MS. DANAE MOORE (Orcid ID : 0000-0003-2129-1452)
DR MICHAEL KEARNEY (Orcid ID : 0000-0002-3349-8744)

Article type : Research Article
Editor : Martijn van de Pol
Section : Climate Ecology

Under the weather? –The direct effects of climate warming on a threatened desert lizard are mediated by their activity phase and burrow system

Running head: Climate warming and the buffering effect of burrow systems

Danae Moore^{A,B}, Adam Stow^A, and Michael Ray Kearney^C

^ADepartment of Biological Sciences, Macquarie University, North Ryde, 2109, NSW, Australia.

^BAustralian Wildlife Conservancy, Newhaven Wildlife Sanctuary, P.M.B. 146, Alice Springs, NT, 0872, Australia.

^CSchool of BioSciences, The University of Melbourne, Parkville, 3010, Vic., Australia.

Corresponding author. Email: danae.moore@bigpond.com; Phone: (08) 89646 000

Key words: climate warming, ectotherm, extreme environments, *Liopholis kintorei*, subterranean refuge use, microclimate, temperature based activity budgets.

Type of Paper: Standard Paper

This is the author manuscript accepted for publication and has undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the [Version of Record](#). Please cite this article as [doi: 10.1111/1365-2656.12812](https://doi.org/10.1111/1365-2656.12812)

This article is protected by copyright. All rights reserved

Abstract

- (1) For ectotherms such as lizards, the importance of behavioral thermoregulation in avoiding thermal extremes is well established and is increasingly acknowledged in modern studies of climate warming and its impacts. Less appreciated and understood are the buffering roles of retreat sites and activity phase, in part because of logistical challenges of studying below-ground activity. Burrowing and nocturnal activity are key behavioral adaptations that have enabled a diverse range of reptiles to survive extreme environmental temperatures within hot desert regions. Yet, the direct impact of recent global warming on activity potential has been hypothesised to have caused extinctions in desert lizards, including the Australian arid zone skink *Liopholis kintorei*.
- (2) We test the relevance of this hypothesis through a detailed characterisation of the above- and below-ground thermal and hydric microclimates available to, and used by, *Liopholis kintorei*.
- (3) We integrate operative temperatures with observed body temperatures to construct daily activity budgets, including the inference of subterranean behavior. We then assess the likelihood that contemporary and future local extinctions in this species, and those of similar burrowing habits, could be explained by the direct effects of warming on its activity budget and exposure to thermal extremes.
- (4) We found that *Liopholis kintorei* spent only 4% of its time active on the surface, primarily at dusk, and that overall potential surface activity will be increased, not restricted, with climate warming. The burrow system provides an exceptional buffer to current and future maximum extremes of temperature ($\approx 40^\circ\text{C}$ reduction from potential surface temperatures), and desiccation (burrows near 100% humidity). Therefore any climate warming impacts on this species are likely to be indirect.
- (5) Our findings reflect the general buffering capacity of underground microclimates, therefore our conclusions for *Liopholis kintorei* are more generally applicable to nocturnal and crepuscular ectotherms, and highlight the need to consider the buffering properties of retreat sites and activity phase when forecasting climate change impacts.

Introduction

Reptiles and other ectotherms have a well-defined temperature range where their performance is optimal (Cowles & Bogert, 1944; Bogert, 1949; reviewed in Huey, 1982). Increasing environmental temperatures through climate warming have thus been predicted to result in localised extinctions through exposure to stressful body temperatures (and through constrictions of the activity budget (Deutsch *et al.*, 2008; Huey *et al.*, 2009; Sinervo *et al.*, 2010).

The use of buffering retreat sites has enabled a diverse range of reptiles to thrive in thermally extreme environments such as deserts (Cowles & Bogert, 1944; Heatwole, 1970; Pianka, 1969; Pianka, 1986; Heatwole & Taylor, 1987; Roger, 2008). Retreat sites are generally microclimates that offer thermal and/or hydric relief from unfavourable environmental conditions. Common retreat sites include sheltering in the shade of vegetation, under bark, under leaf litter or within a burrow. For lizards living in such these regions, where the risk of overheating or desiccation is high, time sequestered within retreat sites may amount to a large proportion of each day (Huey, 1982; Huey *et al.*, 1989; Kerr *et al.*, 2004). The thermal and hydric properties of retreat sites may therefore have a substantial impact on the physiological performance and development of an individual (Dawson, 1975; Huey and Slatkin, 1976; Huey, 1982; Lynch & Gabriel, 1987). In desert environments, where deep shade is rare and vegetation is sparse, burrow construction is common and provides a cool retreat during the day when surface temperatures are unfavourably hot (Heatwole, 1970; Huey *et al.*, 1989). Burrows may also permit the maintenance of higher body temperatures at night or during cooler days (Heatwole & Taylor, 1987; Hertz, 1992; Sunday *et al.*, 2014).

A burrowing habit in conjunction with a crepuscular (active during dawn and dusk) and or nocturnal activity phase, provides even greater buffering from climate extremes than burrowing alone. Nocturnal lizards often retain ancestrally high thermal preferences and activity is typically limited by low rather than high temperatures (Pianka & Pianka, 1976; Autumn *et al.*, 1999), while burrows and other retreat sites can provide thermoregulatory opportunities during the day (Bustard, 1967; Dial, 1978; Webb & Shine, 1998; Kearney *et al.*, 2000). Recent research has highlighted that most reptiles would not be able to survive the warmest potential body temperatures within exposed habitats, and that a reliance on behaviors and or habitats that provide a buffer to current and potential increases in extreme operative temperatures is therefore critical (Huey *et al.*, 2009; Kearney *et al.*, 2009; Huey *et al.*, 2010; Scheffers *et al.*, 2014; Sunday *et al.*, 2014; Grimm-Seyfarth *et al.*, 2017).

Predictive models are frequently relied upon to generate broad-scale conclusions around the extinction risks for ectotherms caused by climate warming (e.g. Thomas *et al.*, 2003; Deutsch *et al.*, 2007; Huey *et al.*, 2009; Sinervo *et al.*, 2010). However, key factors such as thermoregulatory capacity, microclimate variability and the use of refuge sites are often overlooked (Buckley, 2013; Kearney, 2013; Sunday *et al.*, 2014; Briscoe *et al.*, 2016). Recent research (Sinervo *et al.*, 2010) argued that climate warming is driving population extinctions of lizards across the globe and that 20% of all lizard species may be extinct by 2080. This research proposed a mechanism for global lizard population extinction under climate warming where activity periods are restricted due to elevated field body temperatures. This activity restriction model, derived from studies of diurnal Mexican *Sceloporus* lizards, was used to predict recent population extinctions in additional lizards globally, irrespective of activity phase. Sinervo *et al.*'s predictions included our study species, the great desert skink *Liopholis kintorei*, an internationally listed vulnerable species (Stirling & Zietz, 1893; IUCN, 2016). The relevance of restricted activity periods for *L. kintorei*, and therefore possibly other species, is questionable given that field observations point to a crepuscular and nocturnal activity phase in this species (McAlpin, 2001; Pearson *et al.*, 2001).

