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Has contemporary climate change played a role in population declines of the lizard *Ctenophorus decresii* from semi-arid Australia?

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Whilst contemporary climatic changes are small in magnitude compared to those predicted for the coming decades, they have already been linked to species range shifts and local extinctions. Elucidating the drivers behind species' responses to contemporary climate change will better inform management strategies for vulnerable and pest species alike. A recent proposal to explain worldwide local extinctions in lizards is that increasing maximum temperatures have constrained lizard activity time in the breeding season beyond extinction thresholds. Here we document a significant population decline and potential local extinction at the warm (northern) range margin of the tawny dragon, *Ctenophorus decresii*, a rock-dwelling lizard from the Flinders Ranges in semi-arid Australia. We developed and tested a biophysical model of tawny dragon thermoregulatory behaviour and drove the model with daily weather data for the period 1990–2009 across the Flinders Ranges. Our results indicate that potential annual activity time has likely increased over this period throughout the historic range, with within-season declines only in the summer months at the northern range limit. However, populations that have declined since 2000 have also likely experienced higher active body temperatures and more stringent retreat-site requirements (deeper crevices) than have regions where the species remains common, during a period of declining rainfall. Our laboratory estimates of thermal preference in this species were insensitive to altered nutritional and hydric state. Thus it is possible that recent population declines are linked to desiccation stress driven by higher body temperatures and declining rainfall. Our study illustrates that simple indices of the impact of climate warming on animals, such as activity restriction, may in fact reflect a variety of potential mechanisms whose ultimate outcome will be contingent on other factors such as water and shelter availability.

1. Introduction

Climate change is predicted to cause the extinction of thousands of species over the coming century, therefore posing a major threat to biodiversity (Dawson et al., 2011). However, contemporary climate change has already been linked to changes in species distributions (VanDerWal et al., 2013), local extinctions (Sinervo et al., 2010), changes to species phenology (Parmesan and Yohe, 2003; Walther et al., 2002), evolution (Bradshaw and Holzapfel, 2006; Parmesan, 2006), and ultimately to alterations to community structure and ecosystems (Walther, 2010). Identifying causal links between contemporary climate change and species' responses is a complex, but vital challenge that could elucidate the proximal causes that may also drive species responses to future climate change (Ibáñez et al., 2006; Thomas et al., 2004). For many species, the causal mechanisms driving their responses to climate change are unlikely to be as simple as limited tolerance to high temperatures (Cahill et al., 2012). However, understanding exactly how a species may be vulnerable to climate change requires knowledge about not only their exposure to climatic changes, but also their sensitivity and ability to adapt to those changes (Williams et al., 2008).

Recently, contemporary global warming was proposed as a major driver of local lizard extinctions through reduced activity time. Sinervo et al. (2010) suggested that restrictions in activity time in the breeding season may be the major cause of 72% of local lizard extinctions since 1975, and may cause the extinction of up to 20% of all lizard species by 2080. Restricted activity time can result in lower opportunities for mating or foraging, placing strain on an individual's ability to meet the energetic demands of growth, maintenance and reproduction (Adolph and Porter, 1993; Kearney et al., 2009). Sinervo et al. (2010) developed a model of activity restriction based on species-specific preferred temperatures and

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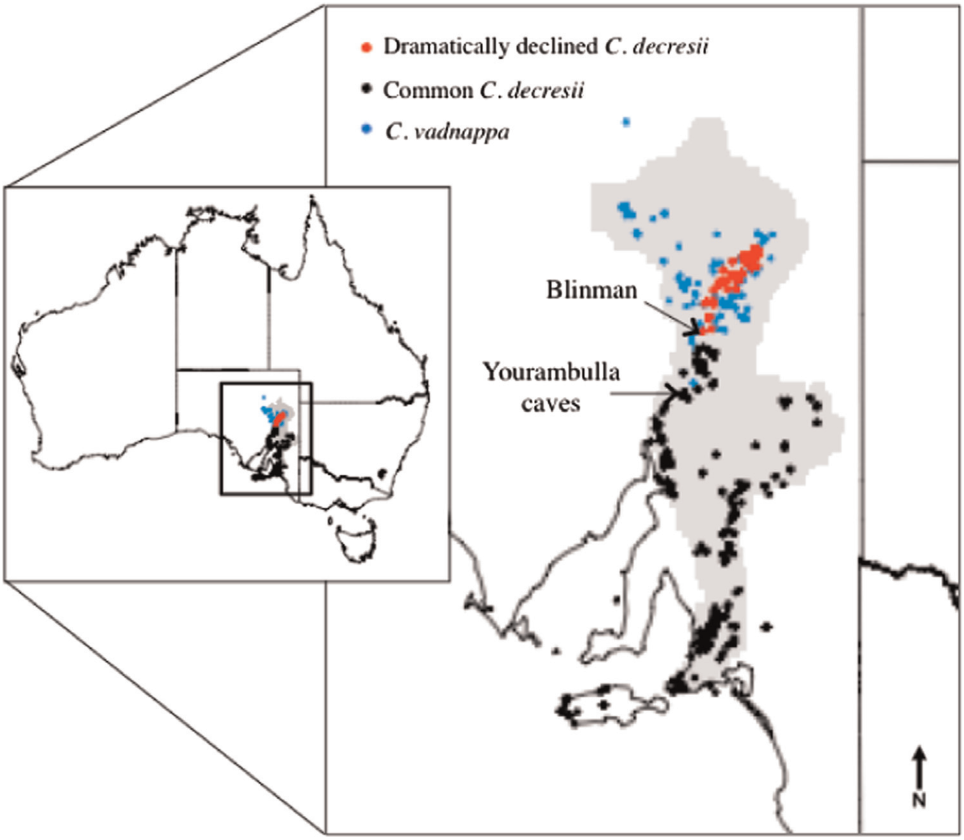

Fig. 1. The distribution of the tawny dragon lizard, *Ctenophorus decresii*, and the red-barred. dragon, *Ctenophorus vadnappa*, in Australia and inset, in South Australia. Red points show locations where the tawny dragon has declined dramatically since 2000 north of Blinman, with locations at which the species remains common in black. Blue points show the distribution of the previously sympatric lizard the red-barred. dragon, *Ctenophorus vadnappa*. Grey shading shows the region where we simulated the effect of climate on the tawny dragon using the software NicheMapR. We conducted a field test of NicheMapR predictions at the Yourambulla cave. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

daily maximum air temperature to explain the hours of activity restriction that each species experienced in the breeding season. As many lizards can adjust their behaviour and use a mosaic of microclimates, or alter the times at which they are active, to buffer themselves against unfavourable climate conditions (Gvozdik, 2012; Huey et al., 1977), this index may overestimate the exposure of lizard species to climate change and underestimate their ability to adapt to those changes through behavioural change (Clusella-Trullas and Chown, 2011; Kearney, 2013).

Here we consider the potential role that contemporary climate change has played in population declines of a lizard from semi-arid Australia, the tawny dragon *Ctenophorus decresii*. This species is found throughout the Flinders, Olary, and Mt Lofty Ranges, and on Kangaroo Island in South Australia (Fig. 1; Cogger, 2014). The tawny dragon is a small (20 g), insectivorous agamid that inhabits rocky areas and is reliant on rocky crevices for shelter (Gibbons, 1979). Their breeding season begins in September, and continues through to December, with the majority of eggs hatching between November and January.

