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► **To cite this version:**

Christopher Brooke, Daniel Fortin, Tineke Kraaij, Hervé Fritz, Margaret Kalule-Sabiti, et al.. Poaching impedes the selection of optimal post-fire forage in three large grazing herbivores. *Biological Conservation*, 2020, 241, pp.108393. 10.1016/j.biocon.2019.108393 . hal-03093391

HAL Id: hal-03093391

<https://hal.science/hal-03093391v1>

Submitted on 25 Nov 2022

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1 **Poaching impedes the selection of optimal post-fire forage by a guild of large herbivores**

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14 Short title: Poaching impedes optimal foraging in herbivores

15 **Abstract**

16 Optimal foraging theory provides a powerful quantitative framework to reveal how foraging
17 options and constraints define the interplay between forager and resource distributions.
18 Although illegal hunting threatened wildlife species all over the globe, few studies have
19 assessed the impact of poaching on the ability of animals to consume the most energy
20 rewarding resources. Thus there is a paucity of information on the impact of illegal hunting
21 on wildlife populations beyond direct animal removal. We assessed how the risk of poaching
22 hinders the ability of common reedbuck (sc name), red hartebeest (sc name), and plains zebra
23 (sc name) to maximise their daily intake of digestible energy in a complex mosaic of post-fire

1 sward patches, in a small fenced nature reserve. Optimality models predict that all species can
2 maximise their intake of digestible energy by feeding in young post-fire patches (29-37 days,
3 depending on species). Movement analysis of GPS-collared individuals indicates that, when
4 far from the likely poacher entry points, all species were able to find and selectively use post-
5 fire patches at the phenological stage that maximized their energy intake. The selection of
6 reedbuck for optimal patches vanished, however, when <3.4 km from likely poacher entry
7 points. Similarly, red hartebeest gradually became much more likely to occur in optimal
8 vegetation patch as the distance to likely poacher entry points increased. Only zebra
9 maximised their daily intake of digestible energy regardless of the distance to likely poacher
10 entry points. Still zebra selected areas of the reserve where poachers were less likely to be
11 encountered, as did the other grazers. Overall, this study demonstrates how the distance to
12 poachers and the forage maturation stage interact to shape the spatial distribution of
13 herbivores. Understanding how herbivores track and use this post fire green-up of vegetation
14 is important for protected area managers areas to understand the trade-offs that herbivores
15 make when foraging. This information has conservation and management significance,
16 especially given that poachers use fires to attract wildlife in post-fire patches. Our study
17 provides protected area managers the potential ability to manipulate and facilitate the
18 environment to benefit herbivores, including in direct response of habitat alteration activities
19 of poachers.

20 Key words: Energy maximisation, herbivores, optimal foraging, anthropogenic fire, habitat
21 selection, protected areas, green wave.

22 **Introduction**

23 Foraging behaviour is fundamental to multiple aspects of theoretical and applied
24 ecology, from spatial and community ecology to ecological conservation and management.
25 Optimal foraging theory provides a robust quantitative framework to understand the dietary

1 choice (MacArthur & Pianka, 1966), and the spatial organisation of consumers (Babin et al.,
2 2011). The theory, however, is most effective for immobile resources, such as dead
3 mealworms consumed by birds or plants by herbivores (Sih & Christensen, 2001). This
4 success is likely linked to the predictability of food distribution, and thus to the ability of
5 consumers to locate and consume optimal resources. In fact, consumers with imperfect
6 information about resource distribution tend to have broader diets than expected for
7 omniscient animals (Fortin, 2003), and to return to recently visited foraging patches (Piper,
8 2011; Merkle, Sigaud, & Fortin, 2015; Merkle, Potts, & Fortin, 2017).

9 Although most plants are immobile, their characteristics change over time, creating
10 strong spatio-temporal structure in ecological stoichiometry (Ellis & Leroux, 2017).
11 Herbivores impact plant availability, while plants can react to herbivory by changing their
12 morphology and chemical composition (Karban & Myers, 1989). Abiotic factors (e.g., air
13 temperature, sunlight, rain, fire) also create rapid changes in plant characteristics (e.g.,
14 biomass, nitrogen, carbon and fibre content, Kim, Jobbágy, & Jackson, 2016; Augustine et
15 al., 2018; Kral et al., 2018; Marshall et al., 2018). Still some herbivores can track those
16 changes. For example, several species of North American large herbivore have been shown to
17 ‘surf’ green-up waves of growing vegetation during spring (Bischof et al., 2012; Raynor,
18 Joern, & Briggs, 2015). Admittedly green-up waves can be rather predictable over space
19 (e.g., gradually occurring at increasing altitudes). By contrast, phenological changes in
20 vegetation following rainfall can display strong stochastic patterns; yet, nomadic Thomson’s
21 gazelles (*Gazella thomsoni thomsoni* Günter) demonstrate an ability to make adaptive
22 movement to match the spatial distribution of the most profitable vegetation patches (Fryxell,
23 Wilmshurst, & Sinclair, 2004; Fryxell et al., 2005). Likewise, fires can create ‘ecological
24 magnets’ that result in the strong selection of post-fire regrowth in recently burned areas
25 (Raynor, Joern, & Briggs, 2015). Foraging optimally may be particularly important in grassy

1 areas where fires are frequent (Hopcraft, Olf, & Sinclair, 2010). In grassland management
2 fire is commonly used, as grazing pressure is often too low to prevent the build-up of
3 moribund vegetation (Sensenig, Demment, & Laca, 2010; Venter, Nabe-Nielsen, et al.,
4 2014). Furthermore, setting up multiple small fires at different times of the year can create a
5 complex mosaic of grass patches at different phenological stages and thus nutrient
6 availability (Shackleton & Mentis, 1992; Venter, Nabe-Nielsen, et al., 2014; Brooke, Kraaij,
7 & Venter, 2018). The ability of grazing herbivores to make timely adjustments to such fine-
8 scale patterns of heterogeneity in dynamic landscapes remains poorly documented.

