Endure your parasites: sleepy lizard movement is not affected by their ectoparasites

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Endure your parasites: sleepy lizard movement is not affected by their ectoparasites

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OS drafted and revised manuscript; SSG collected data, drafted and revised manuscript; AS drafted and revised manuscript; CMB primary supervisor of project, sourced funding and jointly conceived research questions.
Short title:
Ectoparasites does not affect lizard movement

Abstract
Movement is often used to indicate host vigour, as it has various ecological and evolutionary implications, and has been shown to be affected by parasites. We investigate the relationship between tick load and movement in the Australian sleepy lizard (*Tiliqua rugosa* Grey, 1825) using high resolution GPS tracking. This allowed us to track individuals across the entire activity season. We hypothesised that tick load negatively affects host movement (mean distance moved day\(^{-1}\)). We used a multivariate statistical model informed by the ecology and biology of the host and parasite, their host-parasite relationship, and known host movement patterns. This allowed us to quantify the effects of ticks on lizard movement above and beyond effects of other factors such as time in the activity season, lizard body condition and stress. We did not find any support for our hypothesis. Instead, our results provide evidence that lizard movement is strongly driven by internal state (sex and body condition independent of tick load), and by external factors (environmental conditions). We suggest that the sleepy lizard has largely adapted to natural levels of tick infection in this system. Our results conform to host-parasite arms race theory, which predicts varying impacts of parasites on hosts in natural systems.
Introduction

Parasites, by definition, gain their energy resources from their hosts, which negatively impacts the host’s health and vigour (Beyer and Grossman 1997; Fenner and Bull 2008). Such impacts in host-parasite relationships drive selection for host defence mechanisms against parasites and parasite specialisation to overcome host defences, resulting in a host-parasite arm race (Dawkins and Krebs 1979). These opposing selection pressures are key drivers of evolutionary and ecosystem processes within host-parasite interactions (Thomas et al. 1999; Brockhurst et al. 2004; Nunn et al. 2004; Martin et al. 2011). The impact parasites have on their hosts varies substantially, ranging from behavioural changes, for instance when parasites manipulate their hosts to increase transmission probability (Poulin 2010, 2013), to population growth regulation (Anderson 1978), substantial reductions in host health (e.g., paralysis (Hamat et al. 2017)), reduced reproductive success (Marzial et al. 2005) and increased mortality (Fraser et al. 2016).

Movement, is a measure often used to indicate host vigour (Angelier et al. 2007; Warren et al. 2011) and has been shown to be affected by parasite load (Fenner and Bull 2008). Here we investigate the relationship between ectoparasites and vigour in a lizard-tick system.

Animal movement drives various ecological processes like dispersal, foraging and species-coexistence (Nathan et al. 2008; Hansson and Åkesson 2014). Thus, understanding how parasites affect movement of their host is essential for broad topics in ecology, with implications for
management and conservation (Poulin 2010; Kays et al. 2015; Dougherty et al. 2017).

Furthermore, a feedback loop between host movement and parasite infection may exist. Before infection, increased host movement can increase the probability of parasite exposure, particularly for parasites that have a free-living infectious stage in the off-host environment or socially transmitted parasites. For example, dispersal events have been suggested to increase parasite and disease spread in both animals and humans (White et al. 2000; Russell et al. 2005; Viboud et al. 2006). Post-infection, parasites can decrease movement by reducing host vigour. For example, O’Dwyer et al. (2014) found a trend towards reduced movements in intertidal snails infected with philophthalmid trematode parasites. Similarly, lizards with experimentally reduced parasite burdens have been shown to move around for longer time periods during observation sessions (Main and Bull 2000; Fenner and Bull 2008). Conversely, there is also evidence that host manipulation by parasites can enhance certain movements or overall activity (Poulin 2013), for example risk taking behaviour in rodents towards cats (Médoc and Beisel 2008) or risky displays by fish infested by trophically transmitted parasites (Lafferty and Morris 1996; Sato et al. 2012).

