When hot rocks get hotter: behavior and acclimatization mitigate exposure to extreme temperatures in a spider

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Abstract. In environments where animals have a high probability of encountering temperatures close to their thermal limits, animals with the capacity to minimize the chances of encountering these temperatures will be advantaged. We investigated the physiological and behavioral mechanisms used by flat rock spiders, Morebilus plagusius, to avoid encountering lethal or sub-lethal temperatures on sandstone outcrops by measuring their critical thermal maximum (CTMax) in spring and summer and quantifying their retreat rock use. Morebilus plagusius has a high CTMax which acclimatizes seasonally (spring CTMax: 48.3°C ± 0.2°C; summer CTMax: 49.6°C ± 0.3°C). By measuring the operative temperatures available to spiders underneath rocks in spring and summer and quantifying retreat rock use by adult spiders we found that random use of rocks by spiders would frequently expose them to temperatures above their thermal tolerances, especially in summer. Spiders non-randomly used rocks as diurnal retreats, with rocks with a large area and a rock substratum being positively correlated with M. plagusius occupancy. Rocks large in area provided cooler daytime shelters than exfoliated rocks with smaller area. Morebilus plagusius uses both physiological and behavioral mechanisms for avoiding lethal temperatures, and neither physiological nor behavioral mechanisms alone are enough to mitigate the increased probability of encountering lethal temperatures in summer. Our results highlight the importance of an integrative approach, incorporating behavioral, ecological and physiological mechanisms in accessing how animals avoid lethal temperatures in thermally extreme environments.

Key words: Arachnid; climate change; CTMax; Hemicloea major; microhabitat; Morebilus plagusius; outcrops; retreat use; Sydney sandstone ridgetop; thermal tolerances; thermoregulation.

INTRODUCTION

Extreme temperature events can impose selective pressure on organisms. Although persistent changes in mean temperature will have chronic effects on fitness, thermal extremes are acute and often result in death (Welbergen et al. 2008, McKechnie and Wolf 2010, Bauerfeind and Fischer 2014). The ability to survive extreme events (thermal or otherwise) will determine whether an individual or population persists in a changing environment (Parmesan et al. 2000, Culumber and Monks 2014, Lynch et al. 2014) because the probability of extreme weather events, rather than higher mean temperatures, correlate with upper thermal tolerances (critical
Thermal maximum, CT\textsubscript{Max}) (Clusella-Trullas et al. 2011).

Thermal performance curves are asymmetrical in shape (Huey and Stevenson 1979). The distance between an animal’s thermal optimum and its upper thermal tolerance is narrower than between the optimum and its lower thermal tolerances. Consequently, a temperature shift above the thermal optimum is more deleterious than the same magnitude shift below the thermal optimum (Martin and Huey 2008). Thus, fitness costs increase when temperatures are above the selected temperature of the organism and animals should thermoregulate more effectively as temperatures become more extreme and approach critical limits (Vickers et al. 2011). Alternatively, through physiological plasticity, individuals can shift the position of their thermal tolerances (reviewed in Angilletta 2009), thus decreasing exposure to extreme temperatures.

Habitat use and physiology are fundamentally linked. The habitat of an animal determines the microclimates available which consequently affects the animal’s physiology (Huey 1991). Using behavior, animals can thus change the microclimates to which they are exposed (Huey 1991, Angilletta 2009). Animals living in thermally extreme environments should therefore have a suite of adaptations that are behavioral (e.g., shuttling, retreat use, reduced activity time; Bozinovic et al. 2000, Melville and Schulte 2001, Fick et al. 2009), morphological (e.g., long legs, posturing, surface area, increased wax layers; Dreisig 1990, Heinrich 1990, Ward and Seely 1996, Greenberg et al. 2012, Sommer and Wehner 2012) and physiological (e.g., high thermal tolerances/heat shock proteins, evaporative water loss; Christian and Morton 1992, Krebs and Feder 1997, Williams and Tieleman 2005) to avoid the lethal effects of these thermal extremes. Species that live in thermally stressful environments are an ideal model for developing an understanding of how animals use these behavioral and physiological strategies to mitigate the probability of encountering these thermal extremes either by behavioral retreat site selection (Kearney and Predavec 2000) or through having high thermal tolerances.

Flat rock spiders, Morebilus plagusius (Family: Trochanteriiidae; formally Hemicloea major; Platnick 2002), are found on the sandstone outcrops of south-eastern Australia (Goldsbrough et al. 2004). Morebilus plagusius is a nocturnal, sit-and-wait predator that uses exfoliated rocks as diurnal retreats (Brunet 1996, Forster and Forster 1999) with adult females often showing strong site fidelity to retreat rocks (Brennan 2002). Morebilus plagusius inhabits outcrops throughout the year and consequently will be exposed to temperatures that approach its thermal limits, particularly in summer. Consequently, M. plagusius that inhabit sandstone rock outcrops can be used to explore how, in environments where there is a high probability of encountering extremely hot temperatures, species mitigate the consequences of exceeding thermal tolerances. We predict that M. plagusius should have either behavioral and/or physiological strategies to cope with the increased probability of encoun-
Our study had four primary aims: (1) to quantify the thermal profiles of exfoliated rocks on sandstone outcrops in spring and summer to describe how rock thermal characteristics change seasonally with particular focus on changes at the extremes; (2) to determine which physical properties of rocks are correlated with the thermal profiles of rocks; (3) to determine if adult female *M. plagusius* use retreat rocks non-randomly on a fine scale; and (4) to quantify changes in the thermal tolerances of adult female *M. plagusius* between spring and summer.