9 Energy maximizing herbivores feeding on post-fire grass swards should avoid old
10 patches because tall, mature plants are low in nitrogen and poorly digestible (Fryxell, 1991).
11 They should also avoid very young vegetation because the low biomass strongly constrains
12 plant intake rate (Bergman et al., 2001). The synergistic impact of these digestive and
13 availability constraints is such that maximum intake rate of digestible energy is achieved by
14 consuming vegetation of intermediate maturation stages (Fryxell, 1991).

15
16 Foragers, however, may not always select plant types having the highest energy value
17 (Sih & Christensen, 2001). Game theory demonstrates the fitness advantages of trading-off
18 food for safety (Vincent & Brown, 2005). At a broad scale, prey may simply avoid areas
19 where they would be exposed to high risk. At a finer scale, fearful consumers may leave
20 foraging patches relatively early (Fraser & Huntingford, 1986; Brown, 1999; Brown,
21 Laundré, & Gurung, 1999; Jacob & Brown, 2000), and they can become less selective for
22 energy rewarding patches. For example, bison (*Bison bison* Linnaeus) are less selective for
23 plants maximizing their energy intake rate where the risk of encountering a wolf (*Canis lupus*
24 Linnaeus) is relatively high (Fortin et al., 2009). Behavioural change to the risk of human
25 encounters is often similar to that of predators (Lima & Dill, 1990). In many ecosystems

1 humans have become the apex predator (Martin, Caro, & Kiffner, 2013), and this
2 phenomenon is well described as predators induced fear on prey (Preisser, Bolnick, &
3 Benard, 2005). Herbivore perception of predation risk is influenced by habitat characteristics,
4 with many herbivores choosing to avoid risky areas (Krishna, Kumar, & Isvaran, 2016).
5 Habitat selection decisions can become rather complex in human dominated systems
6 (Krishna, Kumar, & Isvaran, 2016), as land-use change may result in habitat loss and the fear
7 of humans may impact the use of some areas (Wilmers et al., 2013) or the time available for
8 feeding (Ordiz et al., 2012). For example, in Murchison Falls National Park (unfenced at the
9 time) in Uganda the effects of illegal hunting outside of the park not only affected the
10 numbers of large herbivores but also attracted individuals to forage outside the confines of
11 the park where the risk of being poached was higher (Oneka, 1990).

12 We tested whether multiple large herbivores could find and make selective use of
13 post-fire sward patches that would maximize their daily energy intake, and we determined
14 whether the risk of encounter with poachers impeded the selection of those patches.
15 Specifically, we first identified the maturation stage of post-fire patches that maximized the
16 daily intake of digestible energy for three sympatric large herbivores, namely, southern
17 reedbuck (*Redunca arundinum* Boddaert, hereafter reedbuck), red hartebeest (*Alcelaphus*
18 *buselaphus* subsp. *Caama* Geoffroy Saint-Hilaire) and plains zebra (*Equus quagga* Boddaert,
19 hereafter zerba) in Mkambati Nature Reserve (hereafter Mkambati). Second, we used GPS-
20 collar information from each of the three herbivores to determine if they selected those
21 patches optimally for energy maximization, and if they did, whether or not there selection
22 varied with the distance to likely poacher entry points on the reserve (as identified by Venter,
23 Nabe-Nielsen, et al., 2014). On Mkambati poachers set fires (with the intention of attracting
24 animals to hunt) further away from reserve infrastructure (Fig. 1) where the likelihood of
25 getting caught is lower (Brooke, Kraaij, & Venter, 2018). Here we test the effect of illegal

1 human activities on the ability/willingness of ungulates to make selective use of energy-rich
2 forage, and discuss the likely consequences for successful conservation of grazing herbivores.

3 **Methods**

4 *Study site*

5 Mkambati Nature Reserve (31.26°S and 29.99°E) is a small (9200 ha) fenced nature
6 reserve situated on the south-east coast of South Africa within the Pondoland Centre for Plant
7 Endemism (De Villiers & Castello, 2013). Mkambati is managed by Eastern Cape Parks and
8 Tourism Agency under a land claim settlement agreement with the local Mkambati
9 community being the land owners (Kepe, 2004). Mkambati is bounded on two sides by major
10 natural rivers (Mtentu River to the north and the Msikaba River to the south) with the only
11 manmade boundary being a fence inland to the west (Shackleton, 1989). High annual rainfall
12 (1200 mm) and mild temperatures (average of 18°C in winter and 22°C in summer) give rise
13 to a mild subtropical climate with relatively high humidity (Shackleton et al., 1991). The
14 vegetation is dominated by Pondoland-Ugu Sandstone Coastal Sourveld interspersed with
15 patches of indigenous forest (scarp and southern coastal forest), wetlands and rocky outcrops
16 (Mucina et al., 2006). The vegetation is nutrient poor resulting from the underlying geology
17 and high levels of leaching (Mucina et al., 2006; Venter & Kalule-Sabiti, 2016). Frequent
18 fires result in a dynamic mosaic of recently burnt, nutrient rich grasses and older, more
19 moribund grasses (Venter, Prins, et al., 2014; Brooke, Kraaij, & Venter, 2018). The peak fire
20 season on Mkambati is during winter and the mean fire return interval of approximately three
21 years (Brooke, Kraaij, & Venter, 2018). These fires create a short-term spike in nutrients
22 (within the first six months after fire) in vegetation (Shackleton, 1989). Most of the fires are
23 ignited by poachers with the intention of attracting herbivores to areas where they are easier
24 to hunt (Shackleton, 1989; Van Wilgen & Forsyth, 2010; Brooke, Kraaij, & Venter, 2018).