Until 2000, the tawny dragon was regularly found north of Blinman in the Flinders Ranges (Brandle, 2001), where it was often locally abundant (Gibbons and Lillywhite, 1981). However, since that time no sightings have been made in this region despite repeated surveys (Table S1). The apparent absence of *C. decresii* in the northern Flinders Ranges contrasts sharply with the remainder of its range, where it is locally abundant in suitable habitat (McLean, 2014; McLean et al., 2014). The species is conspicuous, with the colour polymorphic males having brightly coloured throats and defending territories from prominent rock perches. Consequently, the species has been the focus of several ecological and evolutionary studies (Gibbons and Lillywhite, 1981; McLean, 2014; Teasdale et al., 2013). Therefore the failure to detect *C. decresii* in surveys of the northern Flinders Ranges since 2000 (consistent with anecdotal information), suggests a marked decline in this northern region of its range and potentially a pole-ward range contraction. Whilst the contraction and expansion of species' range boundaries is a natural phenomenon over the long term, rapid changes can often be explained by environmental or biotic interactions (Davey et al., 2013). A pole-ward range contraction is the directional effect expected if increasing temperature or decreasing rainfall were responsible, particularly in this area of Australia, as inland regions have experienced the fastest rates of climate warming over the past 50 years (Burrows et al., 2014; Chen et al., 2011).

The region north of Blinman is recognised as a separate bioregion from the region immediately south where the tawny dragon is still common (Laut et al., 1977). The climate of the northern region is more arid (Brandle, 2001; Schwerdtfeger and Curran, 1996), and the divide between these two regions also corresponds to phenotypic divergence in skinks and geckos (Chapple et al., 2008; Sistrom et al., 2012), suggesting the climate between these two regions may be distinct enough to drive differential evolution in lizards.

Prior to its apparent range contraction, the tawny dragon was found in sympatry and in similar density to a related species north of Blinman, the red barred dragon, *Ctenophorus vadnappa* (Gibbons and Lillywhite, 1981). The two species are similar in morphology and ecology, but perhaps not in their physiology as the red barred dragon generally inhabits hotter and drier regions than the tawny dragon (Fig. 1; Brandle, 2001). Studies on related and sympatric

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lizard species in Australia have found that arid adapted species become more abundant during periods of low rainfall, whilst mesic adapted species become more abundant after periods of high rainfall (Dickman et al., 1999; Read et al., 2012). Additionally, studies of related *Ctenophorus* species have shown that mesic adapted species are similarly successful at regulating their body temperature during hot weather compared to arid adapted species, but that their rate of cutaneous water loss is almost three times as great at high body temperatures (Bradshaw, 1977). Therefore, water may be an important driver of the relative abundance and distribution of sympatric *Ctenophorus* species in Australia.

The overall aim of this study was to evaluate the impact contemporary climate change may have had on tawny dragon thermoregulation and activity time, and if these impacts may be linked to the tawny dragon's recent decline north of Blinman. We first assess the exposure of tawny dragons to recent, broad-scale contemporary climatic changes north of Blinman, and compare these to changes in a nearby region where they are still abundant. Second, we create a biophysical model of the effect of climate on tawny dragon physiology and behaviour, and field-test its accuracy. Finally, we apply this biophysical model to assess the impact of contemporary climate change north of Blinman on tawny dragon thermoregulation and activity time.

2. Materials and methods

2.1. Assessing tawny dragon exposure to broad-scale contemporary climate change

We tested for recent shifts in temperature and rainfall at 40 locations within the distribution of the tawny dragon, spanning the latitudes 30°S to 33°S and longitudes 137°E to 141°E. Of these locations, 20 were north of Blinman where the tawny dragon has undergone a marked decline since 2000 (northern region). The remaining 20 were within a similar sized area immediately south, where the tawny dragon is still locally common (southern region). At each location we extracted interpolated (5 km grid) daily maximum and minimum temperatures (°C) and rainfall (mm) from the Australian Water Availability Project (AWAP) weather database (Jones et al., 2009) for the 20 years from 1990 to 2009. We chose this period as it spans the period over which population declines were observed, and also includes the data on solar radiation necessary for the biophysical modelling (daily solar is only available from 1990).

2.2. Measurement of thermal preference and tolerance and its sensitivity to food and water restriction

We captured 40 adult tawny dragon lizards from Bailey's Gorge (32.205°S, 138.009°E) and Warren's Gorge (32.186°S, 138.010°E), South Australia in October 2011. Lizards were individually housed at the University of Melbourne in opaque plastic containers with a wire mesh lid ($50 \times 35 \times 60 \text{cm}^3$). They were fed two crickets (*Acheta domesticus*) and misted with plentiful water three times a week, and maintained on a 12:12 light:dark photoperiod with additional basking lamps for 9.5 h daily. For the duration of these experiments, during the day the enclosures were approximately 31 °C and temperatures could reach 40 °C underneath the basking lamps. At night the temperature fell to approximately 16 °C. These conditions are similar to those in the field during the March–early April period.

Previous studies have shown that body mass loss of 10% or more can alter lizard thermoregulatory preferences (Crowley, 1987), with some species able to tolerate up to 35% body mass loss from desiccation (Mautz, 1982). We aimed to reduce initial body mass by a maximum of 15%. All lizards were weighed to 0.01 g and their snout to vent length measured. They were randomly assigned to one of four treatment groups with 10 lizards per group, split evenly across sexes: (1) *Control*-fed and misted with water as usual, (2) *Water*-fed as usual, but not misted with water, (3) *Food*-given one-third their usual food (one cricket, twice a week), but misted with water as usual; or (4) *Food/water*-Given one-third their usual food (one cricket, twice a week) and not misted with water. The treatments were imposed for 24 days (plus two extra days in the thermal gradient).

We used a thermal gradient to measure each lizard's thermoregulatory preferences, both before treatment (baseline) and immediately after the 24-day treatment period. For a description of the thermal gradient see Kearney and Predavec (2000). Each lizard was placed in the thermal gradient for 48 h, which provided substrate temperatures ranging from 16 to 51 °C with the lighting cycle identical to the conditions under which they were housed, including access to a small basking lamp for 9.5 h each day. We fasted all lizards (regardless of treatment) for three days before placing them in the gradient to ensure they were post-absorptive, as feeding can affect thermoregulatory preferences (Huey, 1982). Body temperature was measured using thermocouples (type T, 40 gauge, Omega Engineering, Delaware, USA) taped to the lizard's back. A data logger (Campbell Scientific, Logan, USA) recorded the thermocouple signals every 30 s. Two lizards were excluded from analyses, as they remained inactive (not thermoregulating). Two additional lizards were excluded from the *water* group because they were accidentally given access to water.

To assess the accuracy of this method over cloacal (internal) temperature, we compared simultaneously measured back and cloacal temperature in 10 lizards over 6.5 h, with body temperature recorded once every 15 min.

To determine thermoregulatory preferences, we used only data from the second day during the period when basking lamps were available, to allow for acclimation. Preferred temperature (T_p) was calculated as the mean body temperature. We excluded any temperature measurement that was more than 3° away from both the measurement preceding it and the measurement that followed. As measurements were only 30 s apart, this ensured that equipment glitches were not mistakenly included. In addition, we visually examined each trace for the presence of outliers.

The voluntary thermal minimum (VT_{min}) and maximum (VT_{max}) were taken as the single lowest and highest value respectively, recorded for each lizard across the entire 48-h period. For each lizard, we calculated the percentage change from before to after treatment for each of these thermoregulatory metrics.

To quantify the extent of dehydration imposed by our treatments, we measured plasma osmolality (the solute concentration of blood) by taking a blood sample from each lizard at the end of the treatment period, accessed from the sinus angularis at the corner of the mouth (Jessop et al., 2009). These blood samples were immediately centrifuged at 10,000 rpm for 2 min and the separated plasma stored in a freezer at −80 °C until analysis. We measured the plasma osmolality of each sample in triplicate using a freezing point osmometer (model 3320, Advanced Micro-Osmometer, MA, USA).