If adult female *M. plagusius* use microhabitat selection as a behavioral strategy for avoiding thermal extremes, we predict that adult female *M. plagusius* should use retreat rocks non-randomly with respect to rock variables that lower the maximum temperatures experienced in crevices beneath rocks. If *M. plagusius* has physiological mechanisms for avoiding thermal extremes, we also predict that it should have high thermal tolerances, and that these thermal tolerances will increase from spring to summer in accordance with the increased probability of experiencing extreme temperatures in summer.

**Methods**

**Adult retreat rock use**

We surveyed sandstone outcrops in three national parks (NP) around Sydney, Australia (Brisbane Waters NP, 33°31’ S, 151°16’ E; Royal NP, 34°06’ S, 151°06’ E; and Blue Mountains NP, 33°40’ S, 150°22’ E) over 25 days between October 2010 and November 2011. All three national parks are in the northern part the geographic range of *Morebilus plagusius* (Platnick 2002) and reach hotter summer temperatures compared to the more southern parts of their range. We identified suitable rock outcrops (>1.5 m²) that were accessible from walking trails and systematically looked underneath all rocks on the outcrops that had at least one axis greater than 100 mm and were small enough to be lifted by a single researcher. Due to the nature of sandstone exfoliation, rocks that were too large to be lifted were rare; most outcrops did not contain this size rock. Of all the outcrops surveyed, we encountered 28 outcrops with at least one *M. plagusius* (Brisbane Water NP, n = 4; Royal NP, n = 10; Blue Mountains NP, n = 14).

We measured a suite of biotic and abiotic habitat variables of rocks inhabited by an adult or subadult (hereafter, adult) female *M. plagusius*: the physical dimensions of the rock (area (length × width) and thickness); the substrate(s) that the rock was on (dirt/sand, leaf litter, bare rock, smaller rocks or moss); distance to the nearest rock, vegetation or cliff edge; canopy cover; and whether there were any other animals beneath the rock. We calculated percentage canopy cover using Gap Light Analyser software v. 2.0 (Frazer et al. 1999) from hemispherical photographs (Nikon Coolpix990 with FC-E8 Fisheye converter, Nikon Corporation) taken vertically from directly on top of the rock surface.

To determine if adult *M. plagusius* were using rocks as a diurnal retreat non-randomly on a fine scale, we measured the same habitat variables of the four rocks (with an axis >100 mm) nearest to the rock occupied by the spider (‘spider rock’) (Schlesinger and Shine 1994). Most of these surrounding rocks were defined as ‘available rocks’ as they were not occupied by *M. plagusius*; however, if one of the four rocks had an adult *M. plagusius* occupying it, it was redefined as a spider rock. When spider rocks were close in proximity to one another, they could overlap in their available rocks, however, we only used rocks once in our analyses.

We mainly surveyed rocks during the morning. This did not introduce temporal bias in sampling as *M. plagusius* do not change their retreat rock during the day. Furthermore, adult female *M. plagusius* show strong site fidelity to their retreat rock (Brennan 2002), and many retreat rocks have evidence of eggsac cases from multiple years (F. T. van den Berg, *personal observation*). Thus the presence of an adult female underneath a rock represents more than daily retreat rock use. We surveyed each outcrop once.

We determined any associations of rock variables with adult *M. plagusius* occupancy by constructing a suite of possible generalized linear models (GLM) from all the linear combinations of predictor variables. We also used Akaike Information Criterion values corrected for small sample sizes (AICc; Burnham and Anderson 2002) to rank the models using the multi-model inference package MuMln (Bartoń 2013) in R v. 2.14.0 (R Core Team 2014) with the presence or
absence of adult *M. plagusius* as the dependent variable. We calculated the Akaike weights \((w_i)\) of each candidate model to determine the relative likelihood of the model given the data. We deemed models with a \(\Delta AICc\) of <4 to have good support given the data (Anderson 2008). We then produced a reduced model by averaging any generated linear combination of variables with a \(\Delta AICc\) value <4 using the MuMIn package (Bartoň 2013). Variables were standardized (to a mean of 0 and standard deviation of 1) before being entered into the GLM so we could determine the relative importance of each variable for predicting whether a rock was a spider rock. To determine the predictive power of the full model we calculated the Cragg and Uhler pseudo-\(R^2\) (Cragg and Uhler 1970) using the pscl R package (Jackman 2012).

**Rock thermal profiles**

We measured the daily thermal profiles of 28 rocks for a three-week period in spring (18 November–8 December 2008) and summer (31 December–20 January 2008). We included rocks occupied by *M. plagusius* \((n = 15;\) based on occupancy at the experiment start) and available rocks \((n = 13;\) selected randomly). The rocks selected were located on two sandstone outcrops (‘Waratah’, 33°38’27” S, 151°15’17” E and ‘Yeomans’, 33°36’53” S, 151°13’47” E) within Ku-Ring-Gai Chase NP, near Sydney, Australia. We chose these outcrops for the study as they each had more than 100 exfoliated rocks (with one axis \(>100\) mm and small enough to be turned) and little evidence of human disturbance.

We measured the temperature beneath each rock every 15 minutes using an i-button (Thermochron, Dallas semiconductor) placed under the center of the rock. Additionally, we measured the length, width and thickness of each rock to determine any relationship between rock physical properties and their thermal regimes.