1 Mkambati management undertakes limited prescribed burning due to the high incidence of
2 fires associated with poaching (Venter, Prins, et al., 2014).

3 *Study species*

4 GPS/VHF satellite collars (African Wildlife Tracking) were fitted to three large
5 herbivore species on Mkambati. These species were reedbuck (small bodied ruminant with a
6 narrow muzzle), red hartebeest (medium bodied ruminant with a narrow muzzle enabling
7 them to selectively crop short grasses) and zebra (medium bodied non-ruminant with a broad
8 muzzle preventing them from selectively cropping short grass) (Appendix 1). Collars were
9 fitted at varying times throughout the study period (2008 – 2016) and recorded GPS positions
10 at fixed time intervals of either 30 or 60 minutes over varying time periods (Appendix 1). All
11 animals were darted by an experienced veterinarian from a Robinson 44 helicopter. Work on
12 red hartebeest and zebra began in 2008 and was approved by and carried out in accordance
13 with the recommendations in the standard protocols of the animal ethics sub-committee of the
14 University of KwaZulu-Natal (Approval number 012/09/Animal). Field work was conducted
15 by or under the direct supervision of author JAV while he was a staff member of Eastern
16 Cape Parks and Tourism Agency as part of the operational activities of the appointed
17 management authority of Mkambati (Eastern Cape Parks and Tourism Agency Act no. 2 of
18 2010, Eastern Cape Province, South Africa). Work on reedbuck began in October 2015 and
19 was approved by and carried out in accordance with the protocols set out by the animal ethics
20 research committee at the Nelson Mandela University (Approval number RA 0214) and with
21 a government issued permit (Threatened or protected species permit number O 02263).

22 *Land cover types and distance to poachers*

23 Mkambati's original vegetation classification recognised six distinct grassland
24 vegetation types (Shackleton, 1989). For the purposes of this study we consolidated these into

1 two grassland types (after Brooke et al., 2018), namely those affected by fire (merged
 2 grasslands; combining *Aristida junciformis*-*Helichrysum mixtum*, *Cymbopogon validus*-
 3 *Digitaria natalensis*, *Festuca costata*-*Albuca setosa*, *Stoebe vulgaris*-*Athanasia calva* and
 4 *Tristachya leucothrix*-*Loudetia simplex* communities) and those not affected by fire (coastal
 5 *Themeda* grasslands, *Themeda triandra*-*Centella asiatica* community). Our assessments of
 6 daily intake of digestible energy only pertained to the merged grasslands that are affected by
 7 fires. Indigenous forests, rocky outcrops and wetlands also occur interspersed throughout the
 8 grasslands (Shackleton, 1989). To assess the influence of poaching, the main form of
 9 predation on the reserve (Venter, Nabe-Nielsen, et al., 2014), we calculated the distance from
 10 each point (both random and observed; see statistical analysis of animal movement for
 11 detailed description) to the nearest likely poacher entry point (personal communication: V.
 12 Mapiya, Mkambati Nature reserve Manager, Eastern Cape, South Africa). The calculation
 13 was performed using the ‘near tool’ GIS using ArcGIS version 10.1 (Esri, 2012).

14 *Daily intake of digestible energy*

15 For the merged grasslands we used the field data provided by Shackleton (1989) to
 16 calculate the biomass (B) and digestibility (D) based on the two grassland communities (T .
 17 *leucothrix* – L . *simplex* and C . *validus* – D . *natalensis* communities) that predominate in
 18 Mkambati Nature Reserve. Biomass increased with the number of days since the last fire
 19 ($days_{post\ fire}$) ($R^2 = 0.67$, $n = 42$) following:

$$20 \quad B = 570.10 \exp\left(\frac{-115.83}{days_{post\ fire}}\right),$$

21 where the proportion of digestibility for ruminants feeding merged grasslands decreased with
 22 $days_{post\ fire}$ ($R^2 = 0.78$, $n = 41$) following:

$$23 \quad D = -9.675 \ln(days_{post\ fire}) + 84.185$$

1 Because equids generally digest a smaller portion of the vegetation than ruminants, we used
2 Eq. 5 of Vermorel & Martin-Rosset (1997) to transform plant digestibility for ruminants to
3 expected digestibility for horses and used the values in subsequent analysis for zebra.

4 Instantaneous intake rate (I , g/min) of vegetation for ruminants was based on a type II
5 functional response (Wilmshurst, Fryxell, & Bergman, 2000):

$$6 \quad I = \frac{R_{max} \times B}{b + B}$$

7 where R_{max} (g/min) is the maximum instantaneous cropping rate and b (g/m²) is the
8 vegetation biomass at which intake is half of the maximum for a given herbivore species, and
9 V is the biomass of vegetation (g/m²). To determine R_{max} and b for our three ruminant species,
10 we developed a relationship based on Table 1 of Wilmshurst, Fryxell, & Bergman (2000).

11 We found that R_{max} and b covaried with body mass (M) following

12 $R_{max} = 0.1617 \times M + 1.9771$ ($R^2 = 0.94$, $n = 15$) and $b = 0.5768 \times M$ ($R^2 = 0.60$, $n =$
13 15). These allometric relationships were then applied to estimate vegetation intake rate for the
14 ruminant species assuming a body mass of 38 kg for reedbuck and 120 kg for red hartebeest.