The critical thermal minimum, CT_{min}, was determined for 8 male lizards. We first acclimated the lizards in a 15 °C room for one hour, then dropped the room temperature setting to 10 °C. When the skin temperature of the lizard fell to 12 °C, the lizard was placed in a plastic container over an ice bath. The CT_{min} was defined as the point when an individual could no longer right itself after being placed on its back, when a final cloacal temperature was taken (Brattstrom, 1968). The critical thermal maximum, CT_{max}, was determined for 4 male lizards by first acclimating them

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in an incubator at 36 °C for one hour, then moving them to a container with four overhead 12 V 36 W dichroic halogen down lights. The temperature underneath these lamps reached approximately 50 °C. The CT_{max} was defined as the point when an individual could no longer right itself after being placed on its back, when a final cloacal temperature was taken.

2.3. A biophysical model of tawny dragon thermoregulatory behaviour

We used the biophysical modelling software NicheMapR (an R version of the modelling software Niche Mapper; see Kearney et al. (2014)) to predict the microclimates available to tawny dragons and how they could affect activity, body temperature and shelter requirements. The microclimate model was driven with interpolated daily meteorological data from the Australian Water Availability Project (AWAP) (Jones et al., 2009) following Kearney et al. (2014). We used the substrate properties for granite from Campbell and Norman (1998) with a rock solar reflectivity of 0.18 (Kearney, unpublished data), a shade range of 0–70% and a height of 1.5 cm above the ground, for local estimates of air temperature, wind speed and humidity.

Parameters for the ectotherm model and their sources are listed in Table 1 (Kearney et al., 2013). In particular, the mean preferred temperature T_p is the body temperature around which the lizard will try to regulate. Lizards would initially become active at the VT_{min} and choose shade accordingly to stay at T_p as much as possible. If in the full shade lizard body temperature would be above T_p, lizards would allow their body temperature to increase until it hit the VT_{max} upon which, they would retreat into a crevice and become inactive. Therefore, the voluntary thermal minima and maxima (VT_{min} and VT_{max}) are the body temperatures between which the lizard can be active above the ground. We also used the VT_{max} as the threshold for determining how deep the lizard needs to descend into rock crevices to avoid dangerously high temperatures. The emergence temperature, T_{bask}, is the minimum body temperature at which a lizard will emerge from its crevice. Finally, the critical thermal minimum (CT_{min}) and maximum (CT_{max}) are the bounds outside of which the lizard would die after a short period of time (Spellerberg, 1972). NicheMapR also uses the CT_{min} to determine how deep the lizard needs to descend into rock crevices to avoid dangerously cold temperatures.

Whilst not experimentally determined in this study, we used an emergence temperature of 24.8 °C which was measured for the related species *Ctenophorus ornatus* by Bradshaw and Main (1968). Therefore, a tawny dragon could be active above the ground in this model when their body temperature was greater than the emergence temperature, 24.8 °C, but less than the VT_{max}, 43.07 °C. We used this temperature range to calculate the hours of activity that were physiologically possible for tawny dragons during NicheMapR simulations.

The integrated spectral reflectance (300–2120 nm) of 10 lizards split evenly across the sexes was measured using an Ocean Optics USB2000 and NIRQuest spectrometer system. The average total reflectance of males was 11.85% (range 7–15.9%) and 16.5% in females (range 10.3–26.2%), and we used an intermediate value of 15% for these NicheMapR simulations.

2.4. Field test of the biophysical model

We tested the ability of our biophysical model to predict field conditions and tawny dragon body temperature by comparing predictions of operative temperature (T_e), to those measured in the field by physical models of tawny dragons, as well as compared to the thermoregulatory behaviour of field-active lizards. We tested NicheMapR when driven by local measurements of weather conditions, as well as when driven by daily gridded AWAP data.

To test operative temperatures available in the field, we first electroformed 12 hollow copper T_e models after the methods of Bakken and Gates (1975). We used a mould taken from one dead tawny dragon and painted these to achieve a total reflectivity of 14%. We compared four copper models to the body temperatures of four live, restrained lizards in the laboratory to measure their respective temperatures when in equilibrium with the environment following Hertz (1992). We used the thermocouple and data logger system described above, at four to five ambient temperatures ranging from 18 to 42 °C (approximately 5 °C apart per test) per lizard/model pair.

Field tests of NicheMapR performance and lizard behaviour were conducted in October 2013 at the Yourambulla Caves in the Flinders Ranges, South Australia (31.952°S, 138.372°E; Fig. 1). This area is representative of the core range of the tawny dragon in the Flinders Ranges, and the species is abundant here (Samantha Walker, pers obs).

Weather permitting, each day at ~08:30 twelve T_e models were randomly placed in one of four microclimate conditions. The models were removed when we finished recording lizard activity for the day, usually between 17:30 and 19:00. These microclimates represent the main options for a thermoregulating tawny dragon: (1) full sun, (2) full shade, (3) a shallow rock crevice (less than

Table 1
Heat/activity budget model parameters for *Ctenophorus decresii*.

Parameter	Units	Value	Source
ε_{body}, skin longwave infrared emissivity	–	1.0	Default
α_{body}, skin solar absorptivity	–	0.857	Spellerberg (1972)
ρ_{body}, flesh density	kg m^3	1000	Default
k_{body}, flesh thermal conductivity	W m^{-1} °C^{-1}	0.5	Default
C_{body}, flesh specific heat capacity	J kg^{-1} °K^{-1}	4185	Default
$F_{body,sky}$, configuration factor body to sky	–	0.4	Porter et al. (1973)
$F_{body,sub}$, configuration factor body to substrate	–	0.4	Porter et al. (1973)
A, lizard surface area	cm^2	$10.4713W_w^{0.688}$ Where W_w is wet weight in g	Porter et al. (1973)
A_{sil}, silhouette area normal to the sun	cm^2	$3.798W_w^{0.683}$ Where W_w is wet weight in g	Porter et al. (1973)
F_{sub}, fraction of surface area contacting the substrate	–	0.1	Assumed
F_{wet}, fraction of surface area that is wet	–	0.01	Assumed
T_{bask}, minimum temperature for leaving retreat	°C	24.8	Bradshaw and Main (1968)
VT_{min}, minimum foraging temperature	°C	27.1	Present study
VT_{max}, maximum foraging temperature	°C	43.1	Present study
T_p, preferred temperature	°C	35.9	Present study
CT_{min}, critical thermal minimum	°C	8.7	Present study
CT_{max}, critical thermal maximum	°C	46.1	Present study

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20 cm deep); and (4) a deep rock crevice (more than 20 cm deep). The models were spread over an area of approximately 500 m^2 each day. The temperature of the T_e models was recorded every hour by a Thermochron iButton temperature logger (DS1922L, Maxim Integrated Products, CA, USA) placed inside each T_e model on a piece of foam. For the deep crevice microclimate, an iButton was placed inside a small cotton bag with fishing line attached. At each site, a portable weather station (Weather Hawk, Campbell Scientific, Australia) was set up in an area that would receive sun all day and set to record wind speed, air temperature and solar radiation at hourly intervals.

Tawny dragon activity observations were made in two ways. Firstly on 8 separate days, after T_e model placement we took a haphazard walk through that area. We used binoculars to scan for lizards and when sighted, recorded the time of any lizard activity. These recordings were made between 08:30 and 18:30. Secondly, on separate days to the recordings mentioned previously, to ensure that we captured times of emergence and retreat we tracked 2 male and 2 female lizards all on separate days with the aid of binoculars until they retreated into a crevice at night (usually between 18:00 and 19:00). When the lizard had not re-emerged for 30 min we deemed them to have retreated for the night. The following morning we returned to the same crevice at ~08:30 and recorded the lizard's emergence time.

