

Short communication

Behavioural flexibility in foraging mode of the spotted sand lizard (*Pedioplanis l. lineocellata*) seems to buffer negative impacts of savanna degradation

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ABSTRACT

In this field experiment we investigate the impact of land use induced savanna degradation on movement behaviour of the spotted sand lizard (*Pedioplanis l. lineocellata*) in the southern Kalahari. Foraging behaviour of lizards was tested in a factorial design (low vs. high prey availability) in degraded and non-degraded habitats.

An interaction between habitat structure and prey availability affected movement behaviour. In degraded habitats with low prey availability and in non-degraded habitats with high prey availability the spotted sand lizard moved more like an active forager. In contrast, in degraded habitats with high prey availability and in non-degraded habitats with low prey availability lizards moved like sit-and-wait foragers. Interestingly, the behavioural flexibility of the spotted sand lizard seems to buffer extreme conditions and negative effects of land use impacts.

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1. Introduction

Degradation caused by heavy land use practices (e.g. heavy grazing by livestock) is common throughout savannas worldwide (e.g. Gillson and Hoffman, 2007; Skarpe, 1990). In particular, heavy grazing induced shrub encroachment at the cost of palatable vegetation is one of the major forms of rangeland degradation (Scholes and Walker, 1993). During the last decades, shrub encroachment has become increasingly evident in the southern Kalahari (Gillson and Hoffman, 2007; Skarpe, 1990) leading to habitat fragmentation (Milton and Dean, 1995) and to declines in abundance and diversity of animals across taxonomic groups (carnivores: e.g. Blaum et al., 2007a, rodents: Blaum et al., 2007b birds: e.g. Sirami et al., 2009, insects: e.g. Blaum et al., 2009).

In contrast, the responses of lizards to savanna degradation are less clear. While some studies found significantly lower lizard abundance and diversity in degraded savanna habitats (e.g. Meik et al., 2002), others found higher lizard abundance and diversity (e.g. Fabricius et al., 2003; Smart et al., 2005). Clearly, the availability of key resources (e.g. food, sites for nesting) are major drivers for changes in abundance and diversity in degraded

habitats, however, these changes are likely to affect also behavioural patterns. For example, lizards may change and enlarge their home ranges in degraded savannas (Wasiolka et al., 2010) due to lower insect prey availability (Blaum et al., 2009; Pianka, 1986). While food availability will determine overall abundance of lizards, it remains unclear whether prey availability alone can trigger such significant changes in space use and which specific movement properties are affected by habitat degradation.

In this study we experimentally analysed the impacts of savanna degradation (i.e. changes in habitat structure and prey availability) in the southern Kalahari on movement behaviour of the spotted sand lizard (*Pedioplanis l. lineocellata*). We focussed on foraging behaviour as a key process determining the survival of lizards. Movement patterns during foraging will be determined by a trade-off between food availability and predation risk. For lizards, the lower prey availability in degraded habitats may increase movement activity to capture sufficient prey. In contrast, the change in habitat structure from grass dominated (non-degraded) to shrub dominated (degraded) increases predation risk by raptors since total vegetation cover and the availability of the lizard's favoured hiding places (dense perennial grass tussocks) are significantly lower.

The study is based on the results of Wasiolka et al. (2010) who found that home range size of the spotted sand lizard is significantly larger in degraded Kalahari savanna habitats than in non-

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degraded habitats. The major aim of the experiment was to distinguish between the effects of changes in habitat structure and prey availability on the lizard's foraging behaviour. In particular, we analysed possible interactions between habitat structure and prey availability on movement behaviour, by manipulating prey availability (low versus high prey availability) in degraded and non-degraded Kalahari savanna habitats. We recorded the distance and duration of each lizard movement, and the time between subsequent movements to calculate four major movement properties that quantitatively describe the foraging strategy of lizards according to Reilly et al. (2007): the mean distance moved/movement, the mean time being active/movement, the percentage time spent moving/observation and the number of moves per minute. We expected lizards in degraded habitats with low structural diversity and low prey availability to move more often and larger distances for the acquisition of prey (i.e. actively wide-foraging strategy), than lizards in non-degraded habitats with high structural diversity and high prey availability (i.e. sit and wait foraging strategy). This means that we expect both, the structural enrichment of the habitat and the provision of additional prey in our experiment to reduce the movement activity of the lizards.