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

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

$$20 \quad I_1 = \frac{I_{IDE} \times T_{max}}{1000}$$

1 where the maximum daily intake is constrained by T_{max} , the maximum time that can be spent
2 foraging in a day (780 min / day, Wilmshurst, Fryxell, & Bergman (2000); and a digestive
3 constraint:

$$4 \quad I_2 = \frac{V_I \times D \times 18.41}{1000}$$

5 where the constant 18.41 kJ/g corresponds to the gross energy content of vegetation (National
6 Research Council, 1996), and V_I is the daily voluntary intake (kg/day) of vegetation given *ad*
7 *libitum* food availability. Meissner & Paulsmeier (1995) showed that V_I (range: 16 and 62 g /
8 $M^{0.9}$ / day) varied linearly with ratio between D and NDF ($D:NDF$). Given that NDF varies
9 linearly with both D and V_I (Wilmshurst, Fryxell, & Bergman, 2000) and that Meissner &
10 Paulsmeier (1995) analysis is based on D with a similar range (0.24 – 0.83) than the one we
11 studied (0.16 - 0.61), we assumed that the ratio $D:NDF$ took its lowest of 0.3 when $D = 0.16$,
12 and its highest value of 2.4 for $D = 61\%$, and increased linearly within that range ($D:NDF =$
13 $0.0467D - 0.447$). On this basis, we converted our estimates of D into $D:NDF$ ratios, and then
14 used the relationship between V_I and $D:NDF$ for grass provided in Table 3 of Meissner &
15 Paulsmeier (1995) to estimate the voluntary intake of vegetation by our two ruminant species
16 (reedbuck and red hartebeest). For zebra, we estimated V_I for our estimates of D based on the
17 relationship between NDF and D and between V_I and NDF (Edouard et al., 2008). Our
18 estimation of V_I were estimated assuming of body mass of 38 kg for reedbuck, 120 kg for
19 hartebeest, and 300 kg for zebra.

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

$$21 \quad I_{DDE} = \min(I_1, I_2)$$

22 *Statistical analysis of herbivore movement*

1 We used step selection functions (SSFs) to determine how foragers selectively adjust
 2 their movements to habitat features. SSFs are based on a comparison between observed (i.e.
 3 recorded by GPS collars) and random steps, with a step being the straight line linking two
 4 successive locations (Turchin, 1998; Fortin et al., 2005). For all individuals, each observed
 5 step was paired with 10 random steps sharing the same starting location but differing in
 6 length and direction (Fig. 2). We used the ‘create random points’ tool of ArcGIS version 10.1
 7 (Esri, 2012) to draw the endpoint locations of random steps within predetermined buffers for
 8 each species (2.5 km for reedbuck, 5.4 km for red hartebeest and 6.2 km for zebra). The
 9 buffers encompassed the 99 percentile of step lengths for each species. The lengths of
 10 random steps were thus drawn uniformly within these buffers, while turning angles were
 11 drawn uniformly over 360° (see Nicosia et al., 2017 for details).

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

14 w

$$15 \quad (x) = \exp(\beta_1 Step_{Length} + \beta_2 \log[Step_{Length}] + \beta_3 \cos(\theta) + \beta_4 F_{IDDE} + \beta_5 D_{Poacher} +$$

$$16 \quad \beta_6 F_{IDDE} \times D_{Poacher})$$

17 where $Step_{Length}$ is step length, and the SSF includes both $Step_{Length}$ and $\log(Step_{Length})$
 18 together with $\cos(\theta)$ is the cosine of the tuning angle between successive steps as suggest by
 19 Nicosia et al. (2017). F_{IDDE} is a dichotomic variable representing the optimal maturation
 20 stage (i.e. number of days after a fire) for the maximisation of I_{DDE} . F_{IDDE} took a value of 1
 21 when the vegetation patch was within 10 days of the maturation stage; otherwise, F_{IDDE} was
 22 set to 0. $D_{Poacher}$ was the distance (km) to the nearest likely poacher entry point. The steps
 23 with a higher SSF score ($w[x]$) are those more likely to be chosen by the animal.

1 GPS locations were recorded for animals at frequent time intervals, and because of
2 this successive steps were not independent of one another; such autocorrelation does not
3 affect β values but may bias their standard errors (Craiu, Duchesne, & Fortin, 2008). By
4 dividing observations into independent clusters (Ling & Wei, 1989; Wei, Lin, & Weissfeld,
5 1989; Fortin et al., 2005) the approach allowed us to calculate robust standard errors of SSF
6 parameters through the use of robust sandwich estimation of the covariance matrix. Analysis
7 of autocorrelation of the deviance residuals for each species showed that autocorrelation
8 disappeared after a lag of 19 fixes (19 hours) in reedbuck, 16 (8 hours) in red hartebeest and
9 25 (12.5 hours) in zebra. On this basis we created 25-30 clusters for each species, which
10 should be sufficient to provide robust variance for regression coefficients (Prima, Duchesne,
11 & Fortin, 2017).

12 A k -fold cross validation was run to determine the model robustness (Boyce et al.,
13 2002; Fortin et al., 2008, 2009). Following Fortin et al. (2009), an SSF was built using 80%
14 randomly selected strata. The SSF was then used to estimate the $w[x]$ scores for the observed
15 and random locations of the 20% withheld strata. The observed and random strata were
16 ranked against each other from 1 to 11 (potential ranks given that each stratum included one
17 observed and 10 random locations) based on their $w[x]$ scores where 1 was the lowest and 11
18 was the highest possible rank. Ranks of these observations were then tallied into 11 potential
19 bins and Spearman rank correlation (r_S) was performed between the bins ranking and its
20 associated frequency. For each of the three study species the process was done 100 times and
21 the mean and range of r_S was reported.

22 **Results** Studied grassland patches were available at a broad range of maturation
23 stages, ranging from 1 to 2949 days after fire. Within this range, we found that grazers should
24 maximize their I_{DDE} by feeding on vegetation patches at relative early maturation stages (Fig.

1 2). Specifically, patches that have burned 29 days ago would be optimal for both reedbuck
2 and zebra, whereas 37 days old patches would be optimal for hartebeest.