For each rock, in both seasons, we created a single 24-hour thermal profile by averaging the four temperatures measured each hour for each day and calculating the mean of the temperature readings for a particular hour over the three weeks. To adequately describe the thermal profile of each rock over the three-week experimental period we also calculated the mean temperature, average weekly maximum and minimum temperatures (average of the maximum or minimum temperatures recorded for each of the three weeks), overall maximum and minimum temperatures (maximum and minimum temperatures recorded in the three-week period), average weekly range, and the average hour of the day that experienced the hottest temperature. We included average weekly maximum and minimum and overall maximum and minimum as separate dependent variables. Average maximum and minimum temperatures describe maximum and minimum temperatures that a saxicolous animal is likely to frequently experience, whereas overall maximum and minimum temperatures are temperatures that are more extreme but less frequently encountered. We compared these thermal variables between seasons using repeated-measures ANOVAs.

To determine if the thermal profile of a rock is affected by its physical dimensions, we performed separate linear regressions between mean temperature, average weekly and overall temperature minimum, maximum and range, and mean hottest hour against rock thickness and area. We analyzed rock thickness and area separately as they are collinear so we were unable to include both terms in a multiple regression. These regressions were performed for spring and summer thermal regimes to determine if relationships were consistent across seasons.

To test whether the maximum temperatures among rocks were more variable than minimum temperatures among rocks, we calculated the difference between each rock’s average weekly maximum temperature and the mean average weekly maximum temperature for all rocks, for each season. We repeated this calculation for the average weekly minimum. We then determined whether the differences away from the mean of maximum temperatures were significantly different from the differences away from the mean of minimum temperatures using a paired-samples t-test. We repeated the analysis to compare the variability in the overall maximum temperatures against the overall minimum temperatures among rocks.

**Critical thermal maximum (**\(CT_{\text{Max}}\)**)

We collected *M. plagusius* from national parks north of Sydney (Ku-Ring-Gai Chase NP and
Brisbane Waters NP) in spring (n = 19; collected between 18 September and 2 October 2008) and late summer (n = 19; collected between 2 March and 4 March 2008) to determine if there was any seasonal acclimatization of upper thermal tolerances. We used CTMax as a measure of upper thermal tolerances (Lutterschmidt and Hutchison 1997b).

We transported spiders to the University of Sydney and measured each spider’s CTMax within 24 hours of collection to minimize any effects of laboratory acclimation (Lutterschmidt and Hutchison 1997b). All CTMax trials were conducted during the photophase as there is diel variation in CTMax (Lutterschmidt and Hutchison 1997b) and *M. plagusius* experience high temperatures beneath rocks during the day.

We weighed spiders prior to testing, placed them individually into 120 mm (diameter) x 65 mm (height) polypropylene containers with air holes, and put them into a temperature-controlled chamber (Clayson IM550) at 25°C for 30 min to minimize any initial shock to the experimental conditions. After 30 min, we raised the temperature of the incubator at a rate of approximately 0.2°C/min.

We observed the spiders every 5 min until they started to display ‘escape behavior’ (Schmalhofer 1999), which we defined as vigorous running around the experimental container or vigorous movements of the forelimbs and trying to crawl up the side of the container. After the onset of escape behavior, spiders were observed twice every 5 min to decrease the chance of missing the CTMax end point. We defined the CTMax end point as the onset of muscular spasms (Lutterschmidt and Hutchison 1997a) and *M. plagusius* experience high temperatures beneath rocks during the day.

As a control, we put six spiders into an incubator set at 25°C and observed their behavior every 5 min and then twice every 5 min when experimental spiders started displaying escape behavior.

We performed linear regressions to determine if mass was correlated with either escape temperature or CTMax and thus if mass needed to be included as a covariate. We conducted a two-tailed t-test (equal variances) to compare the mean escape initiation temperature for each season. We performed a two-tailed t-test (unequal variances) to determine if the mean CTMax was different between spring and summer. We conducted a two-tailed Pearson correlation between each spider’s escape temperature and CTMax to determine if there was a positive association between the two variables. Additionally, we performed an analysis of covariance (ANCOVA) in JMP (v. 9, SAS Institute, Cary, NC) with escape temperature as the covariate and CTMax as the dependent variable to determine if the slope of the correlation between escape temperature and CTMax was the same in spring and summer. To account for multiplicity, we applied a Bonferroni correction to all CTMax analyses using p = 0.0125 to retain an a = 0.05 (Rice 1989).

We performed all statistical analyses in SPSS (v.16, Chicago, Ill. USA) and all results were considered significant if P < 0.05 unless otherwise specified. When comparing means (ANOVAs or t-tests) we checked data for homogeneity of variances using a Levene’s test. When the test of homogeneity was significant, we performed t-tests assuming unequal variances. All data are presented as mean ± standard error.
RESULTS

Retreat rock selection by adult Morebilus plagusius

We measured 379 rocks, 82 of which were occupied by an adult M. plagusius. The GLM generated 26 models with a ΔAICc < 4 (Appendix A). The Cragg-Uhler pseudo-\( R^2 \) for the full model was 0.60. In the reduced model, the area of the rock and the substrate under the rock had relatively large importance (Fig. 1). Spider rock occupancy was positively associated with the area of the rock and whether the rock was on a bare rock substrate, but negatively associated with rocks on a substrate of dirt/sand or leaf litter (Fig. 1). The canopy openness, distance to nearest rock/vegetation/cliff edge, height of the rock, presence of other animals (spiders or non-spiders), or whether the rock was on a substrate of moss or smaller rocks did not predict whether a rock was occupied by an adult M. plagusius as the confidence intervals associated with their coefficients overlapped zero (Fig. 1).