Here we aim to further understand the potential role of climate warming as a threatening process for non-diurnal lizards living in extreme desert environments, by investigating the thermal constraints for *L. kintorei*. This species was chosen as a case study species because it is known to be a crepuscular and nocturnal lizard, and constructs and maintains a deep burrow-system. Specifically, we assess if the reported local extinctions for *L. kintorei* could be explained by a restriction of activity period due to an increase in field body temperatures. We then assess the potential for future activity restrictions under a climate warming scenario. In addition, we evaluate the extent to which the burrow system constructed by *L. kintorei* provides a buffer against current extreme maximum temperatures and those predicted by future climate warming.

To achieve these objectives we characterised the thermal surface environment within *L. kintorei* habitat and the thermal and hydric conditions of their burrow systems. We concurrently collected field body temperatures from adult *L. kintorei*. We use these three temperature data sets to infer the location of the skink within the burrow system or on the surface, thereby indirectly deriving daily activity budgets and determining their activity phase. Finally, we consider a climate warming scenario and estimate: 1) current and future potential activity times within four micro-habitats by calculating the total hours observed within the voluntary foraging body temperature limits (27.1 °C – 37.6 °C) at dawn, dusk, day and night,

and; 2) current and future thermal stress levels experienced within the burrow system by comparing thermal tolerance limits (maximum body temperature) to burrow system temperatures at various depths.

Materials and Methods

Study species and site

Liopholis kintorei is a large (200 mm snout to vent length, up to 350 g), long-lived skink. It is restricted to sandy and gravelly habitats within the western desert regions of Australia (McAlpin, 2001; Chapple, 2003). It is an obligate burrower that constructs and maintains a deep (up to 80 cm) and complex burrow system. The burrows are occupied by family groups of close relatives, often consisting of an adult pair and two age cohorts of individuals (McAlpin *et al.*, 2011; Dennison, 2015). No field data exists to determine their primary activity phase, however, limited field observations suggest a crepuscular and nocturnal habit during warmer months, with a period of hibernation during the winter months (McAlpin, 2001; Chapple, 2003).

Our study was conducted at Newhaven Wildlife Sanctuary in central Australia, Northern Territory (22.72°S, 131.17°E; Fig. 1). This property is managed for conservation by the Australian Wildlife Conservancy (AWC). On Newhaven *L. kintorei*'s preferred habitat is semi-saline spinifex sandplains; this vegetation community is typically homogenous and is dominated by hummock grass *Triodia pungens*. This study was conducted at a 75 ha study site where *L. kintorei* was known to be locally abundant.

Fig. 1 Newhaven Wildlife Sanctuary (a) showing the location of the 75 ha study site (closed square). The shaded grey areas indicate potential *Liopholis kintorei* habitat and the hatched areas indicate ephemeral salt lakes. The inset map (b) shows the location of Newhaven Wildlife Sanctuary within Australia.

Newhaven's climate is arid tropical, with annual air temperatures ranging from -2 to 46 °C (measured at 1.2 m from the ground) and highly variable annual rainfall (range 66 to 951 mm in the last 50 years) falling mainly in the summer (Stafford-Smith & Morton, 1990; Latz *et al.*, 2003; Bureau of Meteorology, 2016).

Local weather data

Local weather conditions were recorded using an automated weather station (WeatherHawk, Campbell Scientific, Inc.) installed at the study site. Air temperature, relative humidity, wind speed and direction, solar radiation and rainfall were recorded at high resolution (every 10 minutes; 1.2 m above the ground) for a 12 month period.

Measuring the operative thermal environment

The available above-ground thermal environment within *L. kintorei* habitat was measured by using physical models (herein referred to as copper models) to estimate operative environmental temperatures (T_e ; Bakken & Gates, 1975; Bakken, 1992; Grant & Dunham, 1988; Shine & Kearney, 2001; Bakken & Angilletta, 2014). Operative temperatures are the

body temperatures an organism would attain if exposed to a particular environment long enough to attain thermal steady state (Bakken & Gates, 1975). Two sizes (210 x 40 mm and 139 x 20 mm, length x diameter) of thin-walled (1 mm) copper pipe were used to represent adult and sub-adult *L. kintorei*, respectively. Temperature sensitive data-loggers (Maxim Thermochron iButton DS1922L) were inserted into each length of copper pipe. The data-loggers were seated in a piece of thin polystyrene to ensure each data-logger sat centrally in the pipe. In an attempt to match the absorptivity of the copper pipe and *L. kintorei* as closely as possible, copper pipes (which were already orange in colour) were capped with plastic end-caps that were painted with an orange colour similar to the dorsal colour of *L. kintorei*.

We sampled the three dominant surface microhabitats within the semi-saline spinifex sandplain: 1) fully shaded, where copper models were placed under a large (~1 m diameter) hummock of soft spinifex *Triodia pungens*; 2) partially shaded, where copper models were placed under a small (~30 cm diameter) hummock of soft spinifex *Triodia pungens*, and; 3) exposed, where copper models were centred within a 2 m² area of cleared vegetation exposed to full sun. A large and small copper model (see description above) was placed within each of the three microhabitats at six randomly chosen locations within the study site. Each copper model was orientated east-west to maximise exposure to the sun, placed on the surface of the sand with the top of the data-logger facing upwards, and set to record the temperature (°C; accuracy ± 0.5 °C) every 30 minutes for a 12 month period—October 2013 to September 2014.

Measuring temperature and humidity within the burrow system

Six occupied *L. kintorei* burrow systems were selected randomly from the study site. The temperature (°C; accuracy ± 0.5 °C) and relative humidity (%; accuracy ± 0.5 %) of each burrow system was recorded at 30 minute intervals for a 12 month period—October 2013 to September 2014. Temperature and humidity data-loggers (Maxim Thermochron iButton DS1923) were taped onto a 2 – 4 m length of high tensile wire and placed down an active burrow entrance (a small hole was cut into the tape to expose the humidity sensor of the data-logger). Data-loggers were attached to the wire approximately 10 cm from the burrow entrance (shallow), at the mid-point of the wire (mid) and at the base of the wire (deep).