3 The movements of the study species were influenced by some level of directional
4 persistence (represented by $\cos[\theta]$), together with the spatial distribution of patches
5 maximizing their I_{DDE} and the distance to the nearest likely poacher entry point (Table 1).
6 The distances to the nearest likely poacher entry point were 4.1 ± 0.8 km (average \pm standard
7 deviation) for reedbuck ($n = 23,216$ observation; $N = 5$ individuals), 4.6 ± 1.2 km for red
8 hartebeest ($n = 95,338$, $N = 9$), and 4.9 ± 1.3 km for zebra ($n = 96,302$; $N = 7$). Among the
9 three species, only zebra selected optimal vegetation patches near the poacher entry points.
10 Furthermore, zebra foraged optimally throughout the rest of the reserve, irrelevant of the
11 distance to the nearest likely poacher entry point. This suggests that zebra were the only
12 species to maximise their energy regardless of the distance to the nearest likely poacher entry
13 point, however the probability of occurrence increases in both optimal and suboptimal
14 vegetation as the distance to likely poacher entry points increases (Fig. 3). By contrast, red
15 hartebeest and reedbuck selected optimal patches only when away from poacher entry points
16 (Table 1). Red hartebeest quickly became much more likely to occur in optimal rather than
17 non-optimal vegetation patches as the distance to likely poacher entry points increased (Fig.
18 3). The SSF predicted a higher probability of occurrence of reedbuck in optimal (i.e. where
19 they could maximise their energy) than non-optimal patches only when distances exceeded
20 3.4 km from the likely poacher entry points (Fig. 3). To verify this relationship, we re-ran the
21 analysis based on subsets of all observations. Consistently with the analysis of all
22 observations (Table 1, Fig. 3), we found an avoidance of optimal patches (F_{IDDE} coefficient: -
23 0.21 ± 0.11 , $p = 0.05$) when restricting the analysis to the observed steps occurring within 3.4
24 km from potential entry points, whereas we observed a strong selection for optimal patches
25 (F_{IDDE} coefficient: 0.35 ± 0.07 , $p < 0.001$) when restricting the analysis to farther locations.

1 **Discussion**

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

9 We showed that all three herbivore species (two ruminants and a non-ruminant) can
10 maximise their daily intake of digestible energy at a relatively early maturation stage of post-
11 fire vegetation. Hack, East, & Rubenstein (2002) pointed out that, as a non-ruminant, zebra
12 can exploit coarse vegetation of low nutrient value; we showed that although they can tolerate
13 low nutrient vegetation, that is not necessarily what they do. Zebra selected vegetation
14 patches maximizing their daily energy intake throughout the reserve, irrelevant of the
15 distance to poachers. The selection of zebra for young vegetation is well documented. In
16 Botswana, zebra adjust their movements to match low to intermediate vegetation green-ups
17 (Bartlam-Brooks et al. 2013). In South Africa, both zebra and red hartebeest spent more time
18 during visits to the burnt rather than unburnt vegetation (Venter, Nabe-Nielsen, et al., 2014),
19 particularly younger vegetation (less than four years in fynbos) (Novellie & Kraaij, 2010).
20 Here we used optimal foraging theory to demonstrate that not only did these herbivores
21 forage in recently burned grassland patches, but they located and selectively exploited the
22 optimal patches for energy maximization within a complex patch mosaic.

23 Testing predictions of energy maximization principles for several grazers informs on
24 how adaptive evolution have shaped the foraging decisions of sympatric species, how current
25 foraging constraints control diet choices, and how much specific habitat attributes (e.g.

1 spatial pattern of risk) can hamper the rate of energy acquisition. Such tests remain rare
2 however. Optimal diet has been identified for multiple large herbivores, without being tested
3 (Wilmshurst, Fryxell, & Bergman, 2000), while many field studies have outlined the
4 preference of large grazers for recently burnt vegetation without assessing the optimal
5 choices or by studying a single herbivore (Fuhlendorf et al., 2009; Allred et al., 2011;
6 Raynor, Joern, & Briggs, 2015). Our multi-species study demonstrates an overlap in the
7 optimal choice of a guild of large grazers, and in their actual choice. Importantly, our study
8 also demonstrates all studied grazers adjust their foraging pattern with respect to the main
9 areas where poachers access the reserve, but with more contrast in selection expressed in
10 highly mobile species (red hartebeest and zebra).

11 On Mkambati, poaching risk decreased with the distance to the poacher entry points
12 (Venter, Nabe-Nielsen, et al., 2014). Outside of protected areas similar poaching tactics have
13 been noted where the incidence of illegal human activities is higher closer to the outside of
14 protected area boundaries rather than areas further away from protected areas (Oneka, 1990;
15 Lindsey et al., 2011; Kiffner, Stoner, & Caro, 2013; Martin, Caro, & Kiffner, 2013).
16 Furthermore Kiffner et al. (2013) found that 62 % of hunters admitted to hunt on the outskirts
17 of their villages or farms. Mortality risk further depends on the main targets of poachers.
18 Smaller species such as reedbuck are not the preferred prey for poachers on Mkambati
19 (personal communication: V. Mapiya, Mkambati Nature Reserve Manager, Eastern Cape,
20 South Africa). Red hartebeest and zebra, however, are more heavily hunted. On Dwesa
21 Nature reserve (150 km south of Mkambati on the coast), pressure from humans resulted in
22 the local extinction of red hartebeest in the 1990's (Hayward, 2009). In fact, human selection
23 for larger prey species such as red hartebeest and zebra is well established (Martin, Caro, &
24 Kiffner, 2013). Additionally poachers are likely to kill more common species (Martin, Caro,
25 & Kiffner, 2013), which on Mkambati are red hartebeest ($n = 386 \pm 7$) and zebra ($n = 222 \pm$

1 4) compared to far fewer reedbuck ($n = 29 \pm 6$) (Peinke & Gerber, 2016). We have shown
2 here how the spatial and species-specific patterns of poaching risk impacted the movement of
3 all three herbivores species.