2. Methods

The study site was situated at the livestock farm "Loch Lemond" (S 27°02'; E 020°44') in the southern Kalahari, South Africa. The savanna vegetation is described as the Auob dune veld and characterised by a continuous grass layer (*Aristida* spp., *Eragrostis* spp., *Stipagrostis* spp.) and a discontinuous woody layer of trees (*Acacia erioloba*, *A. haematoxylon*) and shrubs (*Rhigozum trichotomum*, *Acacia mellifera*) (Mucina et al., 2005). Mean annual rainfall is 174 mm and extreme temperatures range from -10.3 °C in winter to 45.4 °C in summer (Van Rooyen, 2001).

The study animal, the spotted sand lizard (*Pedioplanis l. lineoocellata*), a medium-sized, diurnal, ground-dwelling lizard (Branch, 1998) is fairly abundant, widely distributed in Southern Africa and is classified as sit-and-wait hunter (Reilly et al., 2007). Lizards were caught with a fishing rod in the degraded habitat. Captured individuals were sexed, measured, and weighed. For relocation of lizards in the experiment, individuals were radio tracked. Only males were selected where the transmitter weight (0.36 g) was below 7.5% of the animals body weight (Kenward, 2001). Other captured individuals were released immediately. Transmitters showed no effect on movement behaviour (Wasiolka et al., 2010).

Fife adult males were large enough (57–64 mm snout-vent length, average body weight: 6.28 g ± 0.50 SE) to carry the transmitters (149 MHz transmitters; type LB-2N, manufactured by Holohil Systems Ltd., Canada). Each individual was temporarily marked (small blue dot of approx. 0.25 cm²) with xylene-free non toxic paint, and transmitters attached at the backs using 100% silicone glue according to Wasiolka et al. (2010). Before each observations, the lizards were once located with a RX 98 Televilt receiver (Televilt, Sweden). The radio tracking was approved by the Northern Cape Nature Conservation Service (Permit No. 078/09). At the end of the observations each lizard was recaptured, transmitters removed and released at the site where they were first captured. Glue and xylene-free paint remains at the skin of the lizards were not removed since they regularly slough off their skin. In the study by Wasiolka et al. (2010) no increased predation risk was observed resulting from the paint remains.

We applied a nested experimental design (within individual animal) to investigate impacts of degradation on movement behaviour. For treatment we used two fully crossed factors: habitat

(degraded and non-degraded) and prey availabilities (low and high prey availability), resulting in four treatment combinations:

1. degraded habitat with unmanipulated, low prey availability
2. degraded habitat with additional prey items
3. non-degraded habitat with removed prey items
4. non-degraded habitat with unmanipulated, high prey availability

We established eight 15 m × 15 m (225 m²) enclosures (two/treatment) using solid plastic fences (50 cm in height) that were dug in the ground. Enclosure size was similar to average home ranges of the lizard (250 m², 90% isopleth) in the study area (Wasiolka et al., 2010). Therefore, no additional water was provided in the enclosures. The enclosures precluded effects during the specific observations due to contact with a different type of habitat aside from interactions with competitors and facilitated recovering the individuals in the field. To avoid trespassing of insects in the enclosures a mosquito-net fence (1 m height) was additionally setup in a distance of 1 m around the enclosure plastic fence.

Vegetation cover differed among degraded and non-degraded enclosures and was determined in four 4 m × 4 m random subplots per enclosure and averaged over the 4 degraded and non-degraded enclosures respectively. Vegetation cover of annual grasses was 7 ± 1% (mean ± SD) in degraded and 1 ± 1% in non-degraded habitat, and of perennial grasses 4 ± 1% in degraded and 36 ± 13% in non-degraded habitat. Shrub cover was 33 ± 9% in degraded and 1 ± 1% in non-degraded habitat. In all enclosures the mean herbal cover was below 0.4% and bare ground above 50%.

