

Prey capture behaviour by pygmy bluetongue lizards with simulated grazing

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Published online: 3 December 2013

Abstract: Endemic biota of native grasslands commonly co-exist with introduced grazing mammals, and often this is seen as a conservation threat. The endangered pygmy bluetongue lizard (*Tiliqua adelaidensis*) is restricted to remnants of native grassland in the mid-north of South Australia, with a long history of sheep grazing. Pygmy bluetongue lizards use ambush predation from their burrow entrances, and prey capture may be more efficient in a habitat with low vegetation density. We experimentally investigated changes in predatory behaviour in this lizard, with different grass density. We maintained and filmed captive lizards, in sequence, in grassed and bare habitat, and in habitat with low and high grass density, and provided them with crickets (*Teleogryllus commodus*) as prey. In habitats with lower grass density lizards emerged from their burrows more, made more prey capture attempts, and these attempts were more often made with the body further emerged from the burrow. We suggest that some grazing by domestic stock might benefit predatory efficiency for this lizard, perhaps by allowing a clearer view of approaching prey when grass density is lower. Our results conform with a previous study of the behaviour of pygmy bluetongue lizards in their natural burrows in the field under different simulated grazing regimes. From a broader perspective, together the results suggest a balance between detrimental impacts and benefits from grazing pressures on grassland lizard species in other geographical regions, and the potential to maintain conservation good will among farming communities.

Keywords: ambush predation strategy; conservation; endangered species; South Australia; *Tiliqua*

Introduction

Anthropogenically induced environmental changes such as habitat loss, fragmentation, and degradation are now considered to be a major threat to a wide array of taxa, including reptiles (Michael et al. 2011). For reptiles these changes can negatively influence their use of the thermal environment, and more broadly, habitat modifications, including those caused by agricultural grazing, can influence the microhabitat characteristics of many ground-dwelling species (Singh et al. 2002).

In many countries agriculture has been one of the leading causes of recent habitat degradation, with native grasslands among the most affected (Mark & McLennan 2005; Scroggie et al. 2012; Böhm et al. 2013). Many studies have highlighted the negative impacts of grazing pressure by domestic stock on endemic grassland flora (Yates et al. 2000; Lansberg et al. 2002) and fauna (Read 2002; James 2003; Castellano & Valone 2006). For instance, in New Zealand, grassland skinks are considered to be among the most threatened lizards (Hitchmough et al. 2010), as exotic pastures have replaced native tussock grasslands, leading to reductions, for lizards, of neonate condition (Hare & Cree 2011), dispersal rates (Berry et al. 2005), dietary breadth (Tocher 2003), and recolonisation of available habitat (Seddon et al. 2011).

Interactions between endemic grassland species and exotic grazers can be complex. For instance, introduced European rabbits (*Oryctolagus cuniculus*) may reduce grassland habitat quality for lizards, but their removal could focus increased predatory attention on grassland lizard populations (Norbury 2001; Norbury et al. 2009). For some grassland species, limited grazing by domestic stock may be beneficial by replicating the impact of large endemic grazers that are now scarce or absent (Rainho et al. 2010). Additionally, relic populations

persist within grazed landscapes and informed conservation management requires an understanding of the impact of grazing on population ecology and behaviour. Several endangered lizard species are now restricted to small fragments of once larger ranges as a result of agricultural modification of grasslands. These include the grand (*Oligosoma grande*) and Otago (*O. ottagense*) skinks that occupy rock outcrops surrounded by grassland in the South Island of New Zealand (Tocher 2009), and the grassland earless dragon (*Tympanocryptis pinguicollis*) that occupies burrows in grasslands of eastern Australia (Dimond et al. 2012).

In this paper we ask whether another endangered grassland lizard, the Australian pygmy bluetongue lizard (*Tiliqua adelaidensis*), is affected by grazing of its habitat. The lizard has an ambush predation strategy (Milne 1999), and we investigated whether there were changes in prey-catching behaviours under simulations of alternative grazing regimes.

Many animals must balance the cost and benefits of investing time and energy into different behaviours such as foraging and territory defence. For ectothermic animals like lizards, thermoregulatory behaviour will also be important, and thermoregulation is a vital precursor to foraging (Herczeg et al. 2008). The availability of warm conditions is critical for digestion of food and for reproductive development (Hare & Cree 2010). The thermoregulatory choices that lizards make can in turn influence their reproductive success, social interactions, and predation risk (Martin & López 2010; Carter et al. 2010). For pygmy bluetongue lizards the critical behavioural choice is whether to be emerged from the burrow, where they can both bask for thermoregulation and detect and capture prey, or to be inside the burrow where they are protected from predation and from extreme climatic conditions.

For many species, the costs of investments into one factor can outweigh the benefits of another. For example, Downes

and Shine (1998) showed that geckos avoided warmer retreat sites (which are usually preferred retreats) that contained predator scent. The risk of predation outweighed the thermal benefits. In our study we asked whether grazing level affected the time that lizards spent emerged and then their subsequent success at prey capture.

One prediction was that lizards would be less likely to risk emergence and foraging activity if less vegetation would leave them more exposed to their own predators. Predation has been recognised as a major threat to many grassland lizards (Lettink et al. 2010a, b; Reardon et al. 2012). Alternatively, the success of lizards in capturing invertebrate prey should be enhanced under simulated grazing, if reduced vegetation cover allowed a wider field of view of passing prey items (although we did not measure field of view in this study). Thus emergence and prey capture might either increase or decrease with less grass cover. The direction of behavioural change could influence conservation management decisions.

The pygmy bluetongue lizard is an endangered reptile endemic to native grasslands in the mid-north of South Australia. It was thought to be extinct until its rediscovery in the stomach of an eastern brown snake (*Pseudonaja textilis*) in 1992 (Armstrong & Reid 1992). Previous records suggested an extended distribution in South Australia that has now contracted to a few isolated remnant patches of native grasslands in a small subset of the previous range (Milne 1999). All known populations are on private properties, and most are exposed to domestic stock grazing (Milne 1999).

Pygmy bluetongue lizards take refuge in, and bask at, the entrance of burrows constructed by lycosid and mygalomorph spiders, and burrows of suitable depth are essential for population persistence (Milne & Bull 2000; Souter et al. 2007). Current species management recommendations identify further agricultural development as a potential threat to the lizard (Milne 1999). Grazing is considered a potential agricultural threat because grazing sheep and cattle can alter the microhabitat architecture, and their trampling can destroy the spider burrows that the lizards rely on for refuge (Souter et al. 2007). Pygmy bluetongue lizards have, however, co-existed with stock grazing for almost 200 years so it is assumed they have some tolerance of grazing (Souter et al. 2007). Current conservation planning recognises a need for a better understanding of the intricate relationship between grazing and the pygmy bluetongue lizard. Overgrazing may remove too much vegetation, compact the soil and cause erosion, consequently directly degrading the microhabitat that surrounds the burrows. Alternatively, the removal of grazing could be a poor management strategy if it results in a reduction of space between grass tussocks that could reduce opportunities for thermal basking and for foraging.

This study is one component of a broader investigation of how grazing impacts the behaviour of the pygmy bluetongue lizard, involving both laboratory and field experiments. The broader aim was to provide results that would allow informed advice to landholders who maintain sheep on properties with populations of this endangered lizard. In previous field studies we have reported that these lizards bask for longer periods of time, and with more of their body exposed out of the burrow, when vegetation around the burrow is reduced (Pettigrew & Bull 2012). However, a deficiency that still remains in the current conservation plan for this species is a lack of knowledge of how different microhabitat states may influence pygmy bluetongue lizard behaviour (such as emergence and foraging), and whether the lizards will alter their behaviour according to

the architecture of their microhabitat. Subsequently, if lizards do alter their behaviour, does this come at a fitness cost to the lizard? From this we might be able to begin to understand what grazing management practice could be used to promote and maintain the optimal microhabitat structure suitable to conserve and promote populations of the pygmy bluetongue lizard. Our focus in this study was on just one of the potential impacts of grazing; it explores how the ambush predation strategy will be affected by reduced levels of vegetation.

Methods

We filmed and monitored pygmy bluetongue lizards in a variety of captive trials in different conditions that represented alternative microhabitat states that might have resulted from different levels of grazing, and investigated whether the lizards showed any alteration in basking and predation behaviour according to the microhabitat they were presented with. The study ran from October 2008 to February 2009, during the spring and summer period when these lizards are active. We collected lizards from their burrows in a semi-arid, remnant native grassland site near Burra, South Australia (33°68' S, 138°94' E), and transported them in individual calico bags 15 km to our trial site. We conducted experimental trials in a room that experienced ambient temperature and light conditions. We filled plastic tanks (base 55 × 40 cm; height 40 cm) to a depth of 20 cm with bricklayers' sand, and inserted two sand-lined plastic tubes (20 cm long; 17-mm internal diameter) vertically into the sand, one at each end of the tank, to provide burrows. For trials that included grass we collected clumps (20–30 cm high) of native speargrass (*Austrostipa* sp.) from the lizard population site, and planted them in the sand substrate. We suspended a 40-watt globe above the middle of each tank approximately 10 cm from the sand surface, and switched it on from 0800 to 1700 hours to provide heating. A digital video camera was mounted above each tank with a field of view that included the entire surface of the tank. We tested two to four lizards at a time in individual tanks in each experimental trial. Each trial lasted 24 h, and included one session in the afternoon of the first day, and a second session in the morning of the second day. No lizard was used more than once, and no more than four lizards were caught and used in trials in any one 24-h period. When each lizard was captured, a rock was used to block the burrow entrance to prevent another lizard from entering that burrow. The burrow was unblocked when each lizard was returned within 24 h, to conform with the permit conditions for capturing this endangered species.

Bare substrate or grass

We tested 30 lizards in each of two alternative treatments, bare substrate or substrate with grass clumps. For the grass treatment we planted 16 grass clumps evenly over the sand surface and at least 2 cm from either burrow entrance. Each lizard was initially exposed to one treatment on the day of capture, allowed to acclimatise to the treatment conditions for 2 h with the heat lamp on, and then filmed for the next 2 h. The following morning lizards were moved to clean tanks and provided with the alternative treatment, using fresh grass clumps and fresh sand. Heat lamps were left on for 2 h before lizard behaviour was filmed for the next 2 h. Half of the lizards were exposed to the bare substrate treatment first and the grass treatment second, and half were exposed to the two treatments in the opposite order.

We placed five live crickets (*Teleogryllus commodus*) (1.0–1.5 cm in length) in the centre of each tank 1 min before filming on each day, and removed any remaining crickets at the end of the 2-h filming session. From the two 2-h recordings we measured both emergence and prey capture parameters. We defined a lizard to be emerged when it was stationary with some part of the body emerged from its burrow entrance, regardless of whether or not the behaviour was for thermoregulation. We recorded the total time spent emerged, and also divided emergence time into time spent in ‘bold’ emergence and the time spent in ‘conservative’ emergence. Following Pettigrew & Bull (2012), bold was defined as when a lizard had more than half of its body exposed out of the burrow, and conservative was when a lizard had less than half of its body exposed. We calculated the percentage of the 2-h filming time each lizard spent emerged, and the percentage of the emergence time each lizard was boldly emerged. We defined a ‘prey capture attempt’ as when a lizard moved rapidly out of its burrow towards a cricket, or turned its head and lunged at a cricket from the burrow entrance. We recorded the time delay before the first prey capture attempt (the time from when the lizard’s head initially emerged from the burrow entrance until when the lizard initiated its first prey capture attempt), the total number of attempts to capture prey, the number of successful attempts, and the number of unsuccessful attempts. We called a prey capture attempt bold if more than half of the lizard’s body was emerged as it lunged at the prey, and conservative if the lizard stayed with less than half of its body emerged during the attempt. We calculated the percentage of total attempts that resulted in a successful capture, and the percentage of attempts that were bold attempts.

To assess the impact of grass cover on emergence and prey capture we used a repeated-measures analysis of variance (ANOVA) for each measured parameter, with treatment (bare or grass) a within-subjects factor, and presentation order (bare first or grass first) as a between-subjects factor.

Low and high grass density

We presented each of 22 lizards with two habitat treatments as in the previous experiment, except that one had low grass density (6 tussocks) and the other had high grass density (14 tussocks) spaced evenly over the tank substrate, and representative of natural grass densities. We filmed 10 lizards for 2 h with no prey, once in the low grass density and once in the high grass density. We filmed the other 12 lizards for 2 h with prey present, once in low and once in high density grass. For those 12 lizards, we provided five medium-sized crickets

1 min before each filming session started, as described in the previous experiment. We filmed half of each group of lizards with the low grass density on the first day and high grass density on the second day, and half in the reverse order. We used repeated-measures ANOVAs for the emergence parameters, with grass density (low or high) as a within-subjects factor, and prey (present or absent) and presentation order (low density grass first or high density grass first) as between-subject factors. We used separate repeated-measures ANOVAs on the prey capture parameters for the 12 lizards that were tested with prey present, with grass density as a within-subjects factor, and with presentation order as a between-subjects factor. For both experiments, proportional data were arcsin-transformed before analysis, and, where necessary, other data were log-transformed to fit the assumptions of normality.

Results

Bare substrate or grass

Lizards spent a significantly higher percentage of the filming time emerged in the bare substrate treatment than in the grass treatment (Table 1; Fig. 1). There was also a significant interaction effect between order and treatment for

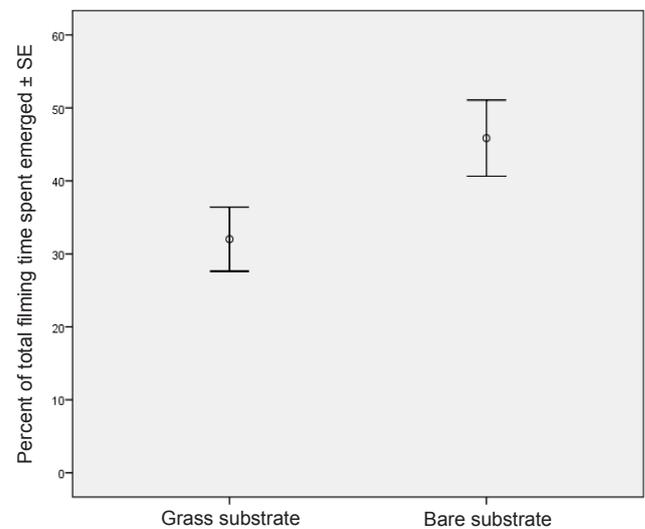


Figure 1. Mean (SE) percentage of time that pygmy bluetongue lizards (*Tiliqua adelaidensis*) spent emerged in the grass and bare substrates during filming sessions.

Table 1. Repeated-measures ANOVAs from the experiment comparing behaviours of pygmy bluetongue lizards (*Tiliqua adelaidensis*) in tanks with bare substrate ($n = 15$) or with planted grass clumps ($n = 15$) (Treatment) presented first (Order). Only the results for emergence and prey-capture parameters that showed significant effects are shown.

| Effect | Percent of overall filming time spent emerged | | | Percent of emerged time spent boldly emerged | | Percent of prey capture attempts that were bold attempts for 17 lizards that attempted to catch prey in both treatments | | |
|-------------------|-----------------------------------------------|----------|-------------|----------------------------------------------|-------------|-------------------------------------------------------------------------------------------------------------------------|----------|-------------|
| | d.f. | <i>F</i> | <i>P</i> | <i>F</i> | <i>P</i> | d.f. | <i>F</i> | <i>P</i> |
| Treatment | 1,28 | 5.83 | 0.02 | 1.45 | 0.24 | 1,15 | 7.79 | 0.01 |
| Order | 1,28 | 0.50 | 0.48 | 0.00 | 0.98 | 1,15 | 0.27 | 0.61 |
| Treatment × Order | 1,28 | 2.48 | 0.12 | 7.51 | 0.01 | 1,15 | 0.96 | 0.34 |

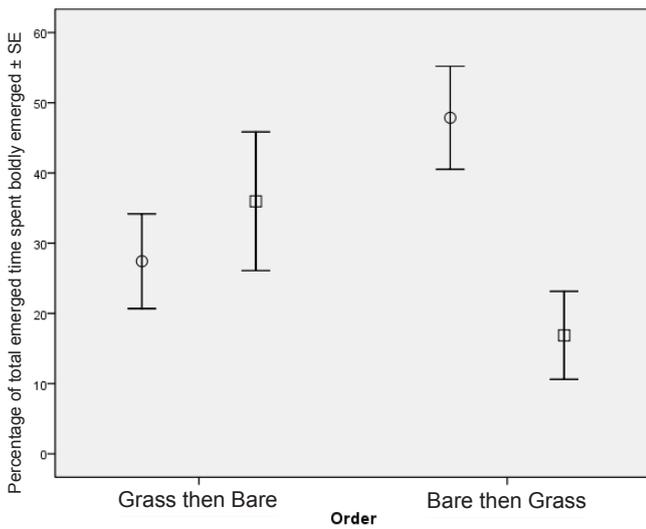


Figure 2. Percentage of total emerged time that pygmy bluetongue lizards (*Tiliqua adelaidensis*) spent boldly emerged in the bare substrate (squares) and grass substrate (circles) when presented with grass substrate first or bare substrate first.