Understanding this feedback between parasite load and host movement within a species (Leung and Koprivnikar 2016) can provide valuable insights into the host-parasite relationship. If there is a negative feedback loop (e.g., where increased movement increases parasite loads, but higher parasite load decreases movement), the system would tend towards intermediate parasite loads, whereas a positive feedback loop (e.g., where increased movement increases parasite loads and parasites cause hosts to move more (e.g., with parasite manipulation of host behaviour (Berdoy et al. 2000), the feedback loop can result in an explosive accumulation of parasites in some hosts.
Many of the above mentioned relationships and examples (but not all) have been demonstrated in the laboratory, but not the field. Here, we aim to fill this gap by working in-situ to upscale these findings to a natural population of sleepy lizards (*Tiliqua rugosa* Gray, 1825). We focus on the effect of parasite load on individual host movement. Working in South Australia, we tracked the movement of free-ranging sleepy lizards infested with two species of parasitic ticks. Previous studies of the effect of parasites in this system supported two complementary hypotheses. Bull and Burzacott (1993) reported a positive relationship between lizard body condition and tick load, and suggested that high quality home ranges simultaneously benefit both lizards and ticks, driving this relationship, and supporting the favourable patch hypothesis. Later, Main and Bull (2000) found evidence for the ‘reduced vigor’ hypothesis by experimentally manipulating lizard tick loads and showing that tick infestation reduced endurance and daily movements in sleepy lizards. While this work demonstrates that heavy tick loads can have a negative effect on lizards, we still do not know whether this effect is present under natural conditions where infestation levels are generally lower, and lizards can compensate for lower vigor by obtaining greater energy resources in high quality home ranges.

Due to the wealth of knowledge surrounding the sleepy lizard – tick system, and following the results of Main and Bull (2000), it is unlikely that ticks increase lizard movement to facilitate their transmission. Consequently, we formulate three predictions: 1) under natural conditions ticks negatively affects lizard movement activity; 2) the effects of ticks on lizard movement increases with decreasing host body condition (Beldomenico et al. 2008; Beldomenico and Begon 2010), such as later in the season when individuals experience particularly harsh environmental conditions (hot and dry) and food resources have dried out; and 3) tick abundance
in the environment, and hence tick load on the lizard, increases over time, further enhancing the influence of ticks on lizard movement later in the season. To test these predictions, we followed the movement behaviour of 55 adult sleepy lizards using GPS tracking devices and simultaneously quantified their naturally occurring tick loads on a fortnightly basis. We then built a multivariate statistical model that incorporated tick-host relationships known from previous studies in this species (and which we detail below) to address these predictions.

Methods

Study site

This study was conducted in a 1.5km² study site near Bundy Bore station in South Australia’s mid-north (33°54’16”S, 139°20’43”E) (Figure 1(A)). This semi-arid region receives an average annual rainfall of about 250 mm (Bull and Baghurst 1998) and its vegetation consists primarily of chenopod shrubland (Bull and Pamula 1998; Leu et al. 2011a). Average monthly high temperatures in winter are ~15 °C and in summer ~32 °C. Winter temperatures regularly drop below 10 °C and summer temperatures regularly climb above 40 °C. In 2009, when our study was conducted, monthly winter and summer temperatures were above average, but annual rainfall equal to the average for the region.

Host parasite system

The host species, the sleepy lizard is a large scincid lizard, with adult snout to vent lengths of up to 350 mm and body mass of up to 1000 g (Bull and Pamula 1996). Adult lizards maintain stable home ranges of approximately 4 ha, with little spatial shift over time (Bull 1995; Bull and
Lizards in the focal population use bushes (*Maireana sedifolia*, and other species), coarse woody or human (corrugated iron sheets) debris, wombat and rabbit warrens as overnight refuges and to avoid adverse weather conditions (Kerr et al. 2003; Leu et al. 2011a).

At our study site, the sleepy lizard is parasitised by two ectoparasitic tick species, *Amblyomma limbatum* Neumann, 1899 and *Bothriocroton hydrosauri* Denny, 1843 (Figure 1(C)). Both tick species are three host ticks, with each life stage, larvae, nymphs and adults, requiring a host individual. All life stages (except adult males) engorge with blood and or lymph while they are attached to their host (Bull and Sharrad 1980). When ticks are fully engorged they detach from their hosts, mostly in the lizards refuges, to moult into the next life stage (Petney et al. 1983; Chilton and Bull 1993b; Kerr and Bull 2006b). Favourable environmental conditions in these host refuges reduce the risks of desiccation for both tick species (Bull et al. 1988; Chilton and Bull 1993a, b). Larvae and nymphs take some time to moult (8-72 days depending on temperature and relative humidity) into the next life stage, during which they are not infectious, before attaching to the next host individual (Chilton et al. 2000). Both tick species rely on host movement and their reuse of refuges to attach to subsequent hosts and do not actively seek out hosts (Petney et al. 1983). Subsequent hosts may be the same or different individuals that use the same refuge. Sleepy lizards repeatedly use a set of overnight refuges, where ticks are transmitted. Furthermore, Leu et al. (2010b) and Wohlfiel et al. (2013) showed that transmission networks based on asynchronous refuge sharing among neighbours predicts individual tick load.