2.5. *Regional application of the biophysical model to assess contemporary climate change impacts*

We used gridded AWAP data to drive NicheMapR simulations of the impact of contemporary climate change on thermoregulation and activity time in the tawny dragon lizard across their distribution, over the 20 years spanning 1990–2009 (see Kearney et al. (2014)). This covered an area from the latitudes 28°S to 35°S and longitudes 136°E to 140°E at 0.05° resolution (~3800 individual locations; Fig. 1). The simulations were run on an IBM iDataplex x86 supercomputer (1120 Intel Sandy Bridge computer cores, running at 2.7 GHz) administered by the Victorian Life Sciences Computation Initiative. From these analyses we computed annual and monthly summaries of the (1) hours of activity, (2) mean body temperature, (3) hours spent above the preferred temperature, Tp, when active, and (4) maximum crevice depth needed to avoid heat/cold stress. At every location, we regressed each descriptor against time using firstly the mean of each year over the 20-year period, and secondly, the mean of individual months over the 20-year period.

All statistical analyses were performed using the program R (version 3.0.2) (R Core Team, 2013). We used the R library packages “nlme” (Pinheiro et al., 2013), “Metrics” (Hamner, 2012), “raster” (Hijmans, 2014), “sp” (Bivand et al., 2013b) and “rgdal” (Bivand et al., 2013a).

3. Results

3.1. *Tawny dragon exposure to broad-scale contemporary climate change*

Significant recent changes in climate were found over the period 1990–2009 (Figs. 2 and 3). Within the northern region, daily maximum and minimum air temperature increased significantly at all 20 locations (Fig. 3). Averaging across all sites, there was a significant linear increase in both daily maximum (linear regression, slope=0.07, $R^2=0.37$, $P=0.003$) and daily minimum (slope=0.05, $R^2=0.33$, $P=0.008$) temperature (Fig. 2). In addition, the number of days above 40 °C increased significantly at 12 out of 20 locations in the northern region (overall regression slope=0.40, $R^2=0.24$, $P=0.029$), and mean daily rainfall significantly decreased at 12 out of 20 locations (overall regression slope=–0.02, $R^2=0.24$, $P=0.017$). Within the southern region, daily maximum temperature increased significantly at 19 out of 20

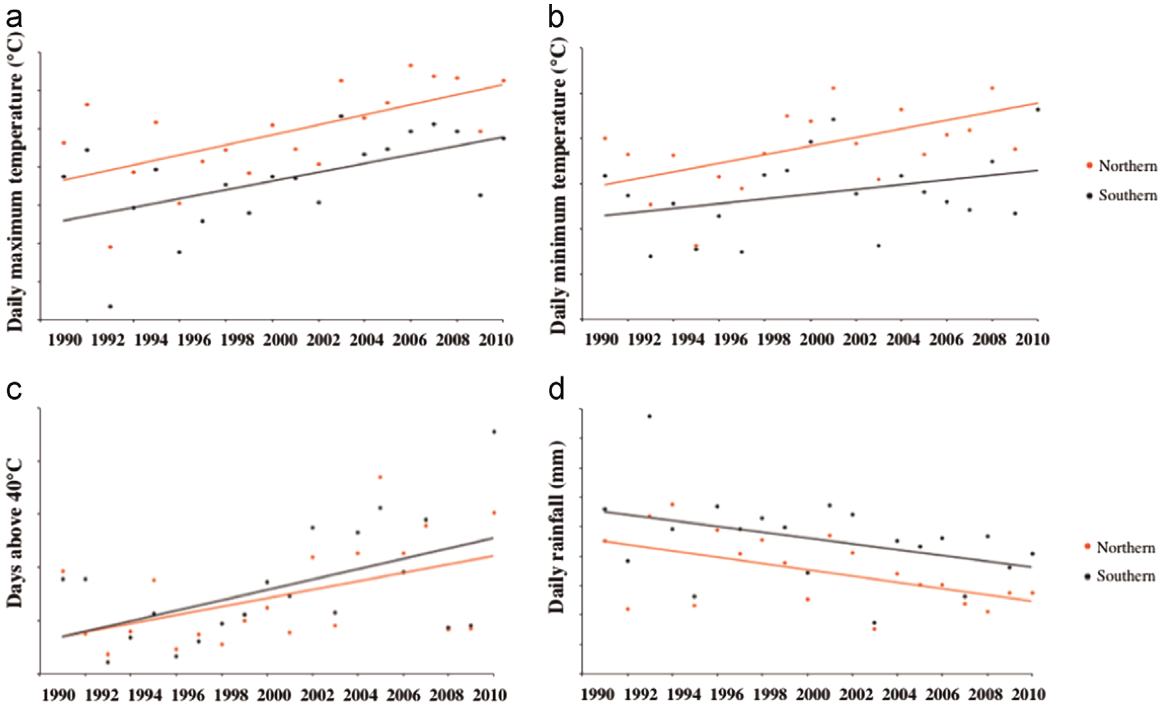

Fig. 2. Historical temperature and rainfall for each year from 1990 to 2009 within the distribution of the tawny dragon lizard. The northern region points shown here in red, represent the mean for each year across 20 locations where the tawny dragon has declined dramatically since 2000, and the southern region points shown in black represent the mean for each year at 20 locations where the tawny dragon remains common for the (a) Daily maximum temperature (°C), (b) daily minimum temperature (°C), (c) number of days above 40 °C; and (d) daily rainfall (mm). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

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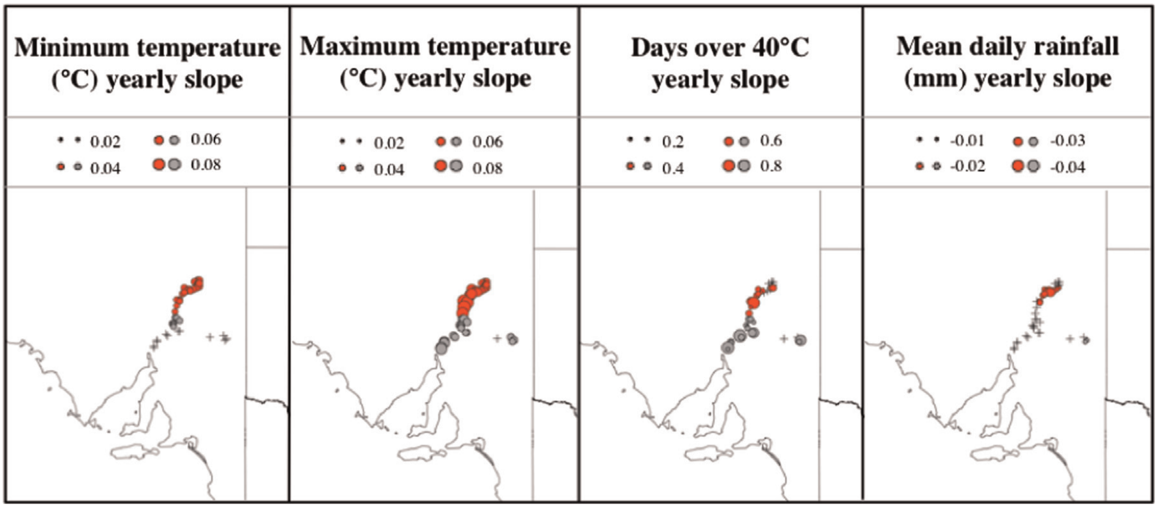

Fig. 3. Linear regression slope of climatic changes over time, for locations within the distribution of the tawny dragon lizard over 1990–2009. Point size is proportional to regression slope at individual locations, and only locations that show significant changes over time ($p < 0.05$) are shown in colour, with locations that showed no significant change over time shown as crosses (+). Red points are locations where the tawny dragon has declined dramatically since 2000, and grey points are where the tawny dragon remains common. All locations shown in colour experienced significant *increases* in daily minimum and maximum temperatures and number of days over 40 °C, and significant *decreases* in mean daily rainfall. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

locations (overall regression slope=0.06, R^2=0.31, P=0.011). Daily minimum temperature increased significantly at 7 out of 20 locations in this region (overall regression slope=0.03, R^2=0.12, P=0.140), and the number of days above 40 °C increased significantly in 17 out of 20 locations (overall regression slope=0.49, R^2=0.28, P=0.017). Mean daily rainfall decreased significantly at 2 of the most eastern locations (overall regression slope=−0.02, R^2=0.157, P=0.083; Fig. 3).