4 As with the other herbivores, zebra tended to avoid moving towards areas where
5 encounters with poachers were most likely. Unlike the other grazers, however, zebra selected
6 optimal vegetation patches throughout the reserve (i.e. they were driven more by energy
7 maximisation than the risk of poaching). Reedbuck and red hartebeest were only selective
8 foragers when relatively far from areas of high poaching risk. Red hartebeest had a much
9 higher probability of occurrence as the distance to likely poacher entry points increased than
10 that of reedbuck (Fig. 3). Reedbuck are known to be sensitive to poachers (du Plessis, Peel, &
11 Child, 2016) and the low shift in probability of occurrence as the distance to likely poacher
12 entry points increased could result from reedbuck having fixed territories (i.e. low mobility)
13 (Skinner & Chimimba, 2005; du Plessis, Peel, & Child, 2016). In risky areas, reedbuck even
14 avoided optimal patches in favour of older, taller vegetation. The preference of reedbuck for
15 tall vegetation and areas that can offer adequate protection has been frequently reported
16 (Skinner & Chimimba, 2005; du Plessis, Peel, & Child, 2016; J A Venter & Kalule-Sabiti,
17 2016). Red hartebeest, a species sought for by poachers, displayed the steepest increase in
18 selection for optimal patches with increasing distance from risky areas (i.e. likely poacher
19 entry points). Overall, these observations for the three large grazers are in line with the
20 general expectation that, when foragers worry about potential threats, they tend to leave risky
21 areas relatively soon, search less intensively for optimal resources, and less rigorously exploit
22 each research patch (Fortin et al., 2009; Bedoya-Perez et al., 2013).

23 Our study provides evidence that poachers not only remove wildlife from protected
24 areas, but they also impact the ecological stoichiometry. On Mkambati, fires are intentionally
25 set with the intention of attracting animals to areas where they could be easily hunted

1 (Brooke, Kraaij, & Venter, 2018). Poachers thus purposely alter plant maturation stages of
2 vegetation by igniting grassland patches, thereby manipulating the chemical composition
3 (e.g. nitrogen concentration), biomass and the digestibility of plant material by large
4 herbivores. Moreover, we showed that poachers can generate spatial patterns in the
5 consumption and assimilation of plant nutrients by large grazers. Given sufficient pressure
6 and limited resources, poachers could have negative effect on the grazer populations that goes
7 beyond the removal of individuals by preventing the use of optimal vegetation. Our study
8 also revealed that the tactic of burning areas to attract grazers would not be as effective for all
9 herbivore species. The approach should not be highly effective for reedbuck as they are
10 habitat specialists (Skinner & Chimimba, 2005; du Plessis, Peel, & Child, 2016) and tend to
11 use older vegetation when near poaching areas. By contrast, burning might be effective for
12 zebra. Zebra have the lowest probability of occurrence near the poacher's entry points;
13 however, their probability of occurrence in an optimal patch at a poacher entry is equivalent
14 to that of zebra in a non-optimal patch located at 5.1 km (i.e., relative probability at 0 km
15 equals that at 5.1 km, Fig 3). Creating optimal vegetation patches near entry point would then
16 have a relatively high probability of being visited by zebra.

17 **Conclusion**

18 We have demonstrated that large herbivores can track the green-up in post-fire
19 vegetation. Zebra are driven by forage quality consistently selectively moving to vegetation
20 patches maximizing their daily intake of digestible energy. By contrast the foraging choices
21 of red hartebeest and reedbuck were negatively affected by poaching with both species only
22 selectively using vegetation patches maximising their energy relatively far from poachers.
23 Furthermore, red hartebeest quickly became more likely to utilize optimal vegetation as the
24 distance to the likely poacher entry points increased. Understanding how herbivores track and
25 use this wave of nutrient rich post-fire vegetation is important for guiding management

1 efforts in protected areas. For example, managers could respond to the manipulation of
2 habitat quality by poachers by setting up their own fires away from poacher entry points. By
3 strategically timing their fires in responses to poachers (e.g., based on Fig. 2), they should be
4 able to maintain grazers away from poachers because, everything else being equal, all three
5 species already avoid poacher entry points (Fig. 3). There has been few comprehensive
6 studies assessing the effects of poaching on wildlife. We showed that, while fire can remain
7 an valuable management tool in small fenced protected areas, managers should account for
8 the fact that poachers also use fire to attract and extract animals from protected reserves. The
9 actions of managers thus might be most effective if they are also done in response to
10 poachers' attempts to alter local resource quality.