Thermal profiles of rocks

Rock thermal profiles were hotter in summer than in spring (Fig. 2). The mean rock temperature, average weekly minimum and maximum temperatures, and overall minimum and maximum temperatures of rocks were significantly hotter in summer than in spring (Table 1). In summer the overall minimum and maximum temperatures were significantly hotter than in spring (Table 1). Rocks had significantly larger average weekly temperature ranges and overall temperature ranges in summer than in spring (Table 1). The mean hottest hour was not significantly different between seasons, peaking around 14:00 each season (Table 1). The variability among rocks in maximum temperatures was greater than that in minimum temperatures in both seasons (Table 2).

There was a significant relationship between rock thickness and mean temperature in spring but not in summer. No measure of physical dimension had any effect on the average weekly minimum temperature in either season. There were significant relationships between the average weekly maximum temperature and rock thickness and area in spring, whereas in summer there were only significant relationships between area and average weekly maximum. Average weekly range was significantly affected by the same measures of physical dimensions as average weekly maximum in spring and summer.
There was a significant relationship between the mean hottest temperature and area in spring and summer. Thickness was a predictor of mean hottest hour in summer only. No other relationship between rock physical dimensions and thermal profile variables was significant (Table 3).

\( CT_{\text{Max}} \)

There was no relationship between spider mass and escape temperature \( (R^2 = 0.05, F_{1,28} = 1.46, P = 0.238) \) or between mass and \( CT_{\text{Max}} \) \( (R^2 = 0.00, F_{1,28} = 0.04, P = 0.854) \) so mass was not used as a covariate in subsequent analyses. Escape temperature was significantly higher in summer than in spring \( (t\text{-test (equal variances): } t(28) = 3.37, P = 0.002) \), with escape behavior being initiated at \( 42.8^\circ \pm 0.4^\circ C \) \( (n = 15) \) for spiders in spring and \( 44.9^\circ \pm 0.5^\circ C \) \( (n = 15) \) in summer. Season had a significant effect on \( CT_{\text{Max}} \) with the mean summer \( CT_{\text{Max}} \) \( (49.6^\circ \pm 0.3^\circ C) \) being higher than the mean spring \( CT_{\text{Max}} \) \( (48.3^\circ \pm 0.2^\circ C) \); \( t\text{-test (unequal variances): } t(21.4) = 3.51, P = 0.002 \). There was a positive correlation between escape

Table 1. Differences between the thermal characteristics (mean temperature, minimum temperature, maximum temperature, temperature range and mean hottest hour) of crevices beneath exfoliated rocks measured in spring and summer.

| Crevise characteristic | Spring          | Summer         | \( F_{1,27} \) | \( P \)     |
|------------------------|-----------------|----------------|----------------|-------------|
| Mean rock temp (°C)    | 23.4 ± 0.9      | 27.5 ± 1.1     | 543.7          | <0.0001     |
| Mean hottest hour (h)  | 14.4 ± 1.3      | 14.1 ± 0.9     | 2.1            | 0.161       |
| Minimum temperature (°C) |               |                |                |             |
| Overall minimum        | 13.5 ± 0.8      | 16.9 ± 1.1     | 371.6          | <0.0001     |
| Average minimum        | 15.8 ± 0.8      | 18.2 ± 1.1     | 184.5          | <0.0001     |
| Maximum temperature (°C) |               |                |                |             |
| Overall maximum        | 42.5 ± 4.3      | 48.7 ± 4.8     | 52.7           | <0.0001     |
| Average maximum        | 40.1 ± 4.0      | 46.1 ± 4.3     | 43.3           | <0.0001     |
| Temperature range (°C) |                 |                |                |             |
| Overall range          | 29.0 ± 4.5      | 31.8 ± 5.5     | 9.7            | 0.004       |
| Average range          | 24.2 ± 4.3      | 27.9 ± 4.9     | 14.3           | 0.001       |

Notes: For minimum and maximum temperatures, and for the temperature range, the average value and overall value have been given because both the normal daily fluctuations and the extremes of the fluctuations may be important for rock dwelling taxa.
There was no significant difference between the seasons in the slope of correlation between escape temperature and CTMax (ANCOVA: season \times escape temperature: F_{1,26} = 3.94, P = 0.06).

**DISCUSSION**

The combination of physiological and behavioral mechanisms decreases the probability of *Morebilus plagusius* encountering stressful hot temperatures. By seasonally acclimatizing upper thermal tolerances and using retreats with milder microclimates, *M. plagusius* persist on sandstone outcrops during summer, when temperatures underneath rocks get hotter. Without this combination of physiological and behavioral mechanisms, the seasonal rise in temperatures during summer would lead to many individuals encountering their upper thermal limits (Fig. 4).

**Seasonal changes in the probability of encountering upper thermal limits**

Our study demonstrates the increased challenges that rock dwelling taxa face in summer in avoiding their upper lethal temperatures by quantifying the seasonal changes in rock temperatures between spring and summer. Rock dwelling taxa that use retreat rocks throughout summer must cope with hotter mean temperatures...