3.2. *Thermal preference and its sensitivity to food and water restriction*

Comparisons between cloacal and dorsal skin temperature showed that dorsal skin temperature was a strong predictor of cloacal temperature (linear mixed-effects model with individual lizard as a random intercept, cloacal temperature range=17–43 °C; r=0.98; regression statistics ± 1 SE; slope=1.069 ± 0.019, intercept=−1.567 ± 0.677, observations=198, groups=10, $P < 0.0001$), with dorsal skin

Table 2
The correlation coefficient (r^2) root mean squared deviation (RMSD) and the standardised root mean squared deviation (RMSD%) of comparisons between NicheMapR predictions and field observations in the Yourambulla caves, South Australia, for (i) portable weather station (WS) data compared to hourly NicheMapR predicted weather conditions when driven by daily climate data from the Australian Water Availability Project (AWAP); (ii) NicheMapR predicted lizard body temperature compared to operative temperature model T_e (lizard thermal mimic) temperature in a variety of microclimates driven by (a) hourly WS input and (b) daily AWAP input; and (iii) NicheMapR predicted lizard activity compared to observed activity when driven by (a) hourly WS input and (b) daily AWAP input. Discrepancy shown is the absolute mean discrepancy.

Model comparisons	df	r^2	RMSD	RMSD%	Discrepancy
(i) WS vs AWAP weather predictions					
Temperature	1,228	0.73	4.69	13.52	3.89 °C
Relative humidity	1,228	0.56	14.89	16.73	10.30%
Wind speed	1,228	0.20	3.80	30.70	2.68 m s^{-1}
Solar radiation	1,228	0.96	92.58	9.36	54.76 W m^{-2}
(ii) Predicted lizard body temperature vs T_e models using (a) WS input and (b) AWAP					°C
(a)					
Full sun	1,80	0.89	3.92	10.32	3.19
Full shade	1,80	0.67	4.66	21.12	3.70
Shallow crevice	1,80	0.61	3.47	15.04	2.71
Deep crevice	1,80	0.76	2.52	16.95	2.08
(b)					
Full sun	1,80	0.88	4.49	11.80	3.72
Full shade	1,80	0.59	5.30	24.03	4.28
Shallow crevice	1,80	0.61	3.47	15.04	2.71
Deep crevice	1,80	0.76	2.52	16.95	2.08
	Observation hours		% correct		
(iii) Predicted activity vs observed using (a) WS input and (b) AWAP					
(a) Surface activity	63		89		
(b) Surface activity	63		89		

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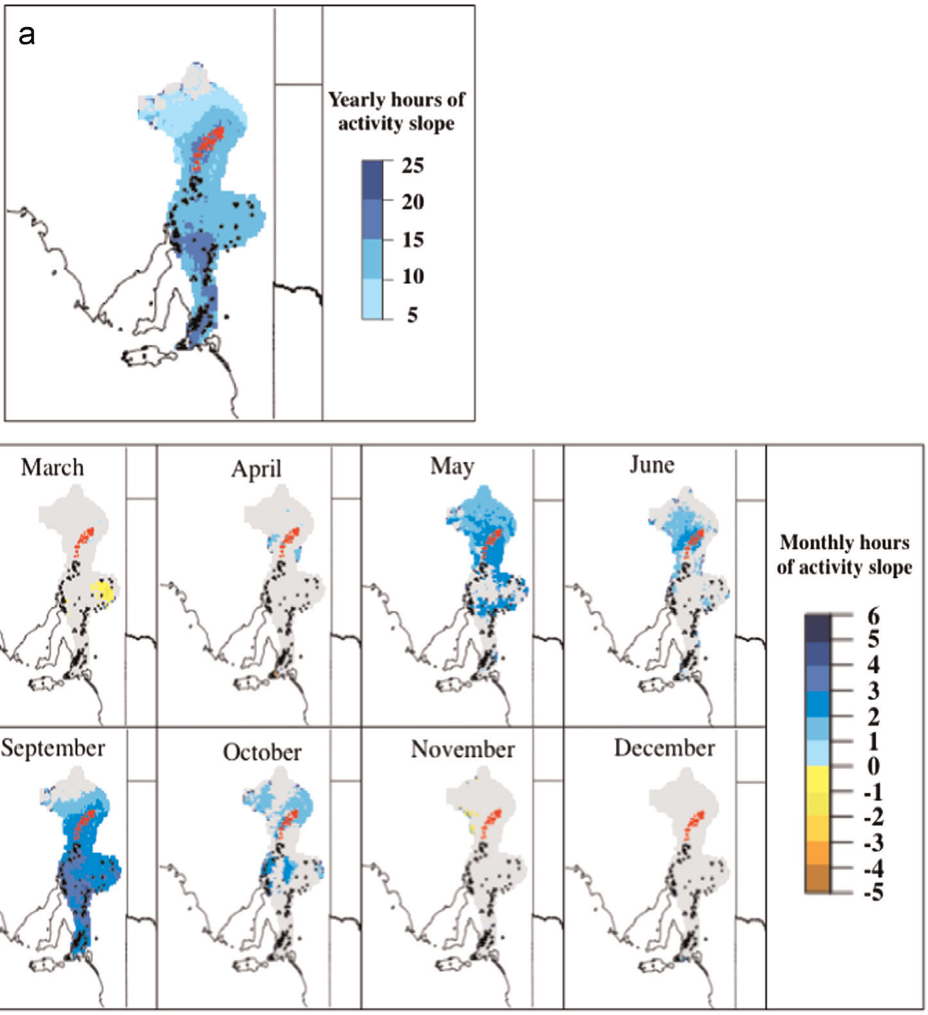

Fig. 4. Regression analysis slope of total hours of activity time of a tawny dragon across their range in South Australia, as simulated by the software NicheMapR. Only locations that show significant change over time ($p < 0.05$) are shown for (a) From the year 1990 to 2009, combining all months; and (b) each calendar month, from the year 1990 to 2009. Red distribution points show locations where the tawny dragon has likely become locally extinct since 2000, with extant locations in black. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

temperature consistently lower than cloacal body temperature. This relationship was used to correct all dorsal skin temperatures, and the summary indices of voluntary preferences are reported in Table 1.