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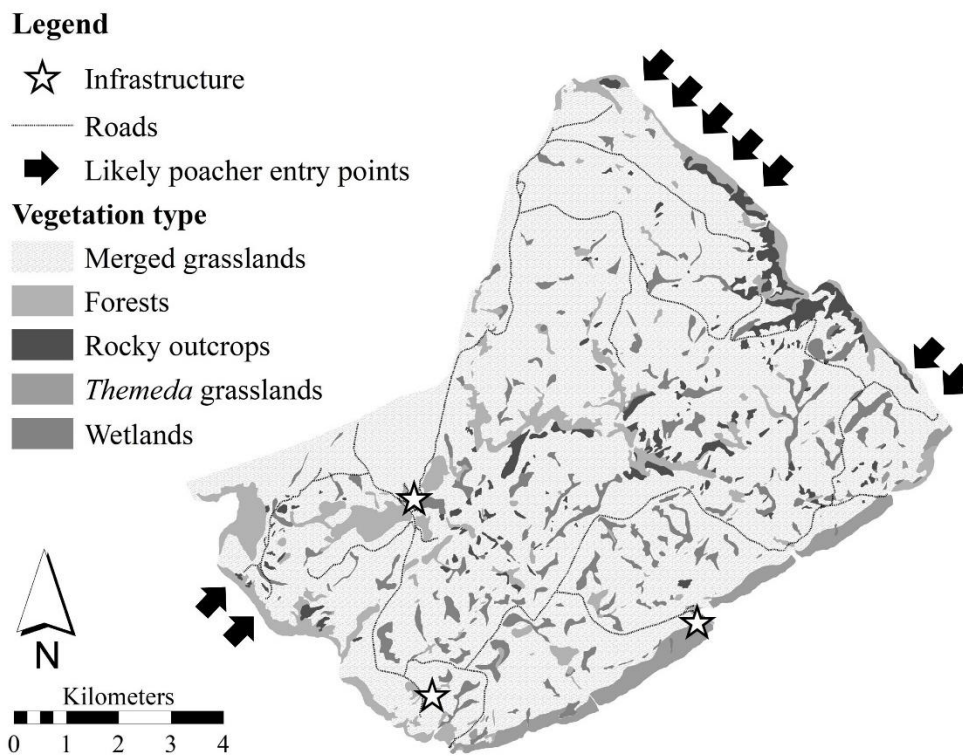
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- 1 Table 1: Step Selection Model (SSF) of GPS satellite collared herbivore species on Mkambati
- 2 Nature Reserve throughout the study period (2008-2016).

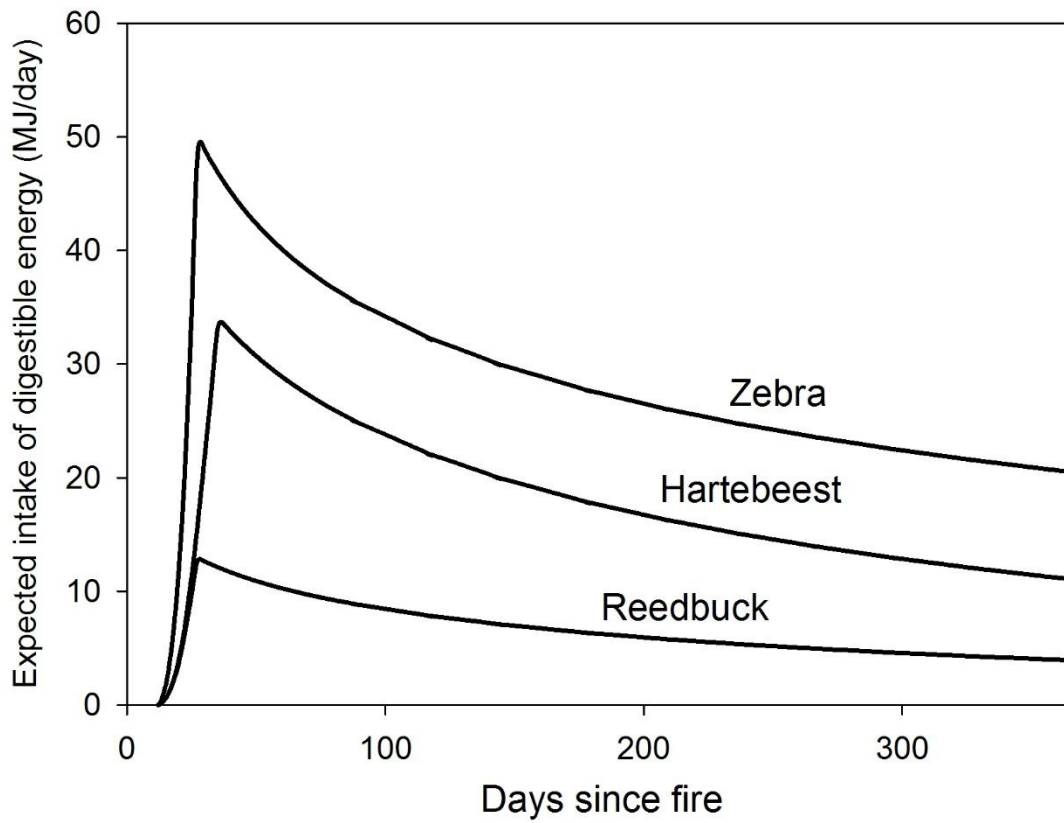
Parameter	β value	Robust SE	SE ratio	X^2	P
Reedbuck					
Log step length (m)	-4.692	0.273	2.761	294.621	<.0001
Step Length (m)	1.056	0.401	2.997	6.943	0.008
Cos(θ) (degree)	0.548	0.069	2.122	63.049	<.0001
F_{IDDE}	-0.286	0.204	0.531	1.968	0.16
Distance to poachers (km)	0.052	0.086	1.738	0.365	0.56
$F_{IDDE} \times$ Distance to poachers	0.089	0.035	0.482	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	101.689	<.0001
Step Length	0.760	0.173	15.403	19.350	<.0001
Cos(θ)	-0.736	0.250	21.893	8.639	0.003
F_{IDDE}	0.294	0.535	3.509	0.301	0.58
Distance to poachers	0.052	0.105	14.236	0.241	0.62
$F_{IDDE} \times$ Distance to poachers	0.376	0.109	2.802	0.001	0.001
k-fold: \hat{r}_S global 0.50 (range: 0.10-0.83) n=100					
Zebra					
				1890.30	
Log step length	-4.186	0.096	1.384	6	<.0001
Step Length	-0.205	0.095	1.266	4.710	0.03
Cos(θ)	1.154	0.041	1.447	793.490	<.0001
F_{IDDE}	0.498	0.146	0.815	11.638	0.0006
Distance to poachers	0.097	0.041	1.205	0.570	0.02
$F_{IDDE} \times$ Distance to poachers	0.038	0.039	0.717	0.946	0.33
k-fold: \hat{r}_S global 0.85 (range: 0.32-0.97) n=100					

1 Figure 1: Reserve map of Mkambati Nature Reserve including vegetation types (Adapted
2 from Shackleton 1989), likely poacher entry points and reserve infrastrucure (buildings on
3 Mkambati).