Food availability was manipulated by addition or removal of prey. Small Orthopterans (<25 mm) are one of the main food sources of the spotted sand lizard and their abundance is lower in degraded habitats than in non-degraded (Wasiolka et al., 2009). For food reduction we removed 60 grasshoppers from the enclosures of the non-degraded habitat (treatment 4), whereas 30 grasshoppers were added in equal spacing to the enclosures of the degraded habitat (treatment 2). The food manipulations were repeated 1 h before each observation. The number of added prey items is based on the average abundance of grasshoppers in non-degraded habitats (Blaum et al., 2009).

Each individual was used in all treatment combinations. The lizards were first exposed either in a degraded habitat with low prey availability or in a non-degraded habitat with low prey availability to exclude effects of saturation (i.e. acquisition of sufficient prey to remain inactive for more than two days) to the next treatment. After half a day, lizards were transposed into an enclosure with the same vegetation structure and composition but higher prey availability. After one and a half day for resting and digestion, the individual was moved to the remaining habitat treatment, again starting with low prey availability to avoid saturation for the last observation. After half a day the reptiles were exposed in an enclosure with the same vegetation characteristics but higher prey availability. The acclimatisation period for each lizards and enclosure was one day.

Individuals were observed in March 2009 for 2 h in the afternoon (15.30–17.30 h), when lizard activity was highest (Wasiolka et al., 2009). We expected lizards originating from degraded habitats to respond more sensitive to the habitat manipulations (the structural enrichment of the habitat and the provision of additional prey).

All individuals were observed for 15 min/treatment. Additionally, minimum distance between observer and lizard was >3 m. For each lizard movement the distance was estimated visually and the movement duration was recorded by the same observer. One lizard movement was defined as a move further than 5 cm away from its previous position until resting longer than 1 s. Postural adjustments, like turning or tail movements, were not recorded. From the

Table 1

Effects of habitat degradation and prey availability on movement behaviour of the spotted sand lizard (MANOVA using habitat structure and prey availability as fixed factors, including their 2-way interaction. Animal ID was used as a random factor to account for individual differences).

	<i>F</i>	<i>P</i>
Animal	$F_{16, 28} = 17.3$	0.093
Habitat structure	$F_{4, 9} = 1.2$	0.358
Prey availability	$F_{4,9} = 1.54$	0.270
Habitat × prey	$F_{4,9} = 6.2$	0.011

For the separate variables the interaction effect was confirmed (MANOVA, between subject effects, univariate tests: interaction (df 1, 12): $4.9 < F < 20.4$, $0.045 > p > 0.001$, main effects not significant).

observations, the following variables were calculated: mean distance/move (m), mean time active/move (s), percentage time spent moving/observation interval (%), and mean number of moves/minute.

All statistical analyses were performed in SPSS (Version 17.0). Data were tested for normality using Kolmogorov-Smirnov-test and for homogeneity of variances using Levene-test. To meet these assumptions the percentage time spent moving was arcsin sqrt-transformed. Since behavioural measurements within one observation time were interrelated, we used a multivariate Analysis of Variance approach to behaviour as response variables. We analysed the effects of habitat degradation and prey availability as fixed factors, included their 2-way interaction, and included animal ID as a random factor to account for individual differences. Results of the MANOVA were reported using Wilk's Lambda.

3. Results and discussion

Interestingly, only the interaction between habitat structure and prey availability affected movement behaviour of the spotted sand lizard (Table 1). Across all animals, each recorded movement property (distances moved, time being active, percentage time

spent moving, and movement frequency), was lowest in degraded habitats with high prey availability (artificially added prey). Highest movement activity was recorded in degraded habitats with unmanipulated low prey availability, and intermediate values in non-degraded habitats (slightly higher movement activity in non-degraded habitats with unmanipulated high prey availability than in the treatment combination with the removed prey, Fig. 1).

Since no predators and escape behaviour of lizards were recorded during our observations, we attribute the majority of movements in the experiment to foraging behaviour.