Neither initial body mass, nor snout vent length differed between the treatment groups ($F_{3,30}=0.59$, $p=0.62$; $F_{3,30}=0.90$, $p=0.45$ respectively). MANOVA of the thermoregulatory descriptors, as well as plasma osmolality and the percentage of body mass loss, revealed that there was a significant difference between treatment groups for at least one of the dependent variables (Λ Pillai$=0.84$, $F_{18,81}=1.75$, $p=0.046$). Individual ANOVAs showed that the percentage of body mass loss differed significantly between groups ($F_{3,30}=5.16$, $p<0.01$), and Tukey's post-hoc comparison revealed that the percentage of body mass loss was significantly higher in the *food/water* group than the *control* group, and the *food* group ($p=0.02$; $p=0.01$ respectively). Plasma osmolality ($\log_{10}$ transformed due to positive skew) also differed significantly between groups ($F_{3,30}=3.39$, $p=0.03$) with the *food/water* group having significantly higher plasma osmolality than the *food* group ($p=0.02$). However, there was no effect of treatment group on the percentage change of any thermoregulatory preference descriptor (VT_{min} $F_{3,30}=1.32$, $p=0.29$; T_p $F_{3,30}=0.91$, $p=0.45$; VT_{max} $F_{3,30}=2.55$, $p=0.07$).

The CT_{min} and CT_{max} were 8.7 °C ± 0.3 and 46.1 °C ± 0.1 (SEM), respectively.

3.3. Operative temperature models and field tests of the biophysical model

T_e models heated and cooled more rapidly than live lizards, as expected due to their lower thermal capacity. However, the steady-state temperature of T_e models and lizard body temperature differed by <1 °C in 83% of the comparisons. The T_e models were a very strong predictor of lizard body temperature (linear mixed-effects model with lizard/model pair as random factor, statistics ± 1 SE; slope$=0.98 \pm 0.02$, intercept$=0.19 \pm 0.63$, $r=0.996$, $N=18$, $P<0.0001$). The random effect of lizard/model pair had an average intercept of 0.37 °C, smaller than the resolution of the iButton® temperature loggers (accurate to 0.5 °C) used for field experiments.

The NicheMapR microclimate model, when driven by the gridded AWAP weather data, successfully reconstructed the hourly variation recorded at the study site by the portable weather station in solar radiation and air temperature (96% and 73%, respectively; Table 2). However, 56% of the variation in relative humidity, and 20% of the variation in wind speed could be captured, the latter being expected because we only had access gridded monthly long-term average wind speed.

NicheMapR hourly predictions explained between 61% and 89% of the variation in T_e model temperatures when driven by the

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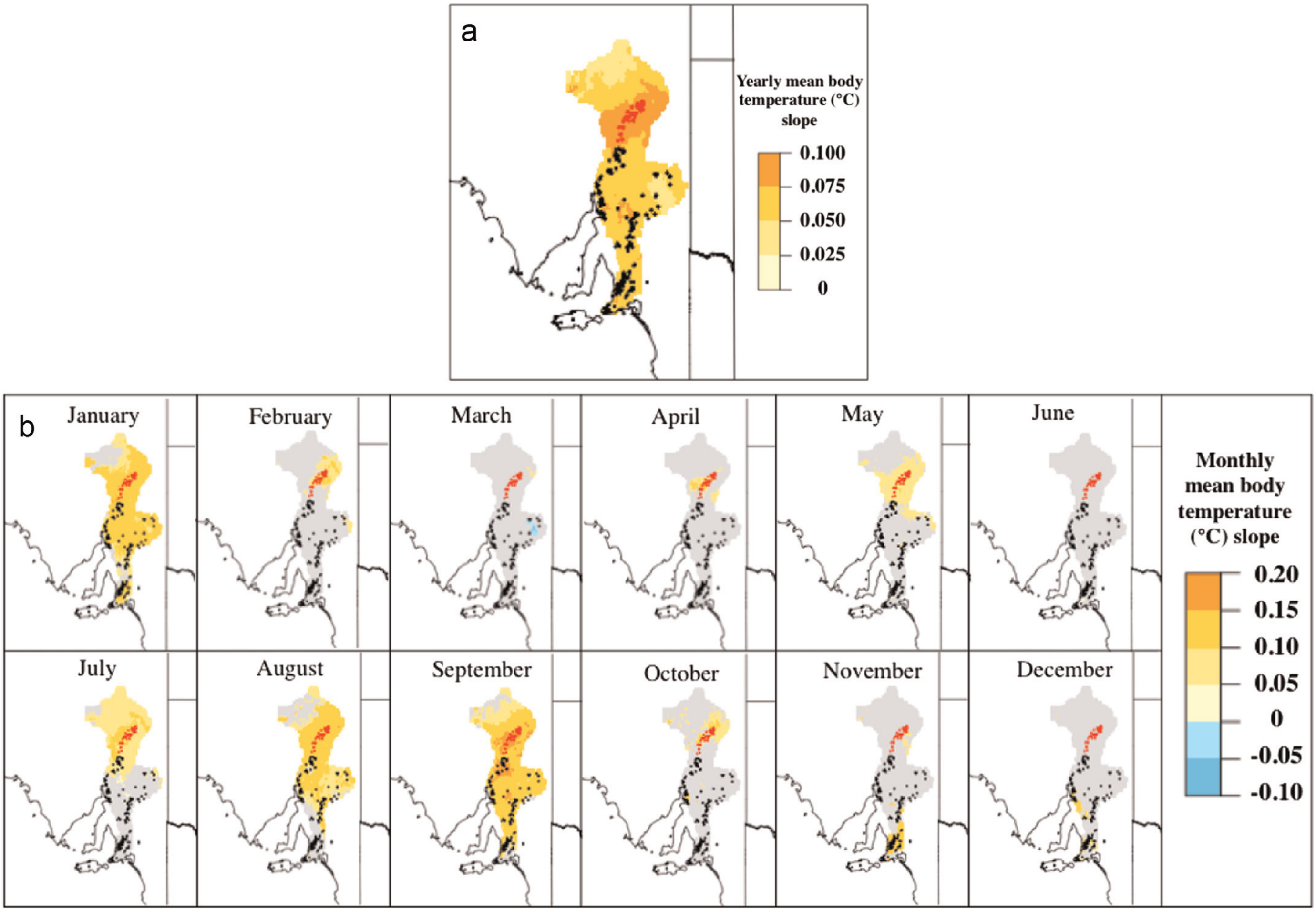

Fig. 5. Regression analysis slope of the mean body temperature of a tawny dragon across their range in South Australia, as simulated by the software NicheMapR. Only locations that show significant change over time ($p < 0.05$) are shown for (a) From the year 1990 to 2009, combining all months; and (b) Each calendar month, from the year 1990 to 2009. Red distribution points show locations where the tawny dragon has likely become locally extinct since 2000, with extant locations in black. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

hourly weather station recordings, and between 59% and 88% when driven by the daily gridded AWAP data (Table 2). Ultimately, NicheMapR was able to predict 89% of the variation in tawny dragon lizard activity patterns, whether driven by the hourly locally-recorded weather station data or the daily AWAP data (Table 2).

3.4. Regional application of the biophysical model to assess contemporary climate change impacts

Hourly landscape-scale simulations of thermoregulatory behaviour from 1990 to 2009 showed that throughout most of the range of tawny dragons, there was a trend of significant linear increases in predicted activity time (Fig. 4a), especially over the months May-September (Fig. 4b). However, the potential activity time in some northern (and potentially extinct) populations was predicted to have decreased significantly in January (Fig. 4b).

Thermoregulating tawny dragons were predicted to experience an overall increase in mean body temperature (Fig. 5a), particularly in January and from July to August (Fig. 5b). Overall, the greatest increase in mean body temperature was in the vicinity of the northern populations (Fig. 5a and b). They were also predicted to have experienced an increase in the time spent above their preferred body temperature (Fig. 6a), particularly in January (Fig. 6b).