Standardised sampling of temperature and relative humidity at a variety of depths across the burrow system was difficult because the construction of each burrow system varies; the actual depths of data-loggers was therefore unknown. We compared sub-surface soil temperature taken simultaneously from the study site to infer the approximate depth of each

data-logger within the burrow system (see below). We thereby inferred that burrow system temperatures recorded from the burrow entrance were between 5 cm – 15 cm deep, those from the mid burrow system were 30 cm – 50 cm, and those from deep with the burrow were between 50 cm to 1 m. We converted relative humidity (%) to vapour density (kg m^{-3}) using the WETAIR subroutine of the NicheMapR package (R Core Team, 2015; Kearney & Porter, 2016), to assess the extent that relative humidity differences were driven by absolute water content of the air.

Measuring the temperature profile of soils within arid spinifex sandplains

The temperature profile of the soil substrate was measured at 6 randomly chosen locations within the study site. Temperatures ($^{\circ}\text{C}$, accuracy $\pm 0.5^{\circ}\text{C}$) were measured at the surface and at depths of 5, 15, 30, 50 and 100 cm. A 1.5 m length of plastic skirting was used to hold the data-loggers (Maxim Thermochron iButton DS1922L) at their pre-determined depths. Temperature data-loggers were covered with a single sheet of OPSITE film (Smith & Nephew) to provide an extra measure of water resistance. Each data-logger was fitted snugly into drilled holes and a layer of gaffer tape was then placed over the back. The exposed side of the data-logger was sprayed with OPSITE before being buried. The front of each surface data-logger faced south and the vegetation was cleared around the data-loggers to create 2 m² area of bare earth that would be continuously exposed to the sun. The temperature was measured at 30 minute intervals for 12 months—October 2013 to September 2014.

Measuring the field body temperatures of Liopholis kintorei

The distribution of *L. kintorei* field body temperature (T_b) was obtained by sampling twenty adult skinks (mean body mass: 217 g), each from a distinct burrow system. Adult skinks were trapped at their burrow system using Elliott traps (Elliott Scientific Equipment). Temperature data-loggers (Maxim Thermochron iButton DS1922L; accuracy $\pm 0.5^{\circ}\text{C}$) and VHF transmitters were attached using *Hyperfix* (Smith & Nephew), a soft, flexible, breathable medical tape. The data-logger and VHF transmitter units had a combined weight of <7 grams, with the total dimensions being 30 x 17 x 5 (L / W / H, mm). The units were fitted laterally on the skink allowing for normal leg movement and so that the skinks could move freely within the burrow system. The surface of the data-logger was placed directly onto the skin of the lizard. Temperature was recorded at fifteen minute intervals from September – December 2013. All skinks were located using a VHF receiver in mid-December, prior to when females

give birth (McAlpin, 2001), at which point the data-loggers and VHF transmitters units were removed.

Our approach uses skin temperature measurements as a proxy for core body temperature measurements. This is justified from a biophysical point of view when the ratio of external and internal resistance to heat flow (the Biot number) in a system under transient heat exchange is less than 0.1, in which case the system can be considered to be of uniform temperature (Porter *et al.* 1973). Following the calculations of Porter *et al.* (1973) for a 217g lizard, one obtains a Biot number of exactly 0.1. Kerr *et al.* (2004) used the same data loggers to estimate body temperature of a larger lizard, *Tiliqua rugosa* (adult mass ~ 700g). They justified this using the findings of Chilton and Bull (1992), who compared internal (cloacal) temperature as measured remotely by thermistor-transmitters with spot measures of surface body temperature for 16 adult *T. rugosa* and obtained a mean difference of 0.5 °C (range -3.8 to 3.8 °C, across a body temperature range of 13.4 °C to 32.2 °C).

Very few records of T_b exist for *L. kintorei* — Pianka (1969) recorded a single field T_b value of 25.2 °C and Henzell (1972) reported a mean T_b of 33.6 °C under laboratory conditions. Due to the difficulties in obtaining individuals of this threatened species for laboratory observations, we assumed the critical thermal max (CT_{max}) for *L. kintorei* to be 43.1 °C by averaging existing published CT_{max} data for *Liopholis inornata* (42.8 °C; Heatwole & Taylor 1987) and unpublished CT_{max} data for *Liopholis slateri* (43.5 °C) . Although these two species differ in body size, they are closely related to *L. kintorei* (Pianka & Giles 1982) and therefore we have used this estimated value as a reference point on our plots.

Activity budget and activity phase

A series of individual time budgets were created where half-hourly mean surface operative temperatures, burrow entrance temperatures, sub-surface soil temperatures (which were used as a proxy for burrow system temperatures when inferring the location of the skinks within a burrow system; Fig. S1), and weather data (rainfall and solar radiation) were plotted against the T_b of an individual *L. kintorei* over a specified period. We developed an algorithm to compute the absolute difference between each available temperature and the body temperature of the individual lizard, to identify the closest of the environmental temperatures to the lizard body temperature. This automated procedure faced ambiguities at sunrise and sunset when operative temperatures and burrow system temperatures were the same within

any half hour period. The prediction were thus manually checked to judge the inferred location and activity state of each individual skink based on the state in the previous time intervals (Fig. S2). Activity states were: 1) active deep in burrow; 2) inactive deep in burrow; 3) active shallow in burrow; 4) inactive shallow in burrow; 5) at burrow entrance, or; 6) on the surface. Activity within the burrow was defined as a change in the depth of location within the burrow system across the half-hour time steps.

To define activity phase from T_b observations, we determined the dawn and dusk time periods based on solar radiation data collected from the remote weather station. We defined these periods to be when solar radiation values were between 1-20 W m⁻² such that dawn and dusk occurred between the hours of 6.00 am and 7.00 am (1 hour), and 6.30 pm and 7.30 pm (1 hour), respectively. Accordingly, diurnal activity was defined as the hours between 7.00 am and 6.30 pm (11.5 hours) and nocturnal activity as the hours between 7.30 pm and 6.00 am (10.5 hours). Pearson's Chi-square test of independence was used to test for statistical independence between activity state and time of day (Quinn & Keough, 2002).

From these data we generated: 1) a mean activity budget; 2) individual activity budgets for 17 lizards, and; 3) daily activity budgets for 10 lizards (those with the most data overall) for a period of a week where most concurrent data was available.

Potential activity times and restrictions under current and future climatic conditions

We estimated monthly and annual proportions of thermally suitable time (i.e. within the range of observed surface body temperatures, 27.1 °C to 37.6 °C, based on our observed data for 2013) during the day, night, dawn and dusk where *L. kintorei* could be active on the surface (either within exposed or deeply shaded habitats), or the burrow system entrance (5 cm to 15cm deep). If conditions were thermally unsuitable (i.e. outside the observed T_b range), inactivity deep within the burrow system was assumed. We did not estimate the proportion of thermally suitable time at mid depths or deep within the burrow system because at these locations T_e never exceeded the voluntary maximum T_b (39.6 °C) of *L. kintorei* under current climatic conditions or future warming scenarios. We also excluded partly shaded surface conditions and focused the analysis on the extremes of T_e —exposed and deeply shaded. We then assessed how this activity potential would change under a projected climate change scenario for the site in 2070. We extracted monthly climate change scenario estimates of maximum air temperature from 6 climate models for our study site (see Briscoe *et al.*, 2016 for details on the climate models used). Although an increased frequency of extreme

high daily temperatures has been predicted for central Australia, we imposed an averaged, uniform increase in maximum air temperature of 2.8 °C in 2070, because there was little variation among the models or between months within models and there remains uncertainty around the nature of these extreme temperature events (Reisinger *et al.*, 2014; Fig. S3). To predict future thermal stress levels, we added the defined increases in temperature to our operative temperature and burrow system temperature data.