### Movement and tick infestation
We captured most of the resident adult lizards (29 males and 26 females) in our study site, and observed their movement throughout the main activity period (Bull and Baghurst 1998), September 2009 – January 2010. We attached a data logger to the dorsal surface of each lizard’s tail using surgical adhesive tape (Leu et al. 2010b) (Figure 1(B)). Data loggers included a GPS unit to record lizard movement, a radio transmitter to allow the recapture of lizards and regular tick counts, and a step counter. GPS locations were recorded every 10 mins when lizards were active and moving, that is when they took at least one step in the previous 10 min. The GPS devices had a median horizontal accuracy of +/- 6m (Leu et al. 2010a). Each data logger (GPS, radio transmitter and step counter units) weighed 37 g, representing 4.9 % of an average 750 g adult lizard body mass. Based on the GPS data, we calculated for each individual, the total distance moved per day (sum of all distances between consecutive locations on that day) and subsequently for each lizard the mean daily distance moved per fortnight (Figure 1(D)). Sleepy lizard movement has previously been quantified by a number of different measures, including steps taken per day (Leu and Bull 2016); daily activity (total number of 10 min intervals during which lizards were recorded active divided by the number of days observed) and daily distance moved (total distance moved in metres divided by the number of days observed) (Leu et al. 2016a); movement activity (distance between consecutive GPS locations) and duration (Leu et al. 2011b); and cotton spooling, sprint speed, endurance, active/inactive behaviour (Main and Bull 2000), all of which measure different aspects of lizard activity. Here our focus was on the mean daily distance moved by lizards on active days, similar to previous studies (Leu et al. 2016a), hence we excluded days on which lizards did not move, i.e. either no steps were taken and hence no GPS locations were recorded, or the total daily distance travelled was 0 m.
Individual lizards could be identified by their unique radio transmitter frequency. We recaptured lizards once every fortnight to record tick loads (number, species and life stage), take morphological measurements and download GPS data. Lizard handling periods (a standard two hour period) were excluded from the GPS data, and lizards released at their point of capture. Handling periods accounted for the period of time lizards were actively handled (~30 mins) and the period of time over which lizard movement was expected to be impacted as a consequence of handling (~1 hour (Kerr et al. 2004)). Larvae, nymphs and adult females have an increasing impact on the hosts because they draw increasing amounts of blood and lymph. Males do not engorge with blood. Following Main (1999), we quantified the differential impact of each life stage and converted each lizard’s fortnightly tick load to a larvae equivalent index. One nymph equalled ten larvae, one adult female equalled 250 larvae, and one adult male equalled one larva (Main 1999). Fortnightly morphological measurements included lizard mass (to the nearest 5 g), and snout-vent length (to the nearest 5 mm). We log transformed these fortnightly morphological measures and used them in a mass on snout-vent length linear regression. We then used the unstandardized residuals from this regression analysis as a measure of each lizard’s fortnightly body condition (Moore et al. 2009). These morphological measures were regressed in one analysis including all lizards and all fortnights, as this provided a better perspective of body condition across the activity season and population.

The first time lizards were captured we also determined each individual’s sex by assessing head morphology, males have substantially longer jaws and broader heads than females (Bull and Pamula 1996). Male sex was confirmed by gently everting their hemipenes where possible.
After the study we removed all data loggers and released all lizards. We observed no damage or irritation to the skin where data loggers were attached and lizards naturally shed their skin in the following months. All lizards were treated using procedures formally approved by the Flinders University Animal Welfare Committee in compliance with the Australian Code of Practice for the Use of Animals for Scientific Purposes and conducted under the South Australian Department of Environment and Natural Resources Permit to Undertake Scientific Research.

