Original article

Behavioural responses of the lizard *Pedioplanis l. lineoocellata* to overgrazing

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ABSTRACT

We studied the effects of overgrazing on the foraging behaviour of the lizard *Pedioplanis l. lineoocellata* (Spotted Sand Lizard), a sit-and-wait forager, in habitats of differing vegetation states to determine the effects of habitat degradation on this species. At high grazing intensity where vegetation cover and diversity is low, the lizard *P. lineoocellata* moves more frequently, spends more time moving and covers larger distances than in habitats where vegetation cover and diversity is high. These behavioural changes in movement patterns can be explained by less abundant prey in habitats with low vegetation cover and diversity. Although morphology, phylogeny and physiology of *P. lineoocellata* should constrain the change in foraging behaviour, the species has modified its foraging strategy from sit-and-wait to actively foraging. We assume that this behavioural flexibility of *P. lineoocellata* is a buffer mechanism enabling the species to use and survive in degraded (unfavourable) habitats.

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1. Introduction

For decades human land use practices, including livestock grazing, game ranching, fire suppression or firewood cutting, in semiarid savannahs of southern Africa have altered the vegetation composition and structure of the system (e.g. Leistner, 1967; Hanley and Page, 1982; Skarpe, 1991; Jeltsch et al., 1996; Dean et al., 1999; Meik et al., 2002). In particular, high grazing pressure by livestock can lead to a reduction of perennial grass cover and herbaceous vegetation and a concomitant increase in area of bare ground (Skarpe, 1990a; Jeltsch et al., 1997; Roques et al., 2001; Wiegand et al., 2005). This situation often favours the establishment of woody shrubs, a phenomenon referred to as shrub encroachment (Skarpe, 1990b; Teague and Smit, 1992; Jeltsch et al., 1996; Dean et al., 1999).

Overgrazing induced changes in vegetation composition and cover often alter environmental conditions and can lead to a decline in abundance and diversity of animals across taxa (e.g. rodents: Blaum et al., 2007a; Blaum and Wichmann, 2007, carnivores: Blaum et al., 2007b,c,d, 2008; birds: Thiele et al., 2008; reptiles: e.g. Busack and Bury, 1974; Reynolds, 1979; Brown et al., 1997; Meik et al., 2002). For lizards, the responses to savannah degradation are less clear. While some studies found a decrease in lizard abundance and diversity (e.g. Busack and Bury, 1974; Reynolds, 1979; Brown et al., 1997; Meik et al., 2002), others found no effects (e.g. Fabricius et al., 2003 (diversity)) and also positive effects of savannah degradation (e.g. Fabricius et al., 2003 (abundance); Smart et al., 2005 (abundance and diversity)). For example, Castellano and Valone (2006) reported for overgrazed areas in arid grasslands

of Arizona that the abundance of *Sceleporus undulatus* and *Uta stansburiana* decreased, whereas the abundance of *Cnemidophorus tigris* abundance was not affected and *Phrynosoma modestum* abundance increased. The decrease in lizards can be explained by a reduction of prey availability. The main prey source of almost all lizard species in the Kalahari (Pianka, 1986) are invertebrates which are declining with grazing impact (Dean and Milton, 1995; Dennis et al., 1998; Seymour and Dean, 1999; Fabricius et al., 2003).

The main focus of recent investigation emphasized the impact of overgrazing and shrub encroachment on lizard community structure, distribution, abundance and prey density (Huey and Pianka, 1977; Jones, 1981; Bock et al., 1990; Brown et al., 1997; Meik et al., 2002; Wasiolka, 2004). But also it is important to investigate behavioural responses of species to habitat alteration to better understand population dynamics on natural and degraded habitats. Behavioural responses can help to understand changes in distribution and abundance of species as well as shifts in population dynamics. Particularly, foraging strategy is a crucial behaviour for the survival of lizard populations under the unpredictable conditions of arid and semiarid savannas. While foraging behaviour of lizards can be classified into two major but contrasting strategies (sit-and-wait versus actively foraging) (e.g. Schoener, 1971; McLaughlin, 1989), shifts in strategies from sit-and-wait to actively foraging and vice versa are limited because of phylogenetic constraints (e.g. Huey and Pianka, 1981; Cooper et al., 1997). In degraded habitats, where prey availability is low, the actively foraging strategy is superior over the sit-and-wait strategy. This leads to the fundamental question: how can sit-and-wait foraging lizards survive in degraded habitats?