Finally, thermoregulating tawny dragons were predicted to have required increasingly deeper crevices on average to escape extremely high temperatures, mainly in the north of their range (Fig. 7a) and particularly in January (Fig. 7b). In the cooler months (July–September), however, this pattern was reversed, with warmer environmental temperatures meaning that they could use shallower crevices in the winter and still avoid cold stress (Fig. 7b).

4. Discussion

This study aimed to determine if contemporary climate change may be responsible for recent local extinctions of the tawny dragon lizard in the northern Flinders Ranges of South Australia, and specifically if their decline may be linked to restricted activity time. Over the past 20 years the northern region where the species has declined dramatically and is potentially locally extinct, has been exposed to increasingly dry and hot weather with more days over 40 °C. These observations are consistent with the findings of other studies for this approximate region of Australia (Braganza et al., 2011). Though these climatic changes were also seen in the southern region, the northern region has experienced overall hotter conditions and decreasing rainfall. Finally, the daily minimum temperature remains largely unchanged since 1990 in all but the northernmost locations within the southern region, but has increased rapidly over the same period throughout the northern region. Together these changes would likely have resulted in tawny dragons experiencing overall higher body temperatures and

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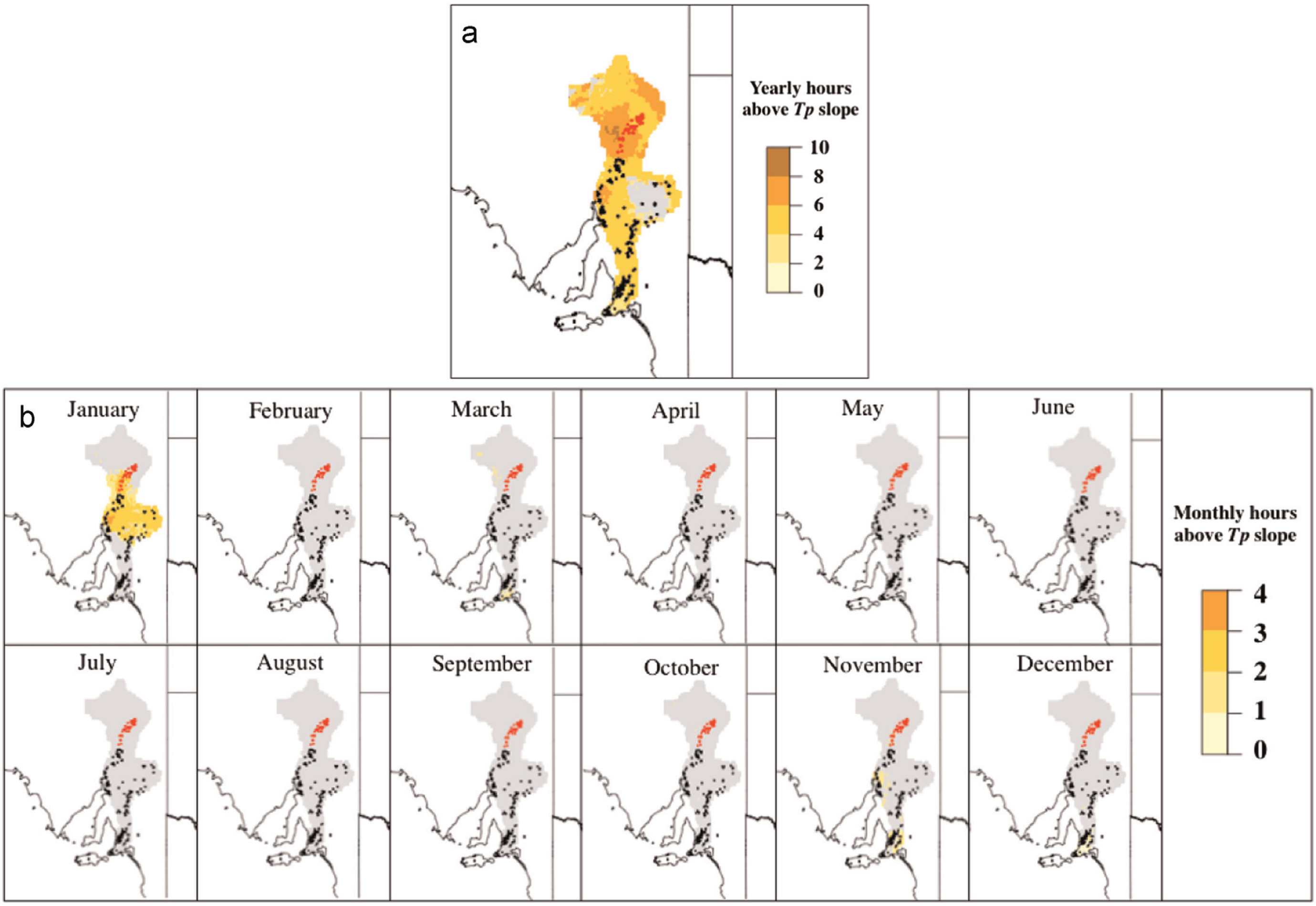

Fig. 6. Regression analysis slope of the number of hours that a tawny dragon would spend above their preferred body temperature, T_p, when active on the surface across their range in South Australia, as simulated by the software NicheMapR. Only locations that show significant change over time ($p < 0.05$) are shown for (a) from the year 1990 to 2009, combining all months; and (b) Each calendar month, from the year 1990 to 2009. Red distribution points show locations where the tawny dragon has likely become locally extinct since 2000, with extant locations in black. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

lower water availability in the northern region. Therefore, tawny dragons in the northern region would likely have had higher water and energetic demands, and would have experienced overall more heat stress than those in the south.

Behavioural thermoregulation is a primary mechanism by which tawny dragons could have buffered themselves against these unfavourable conditions. However, despite losing significant body mass and being dehydrated, tawny dragons in this study showed no change in their thermoregulatory preferences in response to food and water restriction. This is in direct contrast to other studies on reptiles with similar sample sizes (Crowley, 1987; Dunlap, 1995; Dupré and Crawford, 1985; Ladyman and Bradshaw, 2003; Lorenzon et al., 1999). Although tawny dragons did not alter their thermoregulatory preferences in this study, individuals with higher body temperatures after the treatment period were more dehydrated, as shown by their higher plasma osmolality. In the wild, tawny dragons may remain active during periods of drought and food restriction of this magnitude, and therefore be particularly vulnerable to negative physiological consequences such as more rapid dehydration and body mass loss. This could have long-term consequences on their fecundity, growth rate and ultimately survival, particularly as prolonged droughts are predicted to become more common as the climate changes (Dunlap, 1995; IPCC, 2013).

In contrast to the hypothesis of Sinervo et al. (2010), our simulations suggest it is unlikely that restricted activity time in the breeding season has caused the decline of northern populations of tawny dragons. This is despite the tawny dragon being exposed to recent significant increases in daily maximum temperatures. Our simulations predict that northern populations of the tawny dragon actually experienced increased activity time over the first half of the breeding season, and no change later in the season. However, climate change may cause population declines even under increased activity time, and with abundant food availability, by increasing mortality rates through predation (due to more time spent active and vulnerable) without compensatory effects on fecundity (Adolph and Porter, 1993; Kearney, 2013).