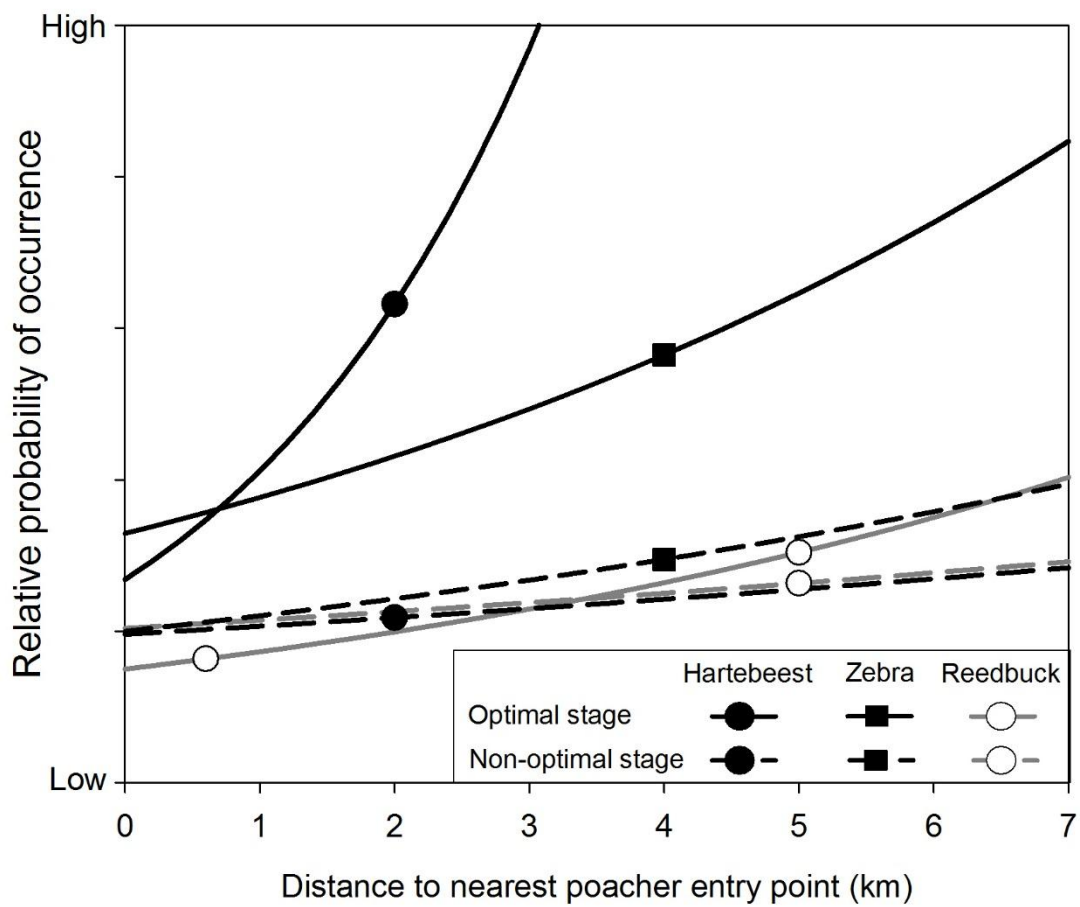


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- 2 Figure 2: Expected intake rate of digestible energy for red hartebeest, zebra and common
- 3 reedbuck on Mkambati Nature Reserve.



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 2 Figure 3: Relative probability of occurrence of three herbivores (red hartebeest, zebra and
 3 common reedbuck) on Mkambati Nature Reserve in relation to the nearest likely poacher
 4 entry point.
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1 Appendix 1: Composition of study species, recording interval, number of observations and length of data collection.

Species	Collar	Digestive strategy	Feeding strategy	Muzzle width	Mean Body Weight	Frequency of recordings	Number of observations	Recorded from	Recorded to
Reedbuck	NAN106	Ruminant ²	Grazer ⁵	31 mm ³	38 kg ²	60 min	3097	Oct-15	Mar-16
	NAN107						5327	Oct-15	Jun-16
	NAN108						4966	Oct-15	Jun-16
	NAN109						5278	Oct-15	Jun-16
	NAN110						4953	Oct-15	Jun-16
Red hartebeest	AU063	Ruminant ²	Grazer ⁵	52 mm ³	120 kg ¹	30 min	9304	Oct-08	May-09
	AU064						18066	Oct-08	Oct-09
	AU065						7060	Oct-08	May-09
	AU066						4360	Oct-08	Jan-09
	AU371						24450	Nov-09	Dec-09
	AU372						19293	Nov-09	Dec-09
	AU373						3398	Nov-09	Dec-09
	AU451						2472	Jun-10	Sep-10
	AU452						7244	Jun-10	Sep-10
	Zebra						AU067	Non-ruminant ²	Grazer ⁵
AU069		17726	Oct-08	Oct-09					

AU070	17836	Oct-08	Oct-09
AU074	15411	Oct-08	Oct-09
AU374	16545	Nov-09	Sep-10
AU375	7438	Nov-09	Sep-10
AU376	4223	Nov-09	Feb-10

1 ¹(Sponheimer et al. 2003), ²(Skinner and Chimimba 2005), ³(Gordon and Illius 1988), ⁴(Janis and Ehrhardt 1988), ⁵(Venter and Kalule-Sabiti 2016)

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