**Table 2.** Differences in the variability in average weekly minimum and maximum temperatures and overall minimum and maximum temperatures among rocks in spring and summer.

| Season  | Variability in temperatures | Statistics |
|---------|-----------------------------|------------|
|         | Minimum                    | Maximum    | t_{27}     | P          |
| Spring  | 0.63 \pm 0.10              | 3.21 \pm 0.45 | 5.68      | <0.001    |
| Overall | 0.56 \pm 0.10              | 3.37 \pm 0.48 | 6.08      | <0.001    |
| Summer  | 0.72 \pm 0.14              | 3.63 \pm 0.41 | 7.28      | <0.001    |
| Overall | 0.83 \pm 0.14              | 3.81 \pm 0.53 | 5.84      | <0.001    |

Note: Variability calculated as the residual distance between the rock maximum (or minimum) temperature for a season and the mean maximum (or minimum) temperature for that season.

**Table 3.** Summary of the spring and summer linear relationships between (a) rock thickness (mm) and (b) rock area (mm\(^2\)) and the dependent variables: mean temperature (°C), average weekly minimum and maximum temperature (°C), overall minimum and maximum temperatures (°C), average weekly range (°C) and mean hottest hour (n = 28).

| Dependent variable | Spring                  |        |          |        |          |            | Summer                  |        |          |        |          |
|--------------------|-------------------------|--------|----------|--------|----------|------------|-------------------------|--------|----------|--------|----------|
|                    | R\(^2\) F\(_{1,26}\) P | Equation       |          | R\(^2\) F\(_{1,26}\) P | Equation       |
| a) Rock thickness (mm) |                        |        |          |        |          |            |                        |        |          |        |          |
| Mean temperature   | 0.16 4.96 0.035*        | −0.0054x + 23.889 | 0.05 1.40 0.247 | ... |
| Average weekly minimum | 0.00 0.00 0.958 | ... | 0.04 1.11 0.302 | ... |
| Overall minimum    | 0.02 0.50 0.486         | ... | 0.02 0.55 0.464 | ... |
| Average weekly maximum | 0.18 5.86 0.023* | −0.0265x + 42.318 | 0.13 3.87 0.060 | ... |
| Overall maximum    | 0.26 9.11 0.006**       | 0.0332x + 45.319 | 0.12 3.55 0.071 | ... |
| Average weekly range | 0.16 5.09 0.033* | −0.0267x + 26.490 | 0.13 3.73 0.064 | ... |
| Mean hottest hour  | 0.07 1.97 0.173         | ... | 0.19 6.26 0.019* | 0.0062x + 13.51 |
| b) Area (mm\(^2\))  |                        |        |          |        |          |            |                        |        |          |        |          |
| Mean temperature   | 0.03 0.90 0.352         | ... | 0.10 2.79 0.107 | ... |
| Average weekly minimum | 0.10 2.77 0.108 | ... | 0.10 2.88 0.101 | ... |
| Overall minimum    | 0.08 2.14 0.156         | ... | 0.12 3.49 0.073 | ... |
| Average weekly maximum | 0.19 6.22 0.019* | −2E-05x + 41.776 | 0.29 10.76 0.003*** | −2E-05x + 48.273 |
| Overall maximum    | 0.25 8.419 0.007**      | −3E-05x + 50.955 | 0.35 13.88 0.001*** | −3E-05x + 50.955 |
| Average weekly range | 0.22 7.42 0.011* | −2E-05x + 26.138 | 0.29 10.43 0.003** | −3E-05x + 30.427 |
| Mean hottest hour  | 0.20 6.36 0.018*        | 5E-06x + 13.914 | 0.24 7.97 0.009** | 4E-06x + 13.679 |

Notes: Significant P values are highlighted in boldface; *P < 0.05, **P < 0.01, ***P < 0.001. Equations are only provided for variables that were significantly affected by the rock physical variable (thickness or area).
Maximum temperatures are more variable between rocks than minimum temperatures, as all rocks equilibrate to similar nighttime temperatures (minimum temperatures), while the maximum temperatures are based on the physical characteristics of the rock (e.g., thickness and area). Using only rock area as a predictor variable, we were able to significantly predict the mean hottest hour, the average weekly range and the maximum (both average and overall) temperatures experienced beneath rocks in spring and summer (Table 2). Thus, the area of the retreat rock used will have a large impact on the probability of a spider encountering potentially lethal upper temperatures. Surprisingly, although rock thickness is correlated with mean temperature, average and overall maximum temperatures, and average weekly range in spring, rock thickness was not significantly related to these thermal metrics in summer.

**Seasonal acclimatization of upper thermal tolerances**

Compared to most other metazoan taxa, *M. plagusius* has a very high CTMax (Hoffmann et al. 2013). This high CTMax assists *M. plagusius* in persisting on thermally stressful sandstone rock outcrops. Most importantly, the CTMax of *M. plagusius* seasonally acclimatizes which decreases the probability of encountering lethal temperatures in summer.

The rate of warming during thermal tolerance trials can affect an animal’s critical thermal limits (Terblanche et al. 2007, Chown et al. 2009, Terblanche et al. 2011). Although the rate of warming we used (0.2°C/min) is a commonly used rate of temperature increase, and thus allows comparisons between *M. plagusius* and other species, it is at the upper end of rates of temperature changes that were recorded by our i-buttons in crevices beneath rocks. As such, our observed CTMax may be higher than the field thermal tolerances of *M. plagusius*, as faster rates of warming produce higher observed tolerances (Terblanche et al. 2007, Chown et al. 2009). However, the consistent methodology between spring and summer CTMax trials demonstrates that there is seasonal acclimatization of upper thermal tolerances in *M. plagusius*, supporting our hypothesis.