In lizards, two different foraging modes can be distinguished: sit-and-wait versus wide-foraging (Reilly et al., 2007). While sit-and-wait foragers wait for mobile prey and only move when prey enters the perceptual range of the lizard; wide-foragers spend much more time in motion to search the prey that is often sedentary and clumped, but unpredictable in their temporal and spatial appearance (Reilly et al., 2007). Although the spotted sand lizard is classified as sit-and-wait forager (Reilly et al., 2007), the variation in movement activity in our experiment indicates a high behavioural flexibility for the acquisition of prey. Indeed, the lizards in our experiment even switched between the two foraging strategies in response to habitat structure and prey availability. In the unmanipulated degraded habitats where prey availability was low, the percentage time spent moving was above 10% and the foraging mode can be classified as wide-foraging (Perry, 1999). In contrast, in degraded habitats where prey was added, lizards apparently recognized the more abundant prey and switched to a sit-and-wait foraging strategy and the percentage time spent moving dropped to less than 1%. Also the duration, distance and frequency of movements were remarkably lower (<1 s/move, <0.1 moves/min and <5 cm/move) compared to the degraded habitat with low prey availability (~ 6 s, 0.7 moves/min and ~ 80 cm/move). In other words, higher prey availability in degraded habitats decreased lizard movement activity.

Although our findings are based on five individuals only, the behavioural flexibility of the spotted sand lizard seems to buffer the extreme conditions in degraded savanna habitats. This behavioural

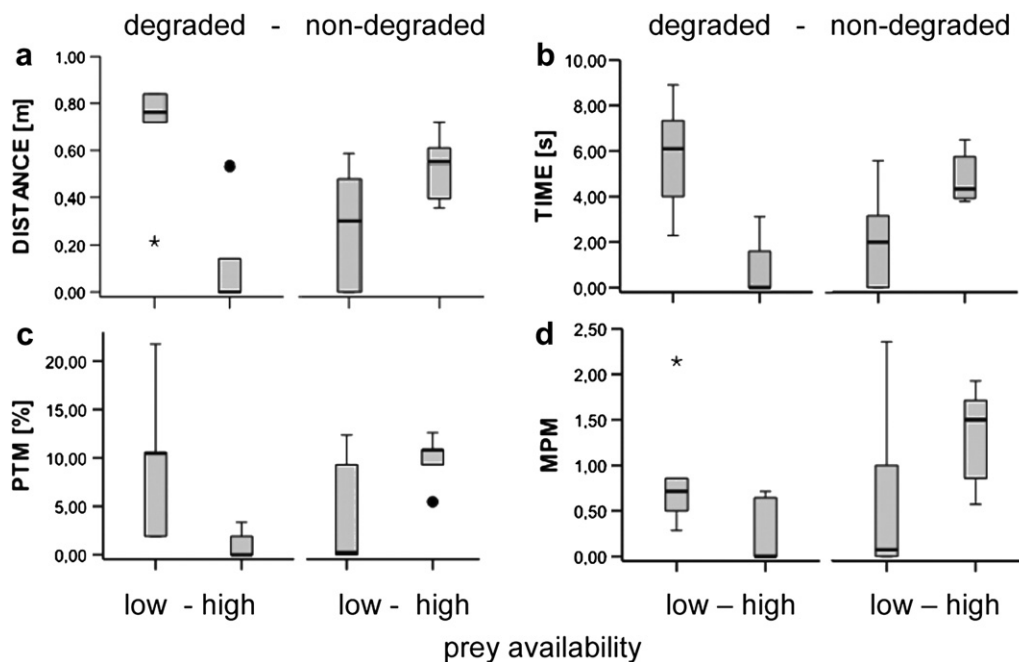


Fig. 1. (a–d): Effects of habitat degradation and prey availability on movement behaviour of the spotted sand lizard in the Southern Kalahari in a repeated measures design ($n = 5$ animals) (a) mean distance moved (MD), (b) mean time being active (MT), (c) mean percentage time spent moving (PTM), (d) mean moves per minute (MPM). Graphs depict median, quartiles, extreme values (circles) and outliers (stars).

flexibility may also explain the non-significant differences in body mass between adult males in degraded and non-degraded habitats ($6.3 \text{ g} \pm 0.14 \text{ SE}$, and $6.6 \pm 0.15 \text{ SE}$) (Wasiolka, 2007). This would have been very unlikely when foraging strategy would have been strictly sit-and-wait. Nevertheless, lizard abundance was significantly lower in degraded habitats and home ranges larger (Wasiolka et al., 2009, 2010).

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