single herbivore (Allred et al., 2011; Raynor et al., 2015). Our multi-species study demonstrates an overlap in the optimal choice of large grazers, and in the actual choices they made. Importantly, our study also demonstrates that all three grazers adjust their foraging pattern with respect to the main areas where poachers access the reserve, but with more contrast in selection expressed in highly mobile species (red hartebeest and zebra).

On Mkambati, poaching risk decreased with the distance to the poacher entry points (Venter et al., 2014a) as did the occurrence of fire (Brooke et al., 2018). Outside of protected areas similar poaching tactics have been noted where the incidence of illegal human activities is higher closer to the outside of protected area boundaries rather than areas further away from protected areas (Martin et al., 2013; Lindsey et al., 2011; Oneka, 1990). Mortality risk further depends on the main targets of poachers and distance from poachers. Smaller species such as reedbeest are not the preferred prey for poachers on Mkambati (personal communication: V. Mapiya, Mkambati Nature Reserve Manager, Eastern Cape, South Africa). Larger species such as eland (*Tragelaphus oryx*, Pallas) are preferred prey by hunter on Mkambati, however red hartebeest and zebra are also readily hunted. On Dwesa Nature Reserve (150 km south of Mkambati along the coast), pressure from humans resulted in the local extinction of red hartebeest in the 1990's (Hayward, 2009). In fact, human selection for larger prey species such as red hartebeest and zebra is well established (Martin et al., 2013). Additionally, poachers are likely to kill more common species (Martin et al., 2013), which on Mkambati are red hartebeest ($n = 386 \pm 7$) and zebra ($n = 222 \pm 4$) compared to rarer reedbeest ($n = 29 \pm 6$) (Peinke and Gerber, 2016). On Mkambati there is a linear relationship ($r^2 = 0.64$) between the number of poaching incidents and the distance to the nearest likely poacher entry point (Venter et al., 2014a). We have shown here how the spatial and species-specific patterns of poaching risk impacted the movement of all three herbivores species.

As with the other herbivores, zebra tended to avoid moving towards areas where encounters with poachers were most likely. Unlike the other grazers, however, zebra selected optimal vegetation patches throughout the reserve. Reedbuck and red hartebeest were only selective foragers when relatively far from areas of high poaching risk. Red hartebeest had a much higher probability of occurrence as the distance to likely poacher entry points increased than that of reedbuck (Fig. 3). Reedbuck are sensitive to poachers (du Plessis et al., 2016) and the slight increase in probability of occurrence as the distance to likely poacher entry points increased could result from reedbuck having fixed territories (i.e. low mobility) (du Plessis et al., 2016; Skinner and Chimimba, 2005). In risky areas, reedbuck even avoided optimal patches in favour of older, taller vegetation. The preference of reedbuck for tall vegetation and areas that can offer adequate protection has been frequently reported (du Plessis et al., 2016; Skinner and Chimimba, 2005; Venter and Kalule-Sabiti, 2016). Red hartebeest, a species sought for by poachers, displayed the steepest increase in selection for optimal patches with increasing distance from risky areas (i.e. likely poacher entry points). Overall, these observations for the three large grazers are in line with the general expectation that, when foragers are concerned about potential threats, they tend to leave risky areas relatively soon, search less intensively for optimal resources, and less rigorously exploit each resource patch (Bedoya-Perez et al., 2013; Fortin and Fortin, 2009).

Our study provides evidence that poachers not only remove wildlife from protected areas, but they also impact the ecological stoichiometry. On Mkambati, fires are intentionally set with the intention of attracting animals to areas where they could be easily hunted (Brooke et al., 2018). Poachers thus purposely alter post-fire vegetation ages by igniting grassland patches, thereby manipulating the chemical composition (e.g. nitrogen concentration), biomass and the digestibility of plant material used by large herbivores. Moreover, we showed that poachers can generate spatial patterns in the consumption and assimilation of plant nutrients by large grazers. Given sufficient pressure and limited resources, poachers could have negative effects on grazer populations that go beyond the removal of individuals by preventing the use of optimal vegetation. Our study also revealed that the tactic of burning areas to attract grazers would not be as effective for all species. The approach should not be highly effective for reedbuck as they are habitat specialists (du Plessis et al., 2016; Skinner and Chimimba, 2005) and tend to use older vegetation when near poaching areas. By contrast, burning might be effective for attracting zebra. Zebra have the lowest probability of occurrence near the poacher's entry points; however, their probability of occurrence in an optimal patch at a poacher entry is equivalent to that of zebra in a non-optimal patch located at 5.1 km (i.e., relative probability at 0 km equals that at 5.1 km, Fig. 3).

5. Conservation implication

We have demonstrated that large herbivores can track the green-up in post-fire vegetation. Zebra are consistently driven by forage quality as they selectively move to vegetation patches that would maximise their daily intake of digestible energy. By contrast the foraging choices of red hartebeest and reedbuck were negatively affected by poaching with both species only selectively using vegetation patches that would maximise their energy when located relatively far away from poachers. Furthermore, red hartebeest quickly became

more likely to utilize optimal vegetation as the distance to the likely poacher entry points increased. Understanding how herbivores track and use this wave of nutrient rich early post-fire vegetation is important for guiding management efforts in protected areas. For example, managers could respond to the manipulation of habitat quality by poachers through setting up their own fires away from poacher entry points. By strategically timing their fires in responses to poachers (e.g. based on Fig. 2), they should be able to keep grazers away from poachers because, everything else being equal, all three species already avoid poacher entry points (Fig. 3). While fire may be a valuable management tool in small fenced protected areas, managers should account for the fact that poachers also use fire to attract and extract animals from protected areas. The actions of managers thus might be most effective if they are also done in response to poachers' attempts to alter local resource quality.

Data accessibility

Animal movement data is available from Afrimove: afrimove.org.

CRedit authorship contribution statement

Christopher F. Brooke:Conceptualization, Data curation, Formal analysis, Project administration, Writing - review & editing.**Daniel Fortin:**Conceptualization, Data curation, Formal analysis, Writing - review & editing.**Tineke Kraaij:**Conceptualization, Data curation, Formal analysis, Writing - review & editing.**Hervé Fritz:**Conceptualization, Data curation, Formal analysis, Writing - review & editing.**Margaret J. Kalule-Sabiti:**Conceptualization, Funding acquisition.**Jan A. Venter:**Conceptualization, Data curation, Formal analysis, Project administration, Writing - review & editing.

Declaration of competing interest

We the authors of “Poaching impedes the selection of optimal post-fire forage in three large grazing herbivores” hereby declare that there are no conflicts of interest hindering the publication of this paper or that have occurred throughout the duration of the study.

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