Comparison of the CTMax with the maximum temperatures recorded by i-buttons beneath the rocks reveals the importance of seasonal acclimatization for increasing the number of thermally suitable rocks available to *M. plagusius* in summer. In spring, only two rocks surveyed had temperatures exceeding the spider’s spring
If no seasonal acclimatization of upper thermal limits occurred between spring and summer, 57% of all rocks in summer would reach temperatures that exceeded the spider’s spring thermal limits. Of these, 69% would on average exceed the mean spring CTMax weekly. Acclimatization of CTMax means that only 43% of rocks in summer reached temperatures exceeding the mean summer upper thermal tolerances of M. plagusius, although 75% of these would exceed the tolerances weekly (Fig. 4). If our CTMax is an overestimation of field thermal tolerances, then the importance of seasonal acclimatization for M. plagusius persistence on outcrops during summer is increased.

Thermal tolerances are affected by temperature treatments in acclimation experiments (e.g., Lutterschmidt and Hutchison 1997b, Beitinger et al. 2000, Piyaphongkul et al. 2014), thus past thermal experience in the field is likely to contribute to the seasonal acclimatization of the CTMax of M. plagusius. However, physiological plasticity in thermal tolerances can also be affected by age, body condition, photoperiod, and hydric conditions (Lutterschmidt and Hutchison 1997b, Terblanche et al. 2011). Any combination of these variables may be the ultimate factors contributing to the seasonal acclimation of the CTMax. However, the proximate result is that CTMax of M. plagusius increases in summer, allowing M. plagusius to persist underneath a greater number of rocks. Understanding the capacity of a population to seasonally acclimatize its CTMax under field conditions is an understudied area of research and deserves more attention (but see Hopkin et al. 2006, Sanabria et al. 2013), especially given the growth of macrophysical models in determining large scale patterns in ecology (Chown and Gaston 2008, Gaston et al. 2009, Kearney et al. 2009). Often these models only use single values of thermal tolerances (although see Sunday et al. 2011) or thermal tolerance values generated under laboratory acclimation conditions that do not capture seasonal variation in temperatures, food availability, reproductive status, field-relevant ramping rates and humidity that may all contribute to the thermal tolerances of a population. Our study demonstrates the need to measure the CTMax of field caught animals in different seasons and incorporate the seasonal variability of thermal tolerances into fundamental niche and macro-physiological models (e.g., Sunday et al. 2011).

Animals will not wait until their thermal tolerances are reached before they respond to increasing temperatures. Many taxa will display escape behavior (e.g., changing activity patterns and seeking thermally suitable microclimates; Fick et al. 2009, Breau et al. 2011, Sinsch and Leskovar 2011) to avoid encountering their CTMax. As the temperature at which escape behavior is initiated is correlated with CTMax for M. plagusius, seasonal acclimatization of thermal tolerances is coupled with a seasonal...
shift in the temperature at which escape behavior to avoid thermal tolerances is initiated. Thus, spiders can stay beneath their rock for longer before the risk of encountering thermal extremes becomes too great and they need to abandon their retreat rock. Throughout spring and summer, *M. plagusius* construct multiple sequential eggsacs that are fixed to the retreat rock (F.T. van den Berg, personal observation). Therefore, needing to abandon a retreat rock due to high temperatures will leave eggsacs unguarded (Pike et al. 2012) and may lead to increased risk of predation from avian predators (as for other saxicolous taxa; Webb and Whiting 2005).

Because of the large increase in maximum temperatures between spring and summer (>6°C), seasonal shift in thermal tolerances alone are not sufficient to prevent *M. plagusius* from encountering lethal temperatures in summer. This is despite the seasonal acclimation of upper thermal tolerances in *M. plagusius* that decrease the possibility of encountering lethal temperatures.

**Non-random retreat use**

Non-random retreat rock use decreases the probability of *M. plagusius* encountering lethal temperatures. Adult female *M. plagusius* use rocks non-randomly, occupying rocks that are larger in area compared to other rocks available on the outcrops. Large rocks experience lower average maximum and lower overall maximum temperatures than small rocks.

Apart from decreasing the probability of encountering maximum temperatures, the non-random use of large rocks will be beneficial for nocturnal ectotherms as these rocks retain their heat until later in the day and provide decreased variability of temperatures at a single point (Table 3), which is important for organisms where movement is limited (e.g., sit-and-wait predators or *M. plagusius* eggs in eggsacs attached to the substratum underneath retreat rocks). Larger rocks may also provide a large thermal gradient, which can be exploited by ectotherms through shuttling behavior (Huey et al. 1989, McGaw 2003, Rock and Cree 2008).

Non-random retreat use is common in animals that live in harsh thermal environments (e.g., Huey et al. 1989, Attum et al. 2013, Campos et al. 2013) and can reduce an animal’s exposure to climatic extremes (Scheffers et al. 2014). Many of these animals are able to modify their retreat to change its thermal properties (Danks 2002, Sinsch and Leskovar 2011, Pike and Mitchell 2013). When animals can change the thermal properties of their retreat through habitat modification, competition for thermally suitable retreats should be minimal. However, when the number of retreats is limited and the physical properties of those retreats are fixed, competition among animals for thermally suitable retreats should be intense, especially when many of the retreats have the potential to exceed an animal’s thermal tolerances.