Yet very few studies have examined the impacts of habitat degradation on foraging ecology of lizards. However, the influence of habitat quality on foraging ecology has drawn some attention in the field of habitat manipulations (e.g. Fair and Henke, 1997; Petren and Case, 1998).

We conducted standardized observations of lizards across a land use gradient in Kalahari savannah habitats, which are characterised by different amounts of vegetation cover, composition, structure and diversity. We addressed the following hypothesis: despite phylogenetic constraints, we expect that the sit-and-wait forager *P. lineoocellata* moves more frequently, spends more time moving and covers larger distances in degraded habitats where prey availability is low.

2. Materials and methods

2.1. Study area and period

The study was conducted after the mating season of *Pedioplanis lineoocellata* from in November 2004 to February 2005 on six privately owned farms (Vry Soutpan (S 27°17′04.0″; E 20°50′19.7″), Swartpan (27°15′36.3″; E 20°46′18.4″), Loch Lemond (S 27°03′40.7″; E 020°45′28.7″); Rea (S 27°01′07.7″,E 20°40′06.6″) Rooiduin (S 26°42′46.3″, E 20°35′10.3″) and Hoekrans (S 26°39′22.0″, E 20°34′55.5″)) around Askham, Northern Cape Province in the vicinity of the Kgalagadi Transfrontier Park in the southern Kalahari, South Africa. The region is

classified as an arid savannah (Van Rooyen, 2001) with an average, annual rainfall of 150–300 mm (Leistner and Werger, 1973) which falls mainly in summer (Werger, 1978). Average temperatures were 27.99 °C in November 2004 and 29.13 °C in February 2005 (Data: BIOTA Weatherstation Farm Alpha, southern Kalahari). The vegetation type is classified as the western form of the Kalahari Thornveld (Acocks, 1988). The typical form is an extremely open savannah with scattered trees of *Acacia erioloba* and *A. haematoxylon*. Other important woody vegetation species are the tree *Boscia albitrunca* and the shrubs *Grewia flava*, *Lycium hirsutum*, *Acacia mellifera* and *Rhigozum trichotomum*. The main grass species are *Aristida* ssp. and *Eragrostis* ssp. in the valleys and *Centropodia glauca*, *Stipagrostis namaquensis*, *Stipagrostis uniplumis*, *Monechma incanum* and *Crotalaria virgultalis* on dunes (Leistner, 1959; Pianka and Huey, 1971; Acocks, 1988).

2.2. Vegetation survey

We chose five different vegetation states which are characterized by different vegetation composition, cover, structure and diversity. These five vegetation states represent vegetation states generated by low - and high- grazing pressure. Vegetation state 1 (low grazing pressure) and vegetation state 5 (high grazing pressure) are two states at opposite ends of the spectrum (Walker et al., 1981; Skarpe, 1990a,b; Moleele and Perkins, 1998). The three other vegetation states are intermediate states (Walker et al., 1981).To quantify the differences in vegetation composition, cover and diversity, we sampled two parallel transects 250 m long and 20–30 m apart in each of the sampled sites of the observation study. Starting after 25 m on each transect every 50 m a 5 × 5-m square was surveyed. Percent ground cover of shrubs, perennial grasses, annual grasses, herbaceous vegetation and bare ground was estimated and the mean calculated. In addition, we calculated the Shannon Index (e.g. Shannon, 1948) to estimate plant diversity. In total we sampled 70 vegetation transects within 35 research sites.

2.3. Behavioural observations

Focal observations took place in dune valleys at sites that differed in vegetation composition, structure and diversity (Table 1). To exclude effects on lizard behaviour by different vegetation composition than the actual study site, each study site was part of a much larger area consisting of similar vegetation composition. The dune valleys where observations took place were at least 80 m wide and 500 m long. Furthermore, the neighbouring dune valleys consisted of similar vegetation composition.

During the study period adult individuals of the lizard *Pedioplanis l. lineoocellata* were observed directly using 8-fold magnifying binoculars. Focal-animal observations were conducted for 2 h during the morning, starting 2 h after sunrise and for another 2 h in the afternoon, starting 3 h before sunset. Lizard observations were equally distributed within these times. During inclement weather conditions (i.e. windy and/or rainy days) no lizard observations took place. Whenever an undisturbed individual of *P. lineoocellata* was encountered it was observed from a distance between 5 and 8 m.

Table 1 – Range of vegetation cover of shrubs, perennial grasses, annual grasses, herbs and bare ground and plant diversity (Shannon Index) for the five vegetation states

Vegetation state	Vegetation cover (%)					Vegetation diversity (Shannon Index)
	Shrubs	Perennial grass	Annual grass	Herbs	Bare ground	
Vegetation state 1	0	31–38	0–1	2–6	57–61	0.72
Vegetation state 2	0–1	19–30	5–8	1–6	57–71	0.78
Vegetation state 3	13–19	3–7	8–12	0–2	65–72	0.51
Vegetation state 4	27–34	1–2	2–10	0–1	60–66	0.31
Vegetation state 5	0–1	0–2	19–32	0–1	75–80	0.22

Individuals of *P. lineoocellata* were observed continuously for 15 min, if possible. To compensate for disturbance of lizards by the observer's presence, the first minute of each observation was omitted from further analyses. Observation time totalled 25.3 h, during which 104 focal observations were performed, ranging from 1 to 14 min in duration. The times each individual spent being active and passive were recorded. In addition, for each individual, the distances (in meters) of individual movements were estimated visually by the same observer. We defined lizard movement when a lizard moved >5 cm away from its previous position and rested >1 s before the next move started. Care was taken to sample each individual only once by walking along the respective dune valley without returning to the same area again.

We observed and measured the following parameters: (i) moves per minute (MPM), (ii) percentage time spent moving (PTM), and (iii) total distance (TD) covered by each individual.

2.4. Prey abundance

Orthoptera smaller than 2.5 cm in body length are one of the main food sources of *P. lineoocellata* (pers. obs.), especially during summer (Pianka, 1986), the investigation period. We surveyed Orthoptera (grasshoppers, locusts) abundance by counting all individuals smaller than 2.5 cm on transects (100 × 3.0 m). We used the same transects as for the vegetation surveys, which were in the same habitats as the focal observations of *P. lineoocellata*. A total of 64 transects were surveyed within the 35 research sites.

2.5. Data analyses

We calculated moves per minute (MPM) and the percentage time spent moving (PTM) to identify foraging mode (Huey and Pianka, 1981; Perry, 1999). For calculations of PTM all behaviour patterns considered as active (e.g. moving and hunting) were combined. To calculate total distance (TD) all distances that an individual moved were added. Only individuals with an observation time of more than 8.5 min were included in the analysis. For observations shorter than 14 min, TD was corrected to 14 min. To evaluate MPM, PTM, TD and Orthoptera abundance the means were compared. Within the five vegetation states, 104 lizard specimens in 35 different research sites were observed. Lizards observed in the same research site were pooled for further analysis (state 1: 21 ind./7 sites; state 2: 26 ind./9 sites; state 3: 20 ind./6 sites; state 4: 19 ind./6 sites; state 5: 18 ind./7 sites). Data were analyzed by means of the statistical program SPSS, Version 12.0 (© SPSS Inc.). To

meet the assumptions of parametric tests, normal distribution and homogeneity of the data, all data sets were ln(x+0.1)-transformed (Underwood, 1997). MPM, PTM, total distance and Orthoptera abundance data were analyzed using one-factor ANOVA (Dytham, 1999). In addition, post-hoc tests (Tukey test) were applied to test for significant differences between the vegetation states. For all tests, a P value of <0.05 was regarded as statistically significant.

3. Results

The results of the vegetation survey show a strong decrease of perennial grass cover in vegetation states 3, 4 and 5. Furthermore, shrub cover increased strongly in states 3 and 4, and there was a strong increase in annual grass cover in state 5. Vegetation diversity increased slightly in vegetation states 1– 2, but strongly decreased within vegetation states 3– 5 (Table 1).

The results of the behavioural study show an overall effect of habitat degradation on lizard movement behaviour. Moves per minute ($F_{4.34} = 8.774$, $P < 0.001$) (Fig. 1a), percentage time moving ($F_{4.34} = 16.856$, $P < 0.001$) (Fig. 1b), total distance ($F_{4.34} = 26.272$, $P < 0.001$) (Fig. 1c) and Orthoptera abundance ($F_{4.34} = 92.508$, $P < 0.001$) differed significantly between vegetation states (Fig. 1d). The Tukey tests show that *P. lineoocellata* moved more frequently, spent more time moving and covered larger distances in vegetation states 3, 4 and 5 than in vegetation states 1 and 2. (Fig. 1a–c). A similar pattern was found for Orthoptera abundance. Orthoptera abundance was lower in vegetation states 3, 4 and 5 than in vegetation states 1 and 2 (Fig. 1d).

4. Discussion

We investigated the impact of overgrazing on the foraging ecology of *Pedioplanis l. lineoocellata*. The results of moves per minutes (MPM) and percentage time spent moving (PTM) showed that the lizard species *P. lineoocellata* moved more frequently and spent more time moving in degraded (vegetation states 3, 4 and 5) in comparison to natural habitats (vegetation states 1 and 2). Additionally, total distance (TD) demonstrated that the lizard covered larger distances in degraded habitats than in natural habitats. Furthermore, our results of prey abundance showed that Orthoptera abundance decreases with habitat degradation. These results support our hypotheses that *P. lineoocellata*: (1) in the search of less
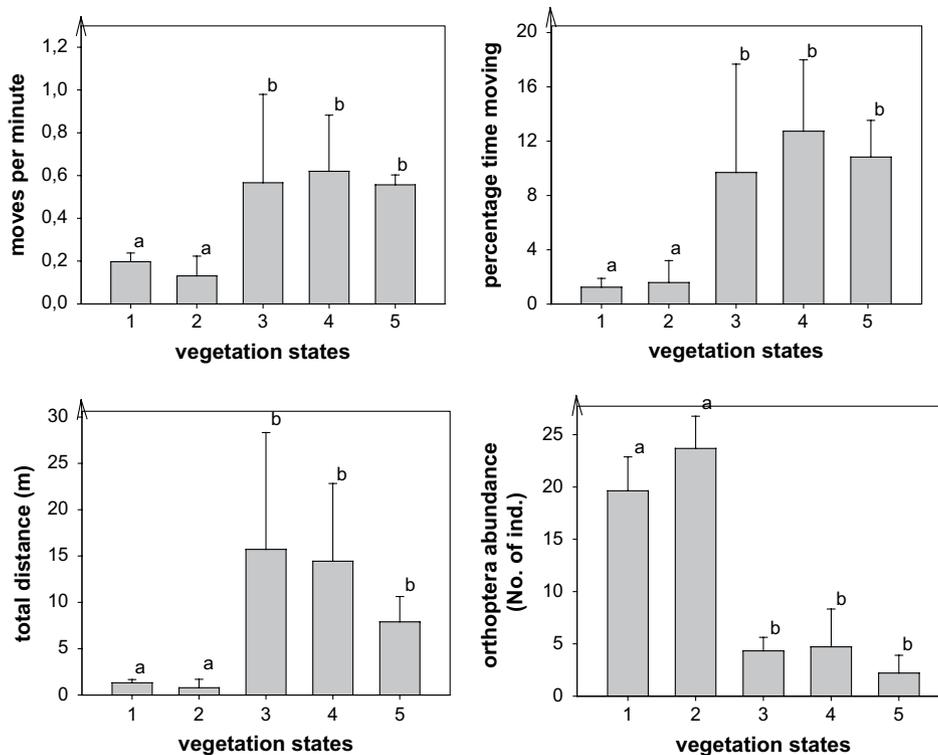
Fig. 1 – (a–d) Means ± SE of moves per minute (MPM), percentage time moving (PTM), total distance (TD) and Orthoptera abundance for the five vegetation states. Different letters (a,b) indicate significant differences between the respective vegetation states (ANOVA, Tukey post-hoc test, P < 0.05). For statistical analysis we used log-transformed data.

abundant prey moves more frequently, and (2) spends more time moving and covers larger distances in degraded habitats.

The results of MPM, PTM and TD point out that the sit-and-wait forager *P. lineoocellata* modifies its foraging strategy on degraded habitats that support less prey compared to natural habitats. The lizards no longer use a clear sit-and-wait strategy (specific for mobile prey), but their behaviour resembles an active foraging strategy (more specific for sedentary food). Perry (1999) considered PTM >10% as the criterion for active foraging. Our results of PTM indicate that the three degraded habitats (9.70 – 12.73%) are higher or close to that level compared to a PTM of 1.54 and 1.64% in natural habitats. These findings are surprising because the type of foraging mode is linked to morphological traits, such as body shape, body weight and relative clutch size (Anderson and Karasow, 1988; Wymann and Whiting, 2002) and further influenced by physiology, predators and competitors (Eifler and Eifler, 1999). Active foragers are more slender, incur higher energy costs and have greater stamina (Cooper and Whiting, 2000; Butler, 2005) than sit-and-wait foragers. In addition the main defence strategy of an active forager is speed compared to the sit-and-wait forager, who relies on crypsis as primary defence (Vitt, 1983). However, it should be noted that values of PTM for *P. lineoocellata* were only slightly higher than the threshold of 10% and are far lower than PTMs of the distinctly active foragers like *Mabuya striata sparsa* (PTM: 41.8%) or *Heliobolus lugubris* with a PTM of 57% (Huey and Pianka, 1981; Wymann and Whiting, 2002). Likewise, MPM (0.57 – 0.62) are lower than typical figures of active foragers (Cooper and Whiting, 1999). However, again, they are 3– 4 times higher

than in less- disturbed habitats (0.13 – 0.19) and still higher than typical figures of sit-and-wait foragers (e.g. *M. spilogaster*: MPM = 0.31). The high values of TD in degraded habitats are typical for active foragers because they cover larger distances as they search for prey (Wymann and Whiting, 2002).

Hence, this lizard species seems to be able to adapt to increasing habitat degradation by changing its foraging mode from a distinct sit-and-wait behaviour closer to an actively foraging mode. Although morphology and physiology of *P. lineoocellata* should constrain the change in foraging behaviour, the species is able to adjust its foraging strategy to the availability and distribution of prey.

This behavioural shift coincides with a decrease in Orthoptera abundance on degraded habitats. A decrease of arthropod density on degraded habitats was also reported by Gandar (1982), Dean and Milton (1995) and Seymour and Dean (1999).

The chance of finding patches with high prey densities or of encountering prey more frequently are higher while moving around than when waiting for prey to pass by (Huey and Pianka, 1981; Cooper and Whiting, 2000). Hence, our results on *P. lineoocellata* support Greeff and Whiting, 2000, who stated that lizards are adept at solving foraging problems, e.g. by shifting their foraging behaviour in response to changes in resource availability.

In the literature only few studies describe shifts in foraging behaviour in response to food availability in lizard species. The few existing studies identified seasonal and short -term shifts (Pietruszka, 1986; Lister and Aguayo, 1992; Eifler and Eifler, 1999; Greeff and Whiting, 2000) in response to fluctuations of

food. We assume that this behavioural flexibility of *P. lineoocellata* is a buffer mechanism enabling the species to use and survive in degraded (unfavourable) habitats. However, the risk of predation increases with the length of foraging activity (Polis, 1988). In addition, active foragers are more prone to encounter predators (e.g. Huey and Pianka, 1981; Wymann and Whiting, 2002; Attum and Eason, 2006). Thus, the increase in activity of *P. lineoocellata* and the decrease of cover can result in higher predation risk (Bentley et al., 2000; Norbury, 2001).

If prey abundance decreases, home range size often increases for reptiles as a compensatory mechanism (Wauters and Dhondt, 1992; Powell et al., 2000). On the other hand, in studies where food availability was experimentally increased, range size remained unaffected (Guyer, 1988; Eifler and Eifler, 1999). As a consequence of a possible increase in home range size (Wasiolka, 2007) and a less abundant prey in degraded habitats (vegetation states 3, 4 and 5), the carrying capacity of *P. lineoocellata* can be reduced for these habitats. We therefore suggest to test if the change in the lizard's foraging strategy (as a buffer mechanism) has the potential to maintain similar population sizes in both, degraded and natural habitats despite the lower prey availability in degraded habitats. Further important steps would be (i) to test our results with manipulative experiments by relocation of sit-and-wait individuals from natural to degraded habitats and vice versa) and (ii) to analyse possible morphological and physiological differences of *P. lineoocellata* (e.g. limb length or speed performance) in natural and degraded habitats.

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