**Model construction**

We constructed our multivariate statistical model informed by previous knowledge of the ecology of the sleepy lizard and its ecto-parasitic ticks as well as their host-parasite relationship. This allowed us to investigate the effects of ticks on lizard movement above and beyond effects of other factors that are known to affect movement. For each fortnight, we calculated the mean daily distance travelled by each lizard, which was our dependent variable. This variable was square root transformed to meet model assumptions (normality, homoscedasticity). Then, to test our first prediction we included total larvae equivalent as a measure of tick load and as one of our independent variables into the model.

Lizard movement activity first increases, then decreases over the course of the season (Firth and Belan 1998; Kerr and Bull 2006c). At the beginning and end of the activity season lizard movement is low due to cool ambient temperatures and low food resources, respectively. We accounted for this non-linear relationship by including a time variable, fortnight, and fortnight$^2$ into our model (both continuous). Lizard sex was included as a fixed categorical factor, because male sleepy lizards have been demonstrated to have higher levels of movement activity than
females (Leu et al. 2011b). Movement activity also varies with body condition (Leu and Bull 2016), which we included in our model. We also included a random intercept and slope for each individual, \((\text{fortnight} \mid \text{lizard id})\), to account for individual differences in movement activity (intercept), as well as individual differences in movement change over time (slope).

In the sleepy lizard, tick load is known to vary with body condition (Bull and Burzacott 1993), and hence we included the interaction term \(\text{total larvae equivalent} \times \text{body condition}\) to test our second prediction that the impact of ticks on lizard movement increases with decreasing host condition. Lastly, we included the interaction term \(\text{total larvae equivalent} \times \text{fortnight}\) to test our third prediction that lizard movement is more strongly affected late in the season because tick abundance in the environment and hence tick load on the lizard increases over time. All continuous independent variables were centred and scaled to allow us to determine their importance relative to one another in the statistical model. We used the “vif.mer” function (Frank 2011) to check for collinearity using variance inflation factors (VIFs), which were generally very low (< 1.07) and below a pre-selected threshold (Zuur et al. (2010) suggest a cut-off of 3). As expected, VIFs were higher for fortnight (20.33) and \(\text{fortnight}^2\) (20.36), due to the polynomial structure of the model, with a clear relationship between the two variables.

Our final model was as follows:

\[
\sqrt{\text{mean daily distance}} = \text{sex} + \text{fortnight} + \text{fortnight}^2 + \text{total larvae equivalent} + \text{body condition} + \text{total larvae equivalent} \times \text{body condition} + \text{total larvae equivalent} \times \text{fortnight} + (\text{fortnight} \mid \text{lizard id})
\]
All statistical analyses and data manipulation was conducted in IBM SPSS Statistics 22 (Corp 2013), or R (R Core Team 2016), using mostly lme4 (Bates et al. 2015), lmerTest (Kuznetsova et al. 2016), and ggplot2 (Wickham 2009) to produce graphs.

Results

Over the duration of this study, the mean number of location records per lizard was 1728 (95% CI 1617-1838), with lizards monitored for a mean of 5.42 (95% CI 5.08-5.8) fortnights over the duration of the season. On average lizards moved a mean daily distance of 215 m (95% CI 203-228m) in a given fortnight over the duration of the season. Mean daily distance moved in a given fortnight ranged from 3-745m/day. Lizard tick loads varied by fortnight, ranging from 0-801 larval units, with a mean of 64 (95% CI 47-81).

We found no evidence to support any of our three predictions on tick load effects; tick load did not affect lizard movement; the effect of tick load on lizard movement was not host condition dependent; and the effect of tick load on lizard movement did not depend on the time in the lizard activity season (Table 1). Our model accounted for lizard ID and fortnight as random effects (intercept and slope (fortnight | lizard id)). Lizard ID explained twice as much of the variance in the intercept than fortnight in the slope (0.15 and 0.08, respectively), suggesting lizards differed from each other more strongly (intercept) than their observed temporal variation (slope) over the duration of the season. Consistent with previous studies, lizard movement varied over the course of the activity season (Table 1). Fortnight had a positive effect, and fortnight\(^2\) a negative effect, implying lower movement at the start of the season and that lizards also walked
less as the season progressed. Lizard movement increased with body condition (Table 1). Female
lizards additionally moved shorter mean distances per day than males (Table 1 and Figure 2).
Interaction effects included in the model were not significant (Table 1).