Although adult spiders use retreat rocks non-randomly, decreasing their probability of encountering extreme upper temperatures, we are unable to discount reasons other than temperature that may be contributing to this non-random retreat use. Alternate hypotheses for why adult spiders are observed non-randomly using larger rocks include the possibility that larger rocks provide spiders with greater protection from predators, increase the probability of encountering prey or, due to their size, are disturbed less by water currents or large vertebrates than smaller rocks. While we are unable to exclude any of these options, laboratory choice trials demonstrate that juvenile *M. plagusius* select retreat rocks based on temperature (Goldsbrough et al. 2004) and adult *M. plagusius* will inhabit and construct eggsacs under much smaller (10 cm²) retreat rocks in the laboratory (F. T. van den Berg, personal observation). Regardless of the ultimate mechanisms for why *M. plagusius* adults are using rocks with larger area, by using these rocks rather than smaller rocks spiders will experience milder thermal conditions.

*M. plagusius* also occupy rocks non-randomly with respect to the substratum, occupying rocks that are on a bare rock substratum and not using rocks that are on leaf litter and/or sand or dirt. The size of the rock does not explain their non-random rock use with regard to substratum type, as rocks with larger area often sit on a combination of dirt/sand, leaf litter and bare rock substratum. Use of bare rock substratum is consistent with other studies of habitat use of *M. plagusius* (Brennan 2002, Goldsbrough et al. 2004), as well as other saxicolous spiders (Goldsbrough et al. 2003, Agnarsson and Rayor 2013).
The use of rocks with bare rock substratum by *M. plagusius* adults may decrease their exposure to potential predators as rocks on soil or dirt are correlated with use by ants, centipedes and coppertail skinks (*Ctenotus taeniolatus*) in these ecosystems (Goldsbrough et al. 2003, Goldsbrough et al. 2006).

Our results highlight that non-random retreat use is important for *M. plagusius* persistence on outcrops. They also demonstrate that the combination of seasonal acclimatization in thermal tolerances and non-random retreat rock use allows the exploitation of more rocks as retreats during summer, which is important when the number of suitable retreat rocks is low.

**Impacts of future increases in extreme temperatures**

Using a combination of non-random retreat rock use and acclimatization in thermal tolerances, *M. plagusius* can persist on sandstone outcrops in summer, as maximum temperatures underneath rocks increase. As the duration of heat waves, the number of hot days, and the magnitude of hot extremes increase with future climate change (Alexander and Arblaster 2009, IPCC 2013) these mechanisms may become increasingly important in determining whether *M. plagusius* will continue to persist during the hottest times on these outcrops. Under such conditions, *M. plagusius* should use even larger rocks, which would buffer them most from fluctuating temperatures and/or increase the capacity to acclimatize its $\text{CT}_{\text{Max}}$. However, despite the capacity of *M. plagusius* to shift its upper thermal tolerances seasonally, its ability to further increase its tolerances may be limited. We would expect that if *M. plagusius* had a greater capacity to shift its physiology to counteract changes in extreme environmental temperatures, then the difference between maximum summer field temperatures and the summer $\text{CT}_{\text{Max}}$ would be close to zero. The small increase in $\text{CT}_{\text{Max}}$ between spring and summer, and the low variability around the $\text{CT}_{\text{Max}}$, suggest that *M. plagusius* has limited physiological capacity to further increase its thermal tolerances (Somero 2010). This low acclimation capacity of thermal tolerances for species with high values of $\text{CT}_{\text{Max}}$ or other thermal tolerance metrics is also shown in the thermal tolerances of crustaceans (Stillman 2003, Hopkin et al. 2006).

Furthermore, the capacity of *M. plagusius* to buffer predicted increases in thermal extremes through non-random retreat use may be limited. Under conditions of increased thermal extremes, the subset of thermally inhabitable rocks will be reduced, being restricted to the very largest of rocks. Large rocks are disproportionately rare on outcrops compared to smaller rocks and the target of anthropogenic bushrock collection (Schlesinger and Shine 1994). Bushrock collection is listed as a key threatening process to biodiversity under the New South Wales Threatened Species Conservation Act 1995.

**Conclusions**

In summer, rock dwelling taxa living on exposed outcrops need to cope with increased mean temperatures and asymmetrically hotter temperatures at the upper end of the distribution compared to spring. To mitigate this seasonal change in maximum temperatures, *M. plagusius* increases its thermal tolerances between spring and summer through seasonal acclimatization. Furthermore, *M. plagusius* uses retreat rocks non-randomly, preferentially using rocks on bare rock substratum and rocks with larger areas compared to the rocks around them. Rocks that are larger in area also provide a less fluctuating thermal environment, retain their heat later in the day and, importantly, experience lower maximum temperatures. By combining non-random retreat rock use and seasonal acclimatization in thermal tolerances, *M. plagusius* can inhabit exfoliated rocks on exposed outcrops throughout summer, when many other taxa will abandon the outcrops.