Buffering effect of the burrow system

We illustrated the current effectiveness of temperature regulation possible by *L. kintorei* with the use of the burrow system by plotting the distribution of adult *L. kintorei* observed field body temperature against sub-surface soil temperatures ranging from 5 cm to 1 m (used as a proxy for burrow system temperatures), and against observed surface operative temperatures within exposed, partly shaded and deeply shaded micro-habitats. In addition, we quantified the frequency, intensity and duration of current and future levels of thermal stress experienced within the burrow system. We compared the observed upper thermal tolerance limit ($T_{vol.max}$) of *L. kintorei*, derived from the activity budget analysis, to the minimum of the hourly maximum temperatures of the burrow system at three depths (deep, mid and burrow entrance) to calculate: 1) the percentage of a year T_e at a given location in the burrow exceeded $T_{vol.max}$; 2) the maximum degrees above $T_{vol.max}$, and; 3) the maximum consecutive hours above $T_{vol.max}$. This allowed us to estimate the extent that the burrow system buffers this species from extreme temperatures under current and future climatic conditions.

Results

Field body temperatures of Liopholis kintorei

We obtained data on the field T_b of 20 individual adult *L. kintorei* between early September and mid December 2013 (mid spring and early summer). Each individual was monitored between three and 50 days resulting in 33 504 T_b temperature data points. Three individual T_b samples were removed from analysis—one skink was preyed upon by a woma python (*Aspidites ramsayi*) and two additional skinks exhibited no movement, suggesting the logger detached early on.

During the study period the minimum and maximum T_b recorded during all activity was 25.7 °C and 39.6 °C, respectively, and the mid 50% T_b ranged from 28.6 °C to 32.1 °C

(Fig. 2). The minimum and maximum T_b recorded during surface activity was 27.1 °C and 37.6 °C respectively and the middle 50% T_b during surface activity ranged from 32.1°C to 34.6 °C (Fig. 2).

Fig. 2 The frequency distribution of observed field body temperatures of adult *Liopholis kintorei*, surface operative temperatures (copper models) and sub-surface soil profile temperatures.

Activity budget and activity phase

The number of days over which T_b was recoded varied in length for each individual skink — ranging between three and 50 days (Fig. S4). Among-individual activity varied, however where observation were longer than 6 days activity budgets showed consistent patterns of high proportions of inactivity within the burrow with relatively smaller amounts of activity at shallow depths within the burrow, at the entrance or on the surface. When surface activity was observed, the proportions were consistently higher during dusk (Fig. S4). Among-day activity varied substantially, with no evidence of synchrony in activity among individuals (Fig. S5).

Mean activity levels varied significantly across the different periods of the day ($\chi^2 = 941.2$, $df = 15$, $P < 0.001$; Fig. 3). *Liopholis kintorei* spent 4 % of their total observed activity time on the surface. The proportion of surface activity was significantly higher during

the hours of dusk (31%) than during the dawn (0%), day (5%) or night (1%) ($\chi^2 = 148$, $df = 5$, $P < 0.001$, $\chi^2 = 963.4$, $df = 5$, $P < 0.001$ respectively). Only 8% of time was spent at the burrow entrance, with proportions similar during the day and night (47% and 49% respectively). A large proportion (88%) of time was spent sequestered within the burrow system where skinks appeared to be inactive for 82% of the time. Most time was spent deep within the burrow, at a depth ranging between 50 cm and 1 m (52%), and 35% of time was spent at shallower depths between 15 cm to 30cm.

Fig. 3 The observed proportion of time an adult *L. kintorei* spends active or inactive within the burrow system, at a burrow entrance or on the surface. The number of hours that each period of the day comprised of is given above the bars.

Annual cycles of surface operative environmental temperatures within arid spinifex sandplains

Maximum T_e values reached 76 °C and 78 °C in exposed conditions for adult and juvenile lizards, respectively (Fig. 4a; Fig S6; Table S1). Deeply shaded habitats were cooler by 22 °C for adults and 24 °C for juvenile lizards. Minimum T_e values measured -3°C for adult and juvenile lizards in exposed conditions — surface conditions were 2 °C warmer in deeply shaded habitats (Fig 4a; Fig. S6; Table S1). High rainfall events, as observed in January, April and, to a lesser extent, July decreased T_e values across all levels of cover (Fig. 4a, Fig. S6).

Fig. 4 Daily mean minimum and maximum surface operative temperatures for adult *L. kintorei* (a); daily mean minimum and maximum temperature within the burrow system (b), and; daily mean minimum and maximum relative humidity within the burrow system (c). Monthly minimum and maximum means and standard deviation are denoted by the open squares and lines. *Liopholis kintorei* voluntary minimum and maximum field body temperatures are denoted by the dashed black lines with the critical thermal maximum indicated by the solid black line.

Annual cycles of temperature, relative humidity and vapour density of the burrow system

Burrow system minimum and maximum temperatures varied by month at all depths following a typical seasonal pattern. The highest monthly maximum temperatures were recorded during the summer season (January and December) and reached as high as 34 °C deep in the burrow, 37 °C at mid depths, and 49 °C at the burrow entrance (Table S2). The lowest monthly minimum temperatures at all depths were recorded in July — temperatures dropped to 14 °C deep within the burrow system, 13 °C at mid depths and 9 °C at the burrow entrance. In some months, following rainfall, monthly maximum temperatures dropped

substantially across all depths following an increase in soil moisture (Fig. 4b). In January, for example, temperature at all depths dropped dramatically after a six day rainfall event where 178 mm of rain was recorded at the study site (Fig. 4b).

Maximum relative humidity occurred mostly deep within the burrow system with levels reducing towards the burrow entrance (Fig. 4c). However, there was a strong interaction between burrow system depth and month on humidity and, in some months, following rainfall, monthly maximum relative humidity levels were highest at the burrow surface (Fig. 4c; Table S3).

Vapour density values within the burrow system followed seasonal air temperature patterns with higher values within the summer months and lower values within the winter months (Fig. S7; Table S4). Vapour density correlated with atmospheric conditions, but was consistently higher within the burrow system at all depths (Fig. S7).