The increased activity of tawny dragons in northern populations over the months July–September occurred concurrently with warmer mean body temperatures and shallower maximum crevice depths. This is due to tawny dragons experiencing significantly warmer winters/early springs over time. If the lizards exploited this extra potential activity time, they may have maintained higher body weights over winter and reached maturity earlier (Jones et al., 1987; Ozgul et al., 2010). Conversely, if they were not able to successfully forage during these months, increased body temperature while over-wintering could have exacerbated body mass loss through increased metabolic and evaporative water loss rates, and therefore poorer survival rates (Brodersen et al., 2011; Fründ et al., 2013). All else being equal, earlier onset of the breeding season may allow newly hatched juveniles greater time for food acquisition and growth before the onset of the next winter, resulting in their better survival through

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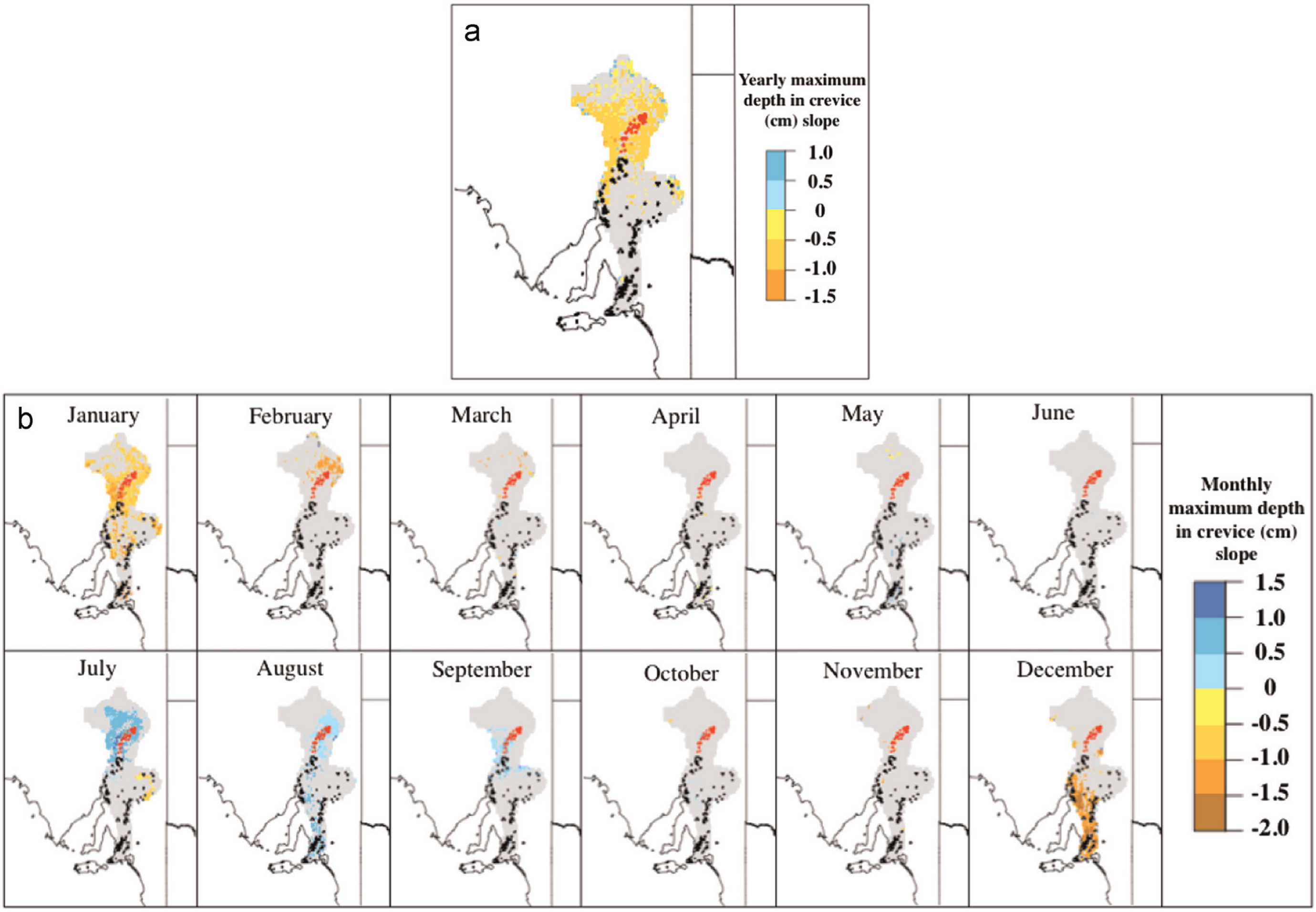

Fig. 7. Regression analysis slope of the maximum depth that a tawny dragon would need to descend into a rock crevice (cm) across their range in South Australia to escape extreme hot/cold temperatures, as simulated by the software NicheMapR. Only locations that show significant change over time ($p < 0.05$) are shown for (a) From the year 1990 to 2009, combining all months; and (b) Each calendar month, from the year 1990 to 2009. Red distribution points show locations where the tawny dragon has likely become locally extinct since 2000, with extant locations in black. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

subsequent hibernation (Ozgul et al., 2010). However, it may also expose gravid females and developing eggs to more frequent cold-snaps, which could negatively impact developing offspring (Michel et al., 2013).

Whilst simulations predict that tawny dragons in northern populations did not experience activity restriction during the breeding season months of September–December, decreases in their activity time were predicted for some populations in January. These decreases in activity time were concurrent with higher mean body temperatures, increased time spent above T_p and greater maximum crevice depths. Even small increases in the time spent at high body temperatures can greatly reduce the lifespan of lizards and increase their mortality rate, thereby increasing the risk of exposed populations to extinction (Munch and Salinas, 2009). Additionally, as body temperature rises above T_p, thermoregulatory effort must increase in order to remain active whilst avoiding lethally hot body temperatures, and therefore the energetic benefits of maintaining activity rapidly diminish (Vickers et al., 2011). As evaporative water loss rate also increases concurrently with temperature, the costs of maintaining activity at body temperatures above T_p over long periods may only be sustainable in high quality habitat with ample amounts of available food and water to compensate for losses, as well as shady habitat suitable for foraging (Huey and Slatkin, 1976; Vickers et al., 2011). As rainfall decreased in northern regions over the 20 year period examined, it is plausible that tawny dragons in these northern populations may not have been able to meet their water needs whilst maintaining their required activity time. Finally, physical performance including sprint speed rapidly decreases at body temperatures higher than T_p, so individuals that remain active above this temperature may expose themselves to higher rates of predation (Hertz et al., 1983). This effect may be particularly important in determining juvenile survival (Husak, 2006), although lizards could potentially behaviourally compensate for changes in performance and predation risk (Lima and Dill, 1990). More generally, the predicted January decreases in activity time and higher mean body temperatures could have a disproportionately greater impact on juveniles, as hatching occurs from November through January.

Another factor potentially contributing to the decline of tawny dragons in northern populations is interactions with the ecologically similar and related species, the red-barred dragon, *C. vadnappa*, with which the tawny dragon was sympatric in the precise region where it now appears to be locally extinct. Increased heat and dehydration stress in January, poorer over-wintering survival and negative impacts on developing offspring may have altered competitive interactions with the more arid adapted red-barred dragon. Water in particular may be an important driver of the relative abundance of sympatric *Ctenophorus* species in Australia (Bradshaw, 1977; Dickman et al., 1999; Read et al., 2012). Future research could investigate this further by quantifying the thermoregulatory preferences and desiccation sensitivities of the red-barred dragon.

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Overall, our analyses suggest that contemporary climate change could potentially have contributed to the decline of the tawny dragon north of Blinman in the Flinders Ranges, but not necessarily through a simple restriction of activity time. The potential proximal mechanisms that we have identified are contingent on habitat features such as shade level, retreat-site quality and food and moisture availability. A deeper understanding of these mechanisms will allow for the effective management of vulnerable and pest species alike, both now and into the future as the climate continues to change.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at http://dx.doi.org/10.1016/j.jtherbio.2014.12.001

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