Our study demonstrates how saxicolous animals, due to their combination of high probability of exposure to high temperatures and limited retreat options, can be a good model for understanding the physiological and behavioral mechanisms animals use to avoid encountering their thermal limits. We highlight how the integration of behavior and physiological adaptive capacity is necessary to explain how animals cope with the change in probability of encountering thermal extremes. As the probability of extreme temperature events are predicted to increase with anthropogenic climate change, both acclimatization capacity and behavioral
mechanisms for avoiding thermal extremes will become increasingly important for animals’ survival.

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### Table A1. Generalized linear models with a ΔAICc < 4 of habitat variables for predicting adult *Morebilus plagusius* rock use: habitat variables included in the model, as indicated by an “X.”

| Model | Height | Area | Dirt/Sand | Rock | Leaf litter | Moss | Small rocks | Distance to escape | Canopy | Other animals |
|-------|--------|------|-----------|------|-------------|------|-------------|-------------------|--------|--------------|
| 1     | ...    | X    | X         | X    | X           | ...  | X           | ...               | ...    | ...          |
| 2     | ...    | X    | X         | X    | X           | ...  | X           | ...               | ...    | ...          |
| 3     | ...    | X    | X         | X    | X           | ...  | X           | ...               | ...    | ...          |
| 4     | ...    | X    | X         | X    | X           | ...  | X           | ...               | ...    | ...          |
| 5     | ...    | X    | X         | X    | X           | ...  | X           | ...               | ...    | ...          |
| 6     | X      | X    | X         | X    | X           | ...  | X           | ...               | ...    | ...          |
| 7     | ...    | X    | X         | X    | X           | ...  | X           | ...               | ...    | ...          |
| 8     | ...    | X    | X         | X    | X           | X    | X           | ...               | ...    | ...          |
| 9     | ...    | X    | X         | X    | X           | ...  | X           | ...               | ...    | ...          |
| 10    | ...    | X    | X         | X    | X           | ...  | X           | ...               | ...    | ...          |
| 11    | ...    | X    | X         | X    | X           | X    | X           | ...               | ...    | ...          |
| 12    | X      | X    | X         | X    | X           | ...  | X           | ...               | ...    | ...          |
| 13    | ...    | X    | X         | X    | X           | X    | X           | ...               | ...    | ...          |
| 14    | X      | X    | X         | X    | X           | X    | X           | ...               | ...    | ...          |
| 15    | X      | X    | X         | X    | X           | X    | X           | ...               | ...    | ...          |
| 16    | ...    | X    | X         | X    | X           | X    | X           | ...               | ...    | ...          |
| 17    | ...    | X    | X         | X    | X           | X    | X           | ...               | ...    | ...          |
| 18    | ...    | X    | X         | X    | X           | X    | X           | ...               | ...    | ...          |
| 19    | ...    | X    | X         | X    | X           | X    | X           | ...               | ...    | ...          |
| 20    | X      | X    | X         | X    | X           | X    | X           | ...               | ...    | ...          |
| 21    | ...    | X    | X         | X    | X           | X    | X           | ...               | ...    | ...          |
| 22    | ...    | X    | X         | X    | X           | X    | X           | ...               | ...    | ...          |
| 23    | X      | X    | X         | X    | X           | X    | X           | ...               | ...    | ...          |
| 24    | ...    | X    | X         | X    | X           | X    | X           | ...               | ...    | ...          |
| 25    | X      | X    | X         | X    | X           | X    | X           | ...               | ...    | ...          |
| 26    | ...    | X    | X         | X    | X           | X    | X           | ...               | ...    | ...          |
Table A2. The log likelihood (logLik), AICc, ΔAICc and Akaike weight ($w_i$) of generalized linear models with a ΔAICc < 4 for predicting adult *Morebilus plagusius* rock use.

| Model | logLik | AICc  | ΔAICc | $w_i$ |
|-------|--------|-------|-------|------|
| 1     | -107.41| 227.03| 0.00  | 0.075|
| 2     | -106.85| 228.01| 0.97  | 0.046|
| 3     | -105.85| 228.08| 1.05  | 0.045|
| 4     | -106.98| 228.25| 1.22  | 0.041|
| 5     | -107.06| 228.41| 1.38  | 0.038|
| 6     | -107.27| 228.84| 1.81  | 0.030|
| 7     | -107.37| 229.04| 2.00  | 0.028|
| 8     | -106.35| 229.10| 2.06  | 0.027|
| 9     | -109.61| 229.38| 2.34  | 0.023|
| 10    | -108.62| 229.46| 2.43  | 0.022|
| 11    | -105.51| 229.51| 2.47  | 0.022|
| 12    | -106.71| 229.80| 2.77  | 0.019|
| 13    | -106.73| 229.84| 2.81  | 0.018|
| 14    | -106.75| 229.88| 2.85  | 0.018|
| 15    | -105.70| 230.89| 3.85  | 0.018|
| 16    | -107.87| 230.04| 3.00  | 0.017|
| 17    | -106.83| 230.05| 3.01  | 0.017|
| 18    | -105.84| 230.16| 3.13  | 0.016|
| 19    | -106.92| 230.23| 3.20  | 0.015|
| 20    | -106.92| 230.24| 3.20  | 0.015|
| 21    | -107.03| 230.44| 3.41  | 0.014|
| 22    | -110.20| 230.57| 3.53  | 0.013|
| 23    | -106.09| 230.67| 3.64  | 0.012|
| 24    | -108.23| 230.75| 3.72  | 0.012|
| 25    | -107.21| 230.81| 3.78  | 0.011|
| 26    | -109.31| 230.84| 3.81  | 0.011|