Potential activity times under current and future climatic conditions

The estimated proportion of time an adult *L. kintorei* could potentially spend active on the surface within exposed or shaded conditions was found to increase by 24% with a warming effect of 2.8 °C by 2070, with proportions changing notably at dawn (+11%) and at night (+28%; Fig. 5). During the primary activity phase period for *L. kintorei*, dusk, we estimated that the amount of thermally suitable time available on the surface will decrease marginally by 2% (Fig. 5). As air temperatures increase, diurnal surface activity will be restricted, resulting in an increased proportion (16%) of time spent deep within the burrow system (Fig. 5).

Fig. 5 The total estimated proportion of time in 2014 (a) and 2070 (b) during the day (11.5 h), night (10.5 h) dawn (1 h) or dusk (1 h), that an adult *L. kintorei* could potentially spend active on the surface, at a burrow entrance, or inactive deep within the burrow system.

When comparing present and future potential activity time across seasons, we predict potential surface activity (in exposed and shaded conditions) to increase across all seasons with a warming effect of 2.8 °C by 2070 (Fig. S8). A 40% increase is predicted during spring (September, October and November) and autumn (March, April and May). Potential surface activity (within exposed habitats) at dusk will become greater during the month of May — under current climatic conditions, activity in this month is restricted to diurnal activity.. Similarly, the proportion of potential activity time in summer (December, January and February) is predicted to increase from 55% to 73%. Although potential activity time during the winter months (June, July and August) is predicted to increase from 14% to 20%, surface activity will remain restricted to the day (Fig. S8).

Buffering effects of the burrow system

The burrow system provides an exceptional buffer against maximum temperature extremes (Fig. 6). Hourly temperatures at mid and deep depths within the burrow system did not exceed the voluntary maximum T_b (39.6 °C) of *L. kintorei* under current climatic conditions and future warming scenarios. The burrow entrance is more exposed to external atmospheric conditions, and measured temperatures exceeded the voluntary maximum T_b (Table 1). Under future climatic warming scenarios we estimated that levels of thermal stress will increase at the burrow entrance, with burrow entrance activity being restricted by 3% by 2070 (Table 1).

Fig. 6 The effectiveness of the burrow system to buffer individuals from temperature extremes is illustrated by observed hourly sub-surface temperatures (as a proxy for burrow system temperature), in comparison with observed surface temperatures.

Table 1 Contemporary and future thermal stress levels where the observed voluntary maximum field body temperature ($T_{vol.max}$) was greater than the burrow entrance operative temperature over a 12 month period.

Indicators of thermal stress at the burrow entrance	2013/2014	2070
Percentage of the year above $T_{vol.max}$	0.4	3
Maximum consecutive hours above $T_{vol.max}$	5	10
Maximum degree in any given hour above $T_{vol.max}$	2	5

Discussion

Although it is well established that lizard species are potentially vulnerable to the impacts of climate warming due to elevated field body temperatures (Grant & Dunham, 1988; Huey *et al.*, 2009; Huey, 2009; Sinervo *et al.*, 2010; Sunday *et al.*, 2014), it is critical that assessments of vulnerability to warming consider species-specific activity phase and the buffering potential of the microhabitats that a species uses (Scheffers *et al.*, 2014). One of our aims was to test the hypothesis of Sinervo *et al.* (2010) that activity restriction through climate warming is generally a threatening process for lizards. We specifically considered *L. kintorei* in this

context because it was a case study presented in Sinervo *et al.* (2010), but our findings will be relevant to many other taxa, particularly species with a nocturnal or crepuscular activity phase and/or that routinely make use of subterranean retreat sites..

Our data lead us to reject the hypothesis that activity restriction due to increased field body temperatures caused the recent local extinctions of *L. kintorei*. First, above-ground temperature does not appear to be limiting surface activity in this species. Indeed, one of the most striking findings of our study is the very low level of surface and burrow entrance activity engaged in by *L. kintorei*, amounting to only 9% of their total activity budget despite 74% of time being thermally suitable. From the limited data available on lizard time budgets, many species, particularly sit-and-wait predators (Huey and Pianka, 1981; Hertz *et al.*, 1988), spend only a fraction (< 30%) of their potential activity period foraging actively, whereas active foragers spend a higher proportion of their potential activity period engaged in vigorous activity. Thus, it may not generally be true that potential activity time is a limiting factor for many lizards.

Second, our data indicate that *L. kintorei* is crepuscular (with similar proportions of diurnal and nocturnal surface activity observed), and we estimated that an increase in air temperature of 2.8 °C by 2070 will actually increase rather than decrease the total potential surface activity times during dawn and dusk. Seasonally, potential activity periods are predicted to increase, particularly in May (late autumn) and September (early spring), thus extending the active season (summer). An examination of individual activity budgets showed a substantial amount of asynchronous daily variation, with surface activity occurring sporadically, indicating that lizard activity patterns were largely independent of each other and thus not tied to particular environmental conditions (for example, all lizards emerging on warm nights). An increase in potential activity time associated with climate warming is likely to be true for most crepuscular or nocturnal lizards as suitable thermal conditions increase (Kearney, 2013).

The dry weather conditions that prevailed over much of the study period may have influenced surface activity of the skinks. Relative humidity, rainfall and soil moisture content are expected to influence surface activity for two primary reasons. First, desiccation risk may restrict surface activity to wetter periods, as was demonstrated experimentally in the Gila Monster *Heloderma suspectum* (Davis & DeNardo, 2009). Second, the primary food source for *L. kintorei* is harvester termites of the genus *Drepanpterns* (McAlpin, 2011), these insects become active in very high numbers on the surface primarily from dusk to dawn during periods of high humidity, and swarming events occur after summer rainfall (Andersen, 2005).

During these times *L. kintorei* may spend more time on the surface at night foraging widely for this high protein food source.

Finally, our data clearly show that burrow system provides an exceptional buffer to extremes of temperature and conditions of low humidity. Maximum burrow system temperatures measured during the study period at mid to deep depths (30 cm – 1m) remained within the estimated voluntary thermal tolerance and estimated lethal limits of this species throughout the year and relative humidity remained high (monthly means ranging from 62% to 97%) deep within the burrow system. Similarly, the temperatures we observed at these depths did not exceed the lethal limits known for any other lizard of the Australian arid zone and generally remained within known voluntary thermal tolerances across scincid and agamid lizards (Warburg, 1965; Greer, 1980; Pianka, 1986; Heatwole & Taylor, 1987).

With the predicted increases in air temperatures under future warming scenarios, the burrow system will continue to provide a buffer for this species, with burrow system temperatures remaining below the observed maximum T_b at mid and deep depths. Thus *L. kintorei*, and the wide range of other taxa that use their burrow systems or that construct their own, even if only at depths of 30 cm, are likely to be buffered from the direct effects of climate warming on body temperature. For these reasons we conclude that threatening processes other than the direct effect of climate warming must be sought to explain the observed loss of *L. kintorei* at some localities (Cadenhead *et al.*, 2015; Moore *et al.*, 2015; Moore *et al.*, 2017).

Although previous studies have inferred the location (e.g. surface vs. retreat site) of individual reptiles based on body temperature and operative environmental temperatures (e.g. Kerr *et al.*, 2004; Davis *et al.*, 2008; Christian & Weavers, 1996), there have been no studies of the thermal biology of a lizard species during periods of inactivity (not hibernating) within a subterranean refuge site. We have demonstrated how two widely used thermal ecology methods (the measurement of operative and field body temperatures), can be combined to make inferences on activity budget of a burrowing species, which are inherently difficult to observe. Although we were not able to validate the activity budgets through direct observation of periods of aboveground activity, the contrast in thermal environments above and below ground is so extreme in magnitude, amplitude and phase (Fig. 4-5) that we could be very confident in our inferences. Moreover, our inference of patterns of surface activity were consistent with the presence of tracks around the burrow system made during routine and concurrent surveys of the burrow systems (Moore *et al.* 2015), and the activity budgets overall were consistent with field observations (McAlpin unpublished data; Pearson, 2001).

This research method has enabled us to assess in detail how the burrow system is used by *L. kintorei* throughout the active season, revealing that it spends the vast majority of its time deep in the burrow where temperatures are generally lowest and humidity highest. In addition, we were able to infer that lizards were inactive (or at least not changing depth) for most of the time spent in the burrow. Thus it appears that *L. kintorei* behaves in a manner that prioritises the conservation of energy and water. The method we developed can be transferred to other reptile, mammal and avian species that construct and maintain a burrow or use existing burrows within the landscape, across a variety of habitats where species specific thermal biology questions are pertinent.

Lizards have been identified as one of the most threatened taxa by climate warming (Huey *et al.*, 2009; Huey *et al.*, 2012; Sinervo *et al.*, 2010). Because our findings reflect the general buffering capacity of underground microclimates, our conclusions for *L. kintorei* are more generally applicable to burrowing ectotherms within desert environments and highlight the need to consider the buffering properties of retreat sites and species-specific activity phase when forecasting climate change impacts. Our study shows how critical it is to ground truth predictive models of climate warming impacts carefully against the microclimates available to a given species. Moreover, predictive models must be able to realistically capture this microclimatic variation in addition to the behavioral thermoregulatory capacity for organisms to exploit it (Sears *et al.*, 2011; Buckley, 2013; Kearney, 2013; Kearney *et al.*, 2014; Briscoe *et al.*, 2016; Kearney & Porter, 2016; Levy *et al.*, 2016a; Sears *et al.*, 2016). It is equally important to test whether activity time is indeed a significant limiting factor from a thermal perspective, and to put activity budgets into the context of the life cycle, phenology and life history (Kearney, 2013; Levy *et al.*, 2016b; Maino *et al.*, 2016). The modelling tools for such analyses are becoming increasingly available, and such analyses will be of particular importance when considering the management of endangered species to ensure the optimum allocation of resources to the most relevant threatening processes.

Acknowledgements

This project was funded by the Australia and Pacific Science Foundation, Trish Macdonald, Joss Haiblen and Australian Wildlife Conservancy. The research was carried out under the Macquarie University Animal Ethics Committee permit ARA 2013/020 and Northern Territory Government Animal Welfare Authority licence 017. We thank volunteers Arlo Stewart, Elia Pirtle, James Maino, Julia Wyllie and Shari May for their valuable assistance

with fieldwork and Georgina Spinaze, Margaret Henley and Linda White for their generous care given at the perfect times. Thank you to Drew Allen who provided analytical guidance and Steve McAlpin and Rachel Paltridge for their ongoing guidance. Thank you also to Josef Schofield, AWC's Newhaven Sanctuary Manager, who gave his full support of the project and provided valuable field assistance together with Eremaea Schofield.

Author's Contributions

All authors conceived the ideas and designed the general methodology. DM collected all field data and led the writing of the manuscript. MK and DM analysed the data. All authors contributed to the drafts and gave their final approval for publication.

Data Accessibility

All data are available from Zenodo: <https://doi.org/10.5281/zenodo.1157165> (Moore et al 2018).

References

- Andersen AN (2005) Termites of Northern Australia. Alice Springs, NT: Barker Souvenirs.
- Autumn K, Jindrich D, DeNardo D & Mueller R (1999) Locomotor performance at low temperature and the evolution of nocturnality in geckos. *Evolution*, 53(2), 580-599.
- Bakken G S & Angilletta MJ (2014) How to avoid errors when quantifying thermal environments. *Functional Ecology*, 28(1), 96–107. doi:10.1111/1365-2435.12149.
- Bakken GS (1992) Measurement and application of operative and standard operative temperatures in ecology. *American Zoologist*, 32, 194-216.
- Bakken GS & Gates DM (1975) Heat-Transfer Analysis of Animals: Some Implications for Field Ecology, Physiology, and Evolution. In: Gates D.M., Schmerl R.B. (eds) *Perspectives of Biophysical Ecology. Ecological Studies (Analysis and Synthesis)*, vol 12. pp. 255-290. Springer, Berlin, Heidelberg.

- Bartholomew George A & Vance A Tucker (1963) Control of changes in body temperature, metabolism, and circulation by the agamid lizard, *Amphibolurus barbatus*. *Physiological Zoology*, 36(3), 199-218.
- Bogert CM (1949) Thermoregulation and ecritic body temperatures in Mexican lizards of the genus *Sceloporus*. *Anales del Instituto de Biología de la Universidad Nacional Autónoma de México*, 20, 415-426.
- Briscoe NJ, Kearney MR, Taylor CA & Wintle BA (2016) Unpacking the mechanisms captured by a correlative species distribution model to improve predictions of climate refugia. *Global Change Biology*, 22(7), 2425-39.
- Buckley LB (2013) Get real: putting models of climate change and species interactions in practice. *Annals of the New York Academy of Sciences*, 1297, 126-138.
- Bureau of Meteorology (2016) 'Climate Data Online'. Available from: <http://www.bom.gov.au/jsp/ncc/cdio/weatherData>. [accessed July 2016].
- Bustard HR (1967) Activity cycle and thermoregulation in the Australian gecko *Gehyra variegata*. *Copeia*, 4, 753-758.
- Bogert CM (1949) Thermoregulation in reptiles: A factor in evolution. *Evolution*, 3(3), 195-211.
- Cadenhead NCR, Kearney MR, Moore D, McAlpin S & Wintle BA (2015) Climate and Fire Scenario Uncertainty Dominate the Evaluation of Options for Conserving the Great Desert Skink. *Conservation Letters*, 9(3), 181-190.
- Chapple DG (2003) Ecology, life-history, and behavior in the Australian scincid genus *Egernia*, with comments on the evolution of complex sociality in lizards. *Herpetological Monographs*, 17, 145-180.
- Chilton NB & Bull CM (1992) The on-host temperature environment for two Australian reptile ticks. *Australian Journal of Zoology*, 40 (6), 583-592.

- Christian KA & Weavers BW (1996) Thermoregulation of monitor lizards in Australia: an evaluation of methods in thermal biology. *Ecological Monographs*, 66 (2), 139-157.
- Cogger H (2014) *Reptiles and amphibians of Australia* (7th ed.). Collingwood, Australia: CSIRO Publishing.
- Cowles RB & Bogert CM (1944) A preliminary study of the thermal requirements of desert reptiles. *Bulletin of the American Museum of Natural History*, 83, 261-296.
- Davis JR, Taylor EN & DeNardo DF (2008) An automated temperature-based option for estimating surface activity and refuge use patterns in free-ranging animals. *Journal of Arid Environments*, 72(8), 1414-1422.
- Dawson WR (1975) On the physiological significance of the preferred body temperatures of reptiles, *Perspectives of Biophysical Ecology*, 12, 443-473.
- Deutsch CA, Tewksbury JJ, Huey RB, Sheldon KS, Ghalambor CK, Haak DC & Martin PR (2008) Impacts of climate warming on terrestrial ectotherms across latitude. *Proceedings of the National Academy of Science*, 105(18), 6668-6672.
- Dennison S (2015) Social organisation and population genetics of the threatened great desert skink, *Liopholis kintorei*. Ph. D. Thesis, Macquarie University, Sydney.
- Dial BE (1978) Aspects of the behavioral ecology of two Chihuahuan desert geckos (Reptilia, Lacertilia, Gekkonidae). *Journal of Herpetology*, 12(2), 209-216.
- Greer AE (1980) Critical thermal maximum temperatures in Australian scincid lizards: their ecological and evolutionary significance. *Australian Journal of Zoology*, 28(1), 91-102.
- Grant BW & Dunham AE (1988) Thermally imposed time constraints on the activity of the desert lizard *Sceloporus merriami*. *Ecology*, 69(1), 167-176.

- Grimm-Seyfarth A, Mihoub JB & Henle K (2017) Too hot to die? The effects of vegetation shading on past, present, and future activity budgets of two diurnal skinks from arid Australia. *Ecology and Evolution*, 7(17), 6803-6813.
- Heatwole H (1970) Thermal ecology of the desert dragon *Amphibolurus inermis*. *Ecological Monographs*, 40(4), 425-457.
- Heatwole HF & Taylor J (1987) *Ecology of reptiles*. Chipping Norton, Australia: Surrey Beatty & Sons Ptl Limited.
- Henzell RP (1972) Adaptation to aridity in lizards of the *Egernia whitei* species-group. Ph. D. Thesis, Adelaide University.
- Hertz PE (1988) Time budgets, thermoregulation, and maximal locomotor performance: are reptiles olympians or boy scouts? *American Zoology*, 28(3), 927-938.
- Hertz PE (1992) Evaluating thermal resource partitioning. *Oecologia*, 90(1), 127-136.
- Huey RB (1982) Temperature, physiology, and the ecology of reptiles. In *Biology of Retilia* (pp. 25-74). Cambridge, UK: Academic Press.
- Huey RB & Pianka ER (1981) Ecological consequences of foraging mode. *Ecology*, 62(4), 991-999.
- Huey RB, Deutsch CA, Tewksbury JJ, Vitt LJ, Hertz PE, Pérez HJÁ & Garland T (2009) Why tropical forest lizards are vulnerable to climate warming. *Proceedings of the Royal Society of London B: Biological Sciences*, 276(1664), 1939-1948.
- Huey RB, Losos JB & Moritz C (2010) Are lizards toast?. *Science*, 328(5980), 832-833.
- Huey RB, Kearney MR, Krockenberger A, Holtum JAM & Williams SE (2012) Predicting organismal vulnerability to climate warming: roles of behavior, physiology and adaptation. *Phil. Trans. R. Soc. B*, 367(1596), 1665-1679.

- Huey RB, Peterson CR, Arnold SJ & Porter WP (1989) Hot rocks and not-so-hot rocks: retreat-site selection by garter snakes and its thermal consequences. *Ecology*, 70(4), 931-944.
- Huey RB & Slatkin M (1976) Cost and benefits of lizard thermoregulation. *The Quarterly Review of Biology*, 51(3), 363-384.
- Humphreys W (1978) The Thermal Biology of *Geolycosa godeffroyi* and Other Burrow Inhabiting Lycosidae (Araneae) in Australia. *Oecologia*, 31(3), 319-347.
- IUCN 2016. The IUCN Red List of Threatened Species. Version 2016-2.
<<http://www.iucnredlist.org>>. Downloaded on 04 September 2016
- Kearney M & Predavec M (2000) Do nocturnal ectotherms thermoregulate? A study of the temperate gecko *Christinus marmoratus*. *Ecology*, 81(11), 2984-2996.
- Kearney M, Shine R & Porter WP (2009) The potential for behavioral thermoregulation to buffer “cold-blooded” animals against climate warming. *Proceedings of the National Academy of Sciences*, 106(10), 3835-3840.
- Kearney MR (2013) Activity restriction and the mechanistic basis for extinctions under climate warming. *Ecology Letters*, 16(12), 1470–1479.
- Kearney MR, Isaac AP & Porter WP (2014) microclim: Global estimates of hourly microclimate based on long-term monthly climate averages. *Scientific Data*, 1, 140006.
doi:10.1038/sdata.2014.6.
- Kearney MR & Porter WP (2016) NicheMapR - an R package for biophysical modelling: the microclimate model. *Ecography*.
- Kerr GD, Bull CM & Cottrell GR (2004) Use of an on board datalogger to determine lizard activity patterns, body temperature and microhabitat use for extended periods in the field. *Wildlife Research*, 31, 171-176.