Discussion

Summary of main result

Our study is based on a rich dataset using GPS data loggers attached to lizards which recorded
host movement in greater detail than previous studies investigating similar questions, and
combining this with repeated measures of lizard tick loads. In contrast to our predictions, we
found no evidence that tick load negatively affected lizard travel distance, and the effect of tick
load was not dependent on host condition or the time in the lizard activity season. Our
interpretation of this results is that lizards have adapted to the natural level of tick infection, and
that the average intensity (number of individual ticks on a given lizard) of ticks is too low to
have a measurable effect on movement patterns. Chronic stress is known to negatively impact
immune system function (Dhabhar 2014). Consequently, we predicted that lizard vigour
(movement) is more strongly affected during periods of chronic stress, for example at low body
conditions or high tick loads, which may occur later in the season due to harsh environmental
conditions, poorer quality food resources and increased tick abundance in the environment.

However, we found no evidence for these predictions. A possible explanation for the lack of tick
effects shown in our study could be that both ticks and lizards are affected by environmental
conditions in a similar manner (both negatively affected by harsh and positively affected by good
environmental conditions). For example, increased temperature and decreased humidity shortens
the time to desiccation for ticks and decreases tick survival when waiting for the next host (Bull et al. 1988; Chilton and Bull 1993a, b). Similarly, temperature and humidity have been shown to influence sleepy lizard activity and movement (Firth and Belan 1998; Kerr and Bull 2006c).

Comparison with earlier findings from the sleepy lizard – tick model system

Our results, demonstrating no impact of ticks on the movement activity of lizard hosts, contrast previous work by Main and Bull (2000) who experimentally manipulated lizard tick load in the field and laboratory, and monitored lizard movements and activity levels. The conclusion of their study was that ticks reduced the daily distance lizards moved, home range size, endurance and sprint speed, and altered basking/active behaviour. However, these effects could not be consistently identified across study sites, lizard age classes, or years (Main and Bull 2000). We argue that increasing tick loads beyond natural levels may increase the level of stress experienced by lizards in a similar manner to a reduction in body condition and food resource availability, as ticks consume host resources. Thus, although the results of Main and Bull (2000) are not consistent with ours or across seasons and sites in their study, their conclusions conform to our original predictions. Whilst the work by Main and Bull (2000) suggests that under some circumstances ticks can impact on lizard movement, our results suggest that overall, under natural conditions, this is not the case.

Parasite effects on movement in other systems

Several studies in other systems also found no effect of parasites on host movement (Hillegass et al. 2010; Mayer et al. 2015; Nelson et al. 2015). For example, Mayer et al. (2015) found no difference in swimming speed of adult keelback snakes (Tropidonophis mairi Jan, 1863) before
and after the removal of the gastrointestinal nematode *Tanqua anomala* Linstow, 1904.

Similarly, Nelson et al. (2015) found no relationship between a range of movement measures (distance travelled per minute, voluntary movements, movements towards prey items, sprint speed and endurance) and lungworm (*Rhabdias hylae* Johnston and Simpson, 1942) infection in multiple anuran species (*Rhinella marina* Linnaeus, 1758, *Cyclorana Australis* Gray, 1842, *Limnodynastes convexiusculus* MacLeay, 1877 and *Litoria nasuta* Gray, 1842). The host-parasite arms race clearly suggests that the effects of parasites on their hosts in natural systems are on a scale from large to small (Dawkins and Krebs 1979). Consequently, studies reporting no impact of parasites on hosts are important as they suggest that in some systems hosts have adapted to natural levels of parasite infection (Mayer et al. 2015; Nelson et al. 2015), at least with regard to the measure of interest.

Nevertheless there are studies which have clearly shown that parasites can reduce host movements. For example, Garrido and Pérez-Mellado (2013) found haemogregarine blood parasite infestation to reduce sprint speed in wild caught Lilford’s wall lizards (*Podarcis lilfordi* Günther, 1874). They suggested that this is the result of the blood parasite reducing haemoglobin concentrations and subsequently lowering the lizards’ capacity for oxygen transportation to muscle tissues, thereby reducing sprint speed (Garrido and Pérez-Mellado 2013). In contrast, there are also reports of parasites increasing host movement. Médoc and Beisel (2008) found that acanthocephalan (*Polymorphus minutus* Goeze, 1782) infection increased both swimming speed and distance covered at the beginning of an escape attempt (first 0.5 sec) in male amphipods (*Gammarus roeseli* Gervais, 1835). They suggested that the acanthocephalan parasite manipulates its host’s vigour to enhance its transmission to a suitable avian definitive host by
increasing the ability of *G. roeseli* to avoid other crustacean predators (Médoc and Beisel 2008).