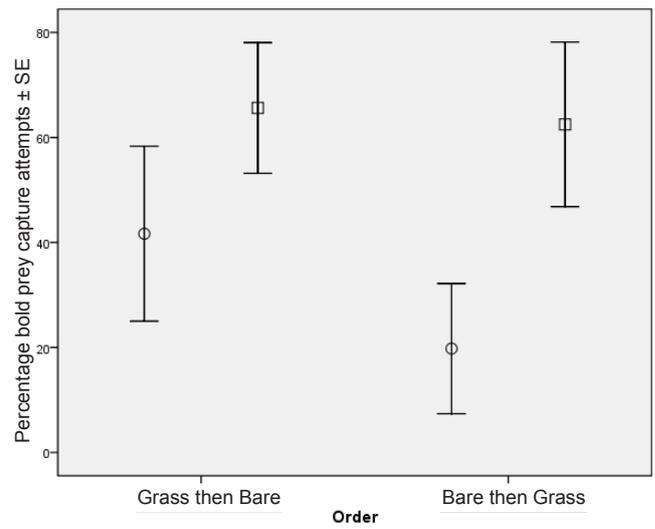


Figure 3. Percentage of total prey capture attempts by pygmy bluetongue lizards (*Tiliqua adelaidensis*) that were bold attempts in the bare substrate (squares) and grass (circles) when grass was presented on Day 1 and bare substrate was presented on Day 2, or when bare substrate was presented on Day 1 and grass was presented on Day 2.

the percentage of total emergence time spent boldly emerged (Table 1). Lizards spent more of their emergence time boldly emerged in the bare substrate treatment than the grass treatment when the grass treatment was presented first, and the reverse when the bare substrate was presented first (Fig. 2). This was probably because lizards generally spent more of their emergence time boldly emerged on Day 2, independent of the treatment. Results from analyses of absolute time emerged and absolute time boldly emerged were similar.

The 30 lizards made a total of 37 prey capture attempts on bare substrate in the 2-h filming sessions and 20 (54%) of those attempts were successful. They made 36 prey capture attempts in the grass treatment with 17 (47%) successful. There was no significant difference between treatments in either the overall number of prey capture attempts ($\chi^2 = 0.01$; d.f. = 1; $P = 0.91$), or in the success rate of the capture attempts ($\chi^2 = 0.34$; d.f. = 1; $P = 0.56$).

The repeated-measures ANOVAs showed no significant effect of treatment or of presentation order on any prey-capture

parameter among the 30 lizards. However, considering only those 17 lizards that made predation attempts in both treatments, a significantly greater percentage of predation attempts were bold attempts in the bare substrate treatment than in the grass treatment and this was consistent across both orders of presentation (Table 1; Fig. 3).

Low and high grass density

For analysis of emergence behaviour, we omitted data from three lizards that did not emerge at all in one of the 2-h filming sessions in the trials without prey (leaving seven lizards in that group for analysis).

For the percentage of filming time spent emerged, there were significant interaction effects of treatment × order and of treatment × prey (Table 2). As in the first experiment, the treatment × order interaction resulted from lizards emerging longest in the treatment that was presented on the second day. The treatment × prey interaction resulted from lizards emerging for longer in low density grass than in high density

Table 2. Repeated-measures ANOVAs from the experiment comparing emergence behaviour of pygmy bluetongue lizards (*Tiliqua adelaidensis*) in tanks with low or high grass density (Treatment), with ($n = 12$) and without ($n = 12$) prey present (Prey), with low grass density presented first or second (Order) (half of each group).

| Effect | Percent of overall filming time spent emerged | | | Percent of emerged time spent boldly emerged | |
|--------------------------|-----------------------------------------------|-------|--------|----------------------------------------------|------|
| | d.f. | F | P | F | P |
| Treatment | 1,15 | 18.06 | <0.001 | 11.64 | 0.01 |
| Order | 1,15 | 1.59 | 0.23 | 0.01 | 0.93 |
| Prey | 1,15 | 0.29 | 0.59 | 3.63 | 0.07 |
| Order × Prey | 1,15 | 0.66 | 0.43 | 0.55 | 0.47 |
| Treatment × Order | 1,15 | 8.56 | 0.01 | 1.36 | 0.26 |
| Treatment × Prey | 1,15 | 10.96 | 0.01 | 9.62 | 0.01 |
| Treatment × Order × Prey | 1,15 | 0.00 | 0.99 | 0.07 | 0.80 |

grass when there were no prey crickets, but emerging for similar times when prey were present (Fig. 4a). There was also a significant treatment \times prey interaction effect for the percentage of emergence time spent boldly emerged (Table 2). Lizards spent more of the emergence time boldly emerged in the low-grass-density treatment than the high-grass-density treatment when there were no prey, but showed no difference when prey were present (Fig. 4b).

The 12 lizards tested with prey made 17 prey capture attempts in the 2-h filming session in the low-grass-density treatment of which 6 (35%) were successful; they made 7 prey capture attempts in the high density grass treatment of which 2 (29%) were successful. In all cases the first successful prey capture happened within a few seconds of the lizard emerging from its burrow. Although there was no significant difference between treatments in the mean number of predation attempts per lizard ($F_{1,10} = 1.31$; $P = 0.28$), there were, overall, significantly more attempts made in the low- than in the high-grass-density treatment ($\chi^2 = 4.17$; d.f. = 1; $P = 0.04$). The overall success rate of attempted prey captures did not differ significantly between low- and high-grass-density treatments ($\chi^2 = 0.10$; d.f. = 1; $P = 0.75$).

The repeated-measures ANOVAs showed no significant effects of treatment, order or treatment \times order interaction for any of the other parameters of prey capture that we measured. In this experiment only 4 of the 12 lizards attempted a prey capture in both treatment types, too small a sample for more detailed comparisons between treatments.

The eight successful prey captures were made during five filming sessions, with four of those sessions (when six prey were captured) in the low-grass-density treatment. We compared the emergence behaviour of the four lizards that captured prey with the eight lizards that did not capture prey in those four low-grass-density sessions. Note that, because prey capture usually occurred soon after the start of filming, most of the emergence we recorded was after prey had been captured. While overall time emerged did not differ significantly between these two groups of lizards, the mean percentage of emergence time spent boldly emerged was significantly higher among the lizards that had captured a cricket (51.4%,

SE 20.3) than among those that had not (6.8%, SE 2.0) ($t = 3.05$; d.f. = 10; $P = 0.01$).

Discussion

Emergence and prey-capture behaviours in these captive trials were similar to those reported from natural populations (Milne et al. 2003; Pettigrew & Bull 2012). Captive pygmy blue tongue lizards in this study emerged for longer in habitats with lower grass density. In the lower grass density, there were more prey capture attempts (in the experiment with low or high grass density) and these attempts were more often made with the body further emerged from the burrow (in the experiment with grass and bare ground). These results suggest that grazing might benefit prey capture by this lizard. The increased number of prey capture attempts might have resulted from a clearer view of approaching prey when grass density was lower.

Pygmy bluetongue lizards spent more of their overall emerged time boldly emerged in the morning of Day 2 than in the afternoon of Day 1 of our trials, regardless of the treatment. We suggest that lizards became more familiar with their cages and less stressed on the second day of captivity. An alternative explanation is that there is a natural diurnal pattern, more bold emergence in the morning than the afternoon, although this has not previously been reported. Our permit conditions restricted us to a 24-h holding period, so we could not allow longer time for acclimatisation, or for us to resolve this question. Nevertheless, although order of treatment presentation was an important influence on the response of lizards to the experimental treatments, here we discuss those trends that can be interpreted as independent of treatment order.

In both experiments we compared lizard behaviour in treatments that differed in the amount of grass cover. In both there were significant trends for lizards to spend more time emerged in the treatment with less grass cover, and for a higher percentage of emerged time to be boldly emerged in the treatment with less grass cover. These results are consistent with trends reported from a field study with manipulation of natural grass cover around burrow entrances, where lizards

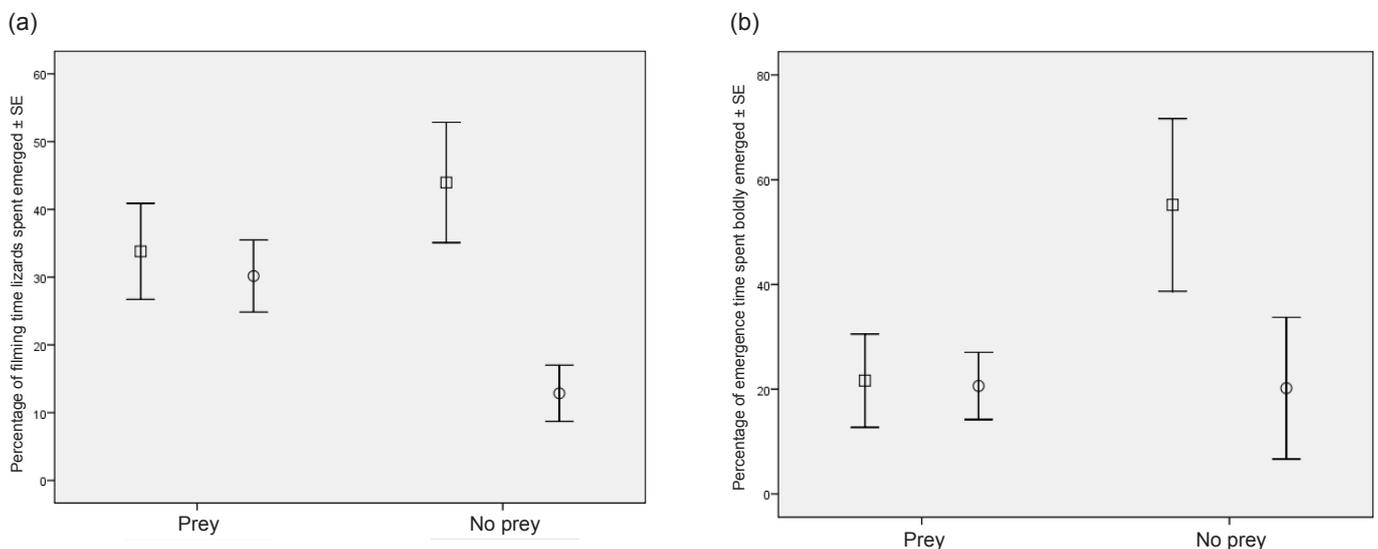


Figure 4. (a) Percentage of time that pygmy bluetongue lizards (*Tiliqua adelaidensis*) spent emerged; and (b) percentage of total emerged time that lizards spent boldly emerged in the low density grass treatment (squares) and the high density grass treatment (circles) when prey was present and when prey was absent during filming sessions.

emerged for longer, and boldly emerged more often when grass was removed (Pettigrew & Bull 2012).

Results from the current study allowed new insights into how prey presence influenced lizard emergence behaviour. In the second experiment lizards emerged more and emerged more boldly in the low- than in the high-grass-density treatment, when no prey were present, but they emerged for similar times in low and high grass density when there were prey in the tanks. That is, the absence of prey seemed to stimulate more confident emergence in the lower than the higher grass density, but when prey were present lizards had equivalent emergence behaviour at both grass densities.

We suggest that a lizard sits at its burrow entrance, initially potentially for thermal basking, but that it remains there to be able to detect and ambush passing prey. Costs of remaining there will include additional risks from bird or snake predators (Fenner et al. 2008a, b), plus energetic costs from higher metabolic rates at warmer body temperatures. Christian and Bedford (1995) have discussed how some lizards can behaviourally reduce metabolic costs by keeping body temperatures lower, when food is scarce. In the pygmy bluetongue lizard, retreating to the cooler environment inside the burrow could lower body temperature, metabolic rate and energetic cost, as well as reducing the predation risk. The benefits of remaining emerged at the burrow entrance are the increased opportunities for prey capture. The time that a lizard chooses to spend at the burrow entrance might result from balancing the relative costs against the benefits.

In circumstances where prey items are present and visible, a lizard may give higher priority to security and thermoregulation, knowing that another meal will be available. If predation opportunities appear scarce, but prey-capture conditions are good (e.g. with low grass density) it may be advantageous to remain emerged at the burrow entrance in case a prey passes by. It may be less advantageous to remain at the burrow entrance when predation opportunities are scarce if prey-capture conditions are less good (e.g. with high grass density), because of the smaller chance of a food reward. In our study, we suggest that the difference in emergence behaviour between high- and low-grass-density treatments when prey crickets were absent represents a shift in the balance of the potential food benefits if a prey did appear against the costs of exposure. We suggest that when grass density was low, lizards either had a broader field of view of where prey might come from, or perceived that any approaching prey was going to be easier to catch, making the potential benefits of remaining at the burrow entrance higher.

A component of that explanation relates to differences in prey capture rates at different grass densities. In the first experiment, lizards were more prepared to leave their burrows and make bold prey capture attempts in the bare substrate (lower grass density) treatment, and, in the second experiment, the overall number of prey capture attempts was significantly higher in the low-grass-density treatment. Both of these results support trends reported from the field study of Pettigrew and Bull (2012) where grass removal improved natural prey capture success in one of the two years examined (with no statistically significant trend in the second year). In combination, these results show that prey captures are easier when grass density is lower, and support the explanation for increased emergence when grass density is lower.

Conflicting evidence comes from the second experiment, low grass density with crickets, where lizards that captured prey early in the filming session spent more of their emergence

time boldly emerged over the next 2 h than did unsuccessful lizards. This contrasts with our suggestion above that lizards will not prolong emergence if they perceive prey are available. Perhaps they emerge more boldly after capturing prey to retain high body temperatures during the initial digestive stages, or perhaps there is natural variation among lizards in the level of boldness, and bolder lizards, those that would emerge boldly anyway, have greater success at catching prey. That is, those four lizards that captured prey were naturally bolder, and would have emerged more boldly than the other lizards whether or not they had caught a cricket. Our analysis highlights the complexities of the factors influencing emergence behaviour and prey capture in these lizards.

In summary our data from laboratory trials in artificial habitats have largely confirmed the trends that we previously reported from field observations and experiments (Pettigrew & Bull 2012), that lizards tend to emerge from their burrows for longer and more boldly when grass density is lower. The results from the current paper suggest that one driver for change of emergence behaviour is an increased opportunity for prey capture when grass is less dense. We found no behavioural change, in either study, to suggest that a reduction in grass density caused lizards to become more cautious as a result of increased potential exposure to predators. We do not know whether lizard mortality from predators is influenced by grass density, but these results suggest that lizard emergence behaviour at the burrow entrance is driven more by prey-capture opportunities than by avoidance of predation risk. Reducing grass density probably increases the likelihood of prey capture by prolonging emergence, particularly when prey are scarce. From that perspective it could be concluded that removal of some grass cover, for instance by sheep grazing, may be beneficial in enhancing prey capture, and has no short-term disadvantages for the pygmy bluetongue lizard.

In a series of studies, we have now started to untangle the interactions between grassland grazing by sheep and behaviour of pygmy bluetongue lizards at their burrow entrances, and to understand some of the mechanisms behind those interactions. We have previously suggested the importance of whether a lizard is in a new or a familiar burrow (Pettigrew & Bull 2011, 2012), and the importance of the year and the time of year when the behaviour is observed (Pettigrew & Bull 2012). Now we add the importance of the perceived prey availability as an additional influencing factor. While these insights into lizard behaviour are themselves of value, and while they may help to explain patterns of behaviour within field populations, they still leave unanswered the management question of the appropriate level of grazing for long-term persistence of lizard populations. We can now confirm that the reduction of grass cover by grazers does not appear to have immediate detrimental impacts on lizard behaviour, and may indeed be beneficial.

However, grazing can have other impacts. For instance trampling by the grazers may destroy burrows, and heavy grazing may reduce the insect food supply, and lead to reduced prey levels for the lizards. Also, Ebrahimi et al. (2012) reported that during a rainstorm pygmy bluetongue lizard burrows were more likely to fill with silt in grazed than ungrazed habitat. Longer term studies of the overall impacts of different grazing levels on lizard population dynamics and on individual lizard fitness and fecundity are now needed.

From a broader perspective these results suggest there could be a balance between the detrimental impacts and the benefits from grazing pressures for other grassland lizard species in other geographical regions. For example, in both

Australia and New Zealand that balance might be affected by conditions that grassland lizards were exposed to before European arrival and the degradation of native grassland habitats for agricultural purposes. In each case lizards may be relatively unaffected by moderate grazing from domestic stock, because large herbivorous marsupial mammals were endemic in Australia, and herbivorous ratite birds (moa) were endemic in New Zealand (Worthy & Holdaway 2002), and sheep may simply replace them for some ecological functions. The positive benefits of grazing by domestic stock for endemic lizards have similarly been reported by Knox et al. (2012) who found that sheep reduced grass density, leading to reduced populations of introduced mice and rats, subsequent reduced predation pressure on endemic geckos, and higher population densities of those geckos. Many conservation management projects are faced with agriculturally modified landscapes, and informed advice, for instance about levels of grazing that are compatible with the continued persistence of target species, will help to maintain the collaboration of local farming communities. The current study of pygmy bluetongue lizards is one example of how this conservation ethic could be promoted in grassland systems around the world, although more data are needed on appropriate levels of grazing pressure.

Acknowledgements

This research was funded by the Australian Research Council, the Nature Foundation of South Australia and the Holsworth Wildlife Research Endowment. We thank Chris Reed for access to the study sites and Alan Pettigrew for help in the field. Our study was conducted with permits from the Flinders University Animal Welfare Committee (permit no. E205) and the South Australian Department of Environment and Heritage (permit no. G250114).

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Received 28 May 2013; accepted 11 September 2013