- Latz P, Paltridge R & Holmes J (2003). Vegetation survey of Newhaven Reserve. A report prepared for *Birds Australia*. Desert Wildlife Services, Alice Springs.
- Levy O, Buckley LB, Keitt TH & Angilletta MJ (2016a) A dynamically downscaled projection of past and future microclimates. *Ecology*.
- Levy O, Buckley LB, Keitt TH & Angilletta MJ (2016b) Ontogeny constrains phenology: opportunities for activity and reproduction interact to dictate potential phenologies in a changing climate. *Ecology Letters*.
- Lynch M & Gabriel W (1987) Environmental tolerance. *American Naturalist*, 283-303.
- Maino JL., Kong JD, Hoffmann AA, Barton MG & Kearney MR (2016) Mechanistic models for predicting insect responses to climate change. *Current Opinion in Insect Science*.
- McAlpin S (2001) 'A Recovery Plan for the Great Desert Skink (*Egernia kintorei*).' Arid Lands Environment Centre: Alice Springs, NT.
- McAlpin S (2011) Social structure and mating systems of the great desert skink, *Liopholis kintorei*. M.Sc. Thesis, Macquarie University, Sydney.
- McAlpin S, Duckett P & Stow A (2011) Lizards cooperatively tunnel to construct a long-term home for family members. *PLoS One* 6, e19041.
- Moore D, Kearney MR, Paltridge R, McAlpin S & Stow A (2015) Is fire a threatening process for *Liopholis kintorei*, a nationally listed threatened skink? *Wildlife Research*, **42**, 207-216.
- Moore D, Kearney MR, Paltridge R, McAlpin S & Stow A (2017) Feeling the pressure at home: predator activity at the burrow entrance of an endangered arid-zone skink. *Austral Ecology* online. doi: 10.1111/aec.12547.

- Moore D, Stow A & KearneyMR (2018) Under the weather? The direct effects of climate warming on a threatened desert lizard are mediated by their activity phase and burrow system. *Journal of Animal Ecology* accepted 10th Jan 2018. doi: 10.5281/zenodo.1157165.
- Morton SR & James CD (1988) The diversity and abundance of lizards in arid Australia: a new hypothesis. *American Naturalist*, 237-256.
- Pearson D, Davies P, Carnegie N & Ward J (2001) The great desert skink (*Egernia kintorei*) in Western Australia: distribution, reproduction and ethno-zoological observations. *Herpetofauna Sydney*, 31, 64-68.
- Pianka ER (1967) On lizard species diversity: North American flatland deserts. *Ecology*, 334-351.
- Pianka ER (1986) Ecology and natural history of desert lizards: analyses of the ecological niche and community structure. Princeton, NJ: Princeton University Press.
- Pianka ER & Giles WE (1982) Notes on the biology of two species of nocturnal skinks, *Egernia inornata* and *Egernia striatata* in the Great Victoria desert. *West. Aust. Nat.*, **15**, 44-49.
- Pianka ER & Pianka HD (1976) Comparative ecology of twelve species of nocturnal lizards (Gekkonidae) in the Western Australian desert. *Copeia*, 1, 125-142.
- Porter WP, Mitchell JW, Beckman WA & DeWitt CB (1973) Behavioral implications of mechanistic ecology. *Oecologia*, 13(1), 1-54.
- Quinn GP & Keough JM (2002) 'Experimental Design and Data Analysis for Biologists.' Cambridge University Press: Cambridge, UK.
- R Core Team (2015) R: A language and environment for statistical computing. R foundation for Statistical Computing, Vienna, Austria.

Reisinger A, Kitching R, Chiew F, Hughes L, Newton P, Schuster S, Tait A, Whetton P
Barnett J, Becken S & Blackett P (2014) Australasia. In 'Climate Change 2014: Impacts,
Adaptation and Vulnerability. Contribution of Working Group II to the Fifth Assessment
Report of the Intergovernmental Panel on Climate Change'. (Eds B. Fitzharris and D. Karoly.)
1371–1438.

Roger M (2008) Retreat site characteristics and body temperatures of *Saurodactylus brosseti*
Bons & Pasteur, 1957 (Sauria: Sphaerodactylidae) in Morocco. Bull. Soc. Herp. Fr, 128, 41-
48.

Sears MW, Raskin E & Angilletta Jr MJ (2011) The world is not flat: defining relevant
thermal landscapes in the context of climate change. Integr Comp Biol, 51,666-675.

Sears MW, Angilletta MJ, Schuler MS, Borchert J, Dilliplane KF, Stegman M, Rusch TW &
Mitchell WA (2016) Configuration of the thermal landscape determines thermoregulatory
performance of ectotherms. Proceedings of the National Academy of Sciences, 113,10595-
10600.

Scheffers BR, Edwards DP, Diesmos A, Williams SE & Evans TA (2014) Microhabitats
reduce animal's exposure to climate extremes. Global Change Biology, 20, 495-503.

Shine R & Kearney MR (2001) Field studies of reptile thermoregulation: how well do
physical models predict operative temperatures? Functional Ecology, 15, 282-288.

Sinervo B, Mendez-De-La-Cruz F, Miles DB, Heulin B, Bastiaans E, Villagrán-Santa Cruz
M,...Gadsden H (2010) Erosion of lizard diversity by climate change and altered thermal
niches. Science, 328, 894-899.

Stafford-Smith M & Morton S (1990) A framework for the ecology of arid Australia. Journal
of Arid Environments, 18, 255-278.

Stirling EC & Zeitz A (1893) Vertebrata. Transactions of the Royal Society of South
Australia, 16, 154-176.

Sunday JM, Bates AE, Kearney MR, Colwell KR, Dulvy KN, Longino JT & Huey RB
(2014) Thermal-safety margins and the necessity of thermoregulatory behavior across latitude
and elevation. *Proceedings of the National Academy of Sciences*, 111, 5610-5615.

Thomas CD, Cameron A, Green RE, Bakkenes M, Beaumont LJ, Collingham YC,...
Erasmus BFN (2004). Extinction risk from climate change. *Nature*, 427 (6970), p.145-148.

Thomas CD, Cameron A, Green RE, Bakkenes M, Beaumont LJ, Collingham YC, Erasmus
BFN (2004) Extinction risk from climate change. *Nature*, 427(6970), 145-148.
doi:10.1038/nature02121.

Warburg MR (1964) Studies on the environmental physiology of some
Australian lizards from arid and semi-arid habitats. *Australian Journal of Zoology*, 13, 563-
575.

Webb JK & Shine R (1998) Using thermal ecology to predict retreat-site selection by an
endangered snake species. *Biological Conservation*, 86 (2), 233-242.

Minerva Access is the Institutional Repository of The University of Melbourne

Author/s:

Moore, D;Stow, A;Kearney, MR

Title:

Under the weather?-The direct effects of climate warming on a threatened desert lizard are mediated by their activity phase and burrow system

Date:

2018-05-01

Citation:

Moore, D., Stow, A. & Kearney, M. R. (2018). Under the weather?-The direct effects of climate warming on a threatened desert lizard are mediated by their activity phase and burrow system. JOURNAL OF ANIMAL ECOLOGY, 87 (3), pp.660-671. <https://doi.org/10.1111/1365-2656.12812>.

Persistent Link:

<http://hdl.handle.net/11343/283648>