Together the relationships in these studies suggest that the effect of parasite infections on host movement is largely dependent on the host-parasite system and type of movement/behaviour being observed or measured.

**Other drivers of sleepy lizard movement**

Whilst tick load did not appear to impact movement activity in the sleepy lizard, we did identify three other drivers of lizard movement. Lizard movement changed over the lizard activity season (change over time) in a non-linear fashion. This is consistent with earlier findings (Kerr and Bull 2006c; Spiegel et al. 2015) and is driven by ambient conditions, predominately temperature (Firth and Belan 1998) and food availability. Movement activity in the sleepy lizard increases from the beginning of the active season, when nights are cold and lizards bask longer to reach suitable body temperatures before they start moving. Following its peak, movement activity decreases again towards the end of the activity season, as ambient temperatures become too hot and food availability is scarce. Lizard sex was a second major driver of movement, with males moving greater daily distances than females and covering larger home ranges (Spiegel et al. accepted). Leu et al. (2011b) found similar differences between sexes and suggested that greater male movement is due to males seeking extra pair matings and/or additional foraging opportunities because costs of pair living are higher for males, or due to males investing more in home range guarding activities such as patrolling it more or marking their home range more frequently than females (Leu et al. 2016b; Sih et al. 2017). Thirdly, we showed movement to increase with lizard body condition. Earlier studies suggested that lizard body condition and tick loads are related (Bull and Burzacott 1993). Here, we included lizard body condition, tick load
and their interaction in our model and did not find a significant interaction effect nor any
collinearity between these variables. Based on this, we were able to distinguish between the
effect of both factors and clearly identified body condition as a strong driver of movement in the
sleepy lizard. Whilst not demonstrated in our study, social interactions are also known to
influence behaviour and movement in the sleepy lizard, for example in monogamous lizard pairs,
where pair partners remain in close proximity for extended periods of time (Leu et al. 2015), or
in social networks, where individuals actively associate with or avoid individual neighbours (Leu
et al. 2010a; Spiegel et al. 2016). Ectoparasitic ticks also have the potential to influence the
relationship between social interaction and movement both directly, by changing host behaviours
such as the frequency of refuge reuse (Leu et al. 2010b), or indirectly by affecting how
conspecific lizards respond to infected individuals (Bull 1990).

Concluding remarks

Parasites are defined as having adverse impacts on their hosts. Nevertheless, several studies have
described exceptions to this (Mayer et al. 2015; Nelson et al. 2015; Taggart 2016; Taggart and
Schultz 2016). Here, we describe another exception in a lizard-tick host-parasite system which
extends our understanding of the complex relationships between hosts, parasites and the
environment by including detailed previous knowledge, frequently unavailable in other systems.
In this study, we chose a single index of vigour, however, it is possible that other aspects of the
lizards’ movement are impacted by tick loads, such as area covered or duration of activity, as
well as non-movement measures. The host-parasite arms race clearly predicts that some parasites
have little or no impact on their host while others have great impacts depending on the state of
the arms race (Dawkins and Krebs 1979). This system is another example of a parasite having little effect on its host.

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References:


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Table 1: Linear mixed model summary showing the effects of sleepy lizard (*Tiliqua rugosa*) sex, body condition, tick load and time in the activity season on the average daily movement of lizards.

SE = standard error

DF = degrees of freedom

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</tbody>
</table>
Figure 1: Sleepy lizards (*Tiliqua rugosa*) and our study site: (A) the location of our study site in South Australia; (B) adult sleepy lizard with GPS unit and radio transmitter taped to tail, note permanent marker pen adjacent lizard for scale; (C) ticks attached to lizard; and (D) movement tracks of a single tagged lizard over the duration of the activity season (green lines), showing example of our dependent variable, the total daily distance moved (red line). Map source data were provided by the Department of Environment, Water and Natural Resources.

Figure 2: Effect of lizard sex on the mean daily movement of male and female sleepy lizards (*Tiliqua rugosa*).
Figure 1:
Figure 2: