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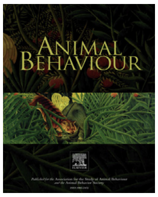

Behaviour of an alpine range-restricted species is described by interactions between microsite use and temperature

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Climate change predictions include increased mean temperatures and increased frequency of heatwaves. Short-term responses to high air temperatures can allow animals to conserve water while maintaining a safe body temperature. For birds, cooling is often through evaporative water loss, which can be physiologically costly. Microsite use is an effective means of conserving water via reducing environmental heat load, so long as there are no negative trade-offs with other necessary functions, such as foraging. We examined behavioural responses to temperature in Cape rockjumpers, *Chaetops frenatus* (hereafter: 'rockjumper'), an alpine specialist bird. We hypothesized that rockjumper behaviours would be temperature and microsite dependent. We collected data on rockjumper microsite use (sun, rock shade), behaviour (activity, foraging, preening, panting) and temperature (air, environmental). Rockjumpers made increased use of rock shade as air temperature increased. However, birds in rock shade foraged less. Depending on where their main food source is located, this suggests that when foraging demands are high, birds may need to remain in the sun despite risks of high thermal load, or else may suffer costs of lost foraging opportunities when using shade. The relationship between air temperature and heat dissipation behaviour (panting) was also mediated by microsite: birds showed significant increases in panting with increasing air temperature only when in the sun. The lack of increase in panting for birds in rock shade suggests that shade seeking may buffer physiological thermoregulatory costs (i.e. water expenditure). Individuals may therefore be able to mitigate some potential negative effects of high temperatures by making use of cooler microsites, although this could come at a cost to foraging.

Under climate change, weather patterns are increasingly characterized by warmer overall temperatures and more intense heatwaves (Easterling et al., 2000). One way in which animals may respond quickly to environmental challenges is by using short-term behavioural responses (Wingfield, 2003). In general, behavioural responses to temperature have been considered typical of ectotherms (e.g. Adolph, 1990; Gifford, Clay, & Powell, 2012; Gilman, Toolson, & Wolf, 2008; Huey, 1991; Huey, Peterson, Arnold, & Porter, 1989; Sears et al., 2016), while endotherms are often assumed to rely primarily on physiological adjustments to regulate their body temperatures (Boyles, Seebacher, Smit, & McKechnie, 2011; Chamane & Downs, 2009; Smit, Harding, Hockey, & McKechnie, 2013). However, when examining potential avenues for mitigating the negative effects of increasing temperatures, Huey et al. (2012) suggested that any terrestrial species in thermally heterogeneous environments could use 'behavioural buffering' (e.g. spending more time in cooler microsites) to help maintain body temperature. Indeed, behavioural buffering is a commonly used behavioural mechanism for coping with high temperatures, along with reducing daily energy expenditure, across both ectothermic and endothermic taxa (Buckley, Ehrenberger, & Angilletta, 2015; Gifford et al., 2012; Mugaas & King, 1981; Sinervo et al., 2010; Visinoni, Pernollet, Desmet, Korner-Nievergelt, & Jenni, 2015).

Interest in behavioural buffering has led to a growing number of studies focusing on how endotherms use microsites to cope with high temperatures, including both birds (e.g. Cunningham, Martin, & Hockey, 2015; Hill, 2006; Martin, Cunningham, & Hockey, 2015; Pattinson & Smit, 2017; Shi, Paull, Broome, & Bates, 2015; Wolf, Wooden, & Walsberg, 1996), and mammals (e.g. Hewson, 1990; Moyer-Horner, Mathewson, Jones, Kearney, & Porter, 2015; and

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see review by ; Cain, Krausman, Rosenstock, & Turner, 2006). Adjusting behaviour in response to weather conditions is vital for maintaining heat balance while also balancing water and energy demands, especially in water-scarce environments (McKechnie & Wolf, 2004; Smit et al., 2013; Williams & Tieleman, 2005; Xie, Turrell, & McWhorter, 2017), and selective microsite use remains the most effective means of water conservation (Williams, Bradshaw, & Schmidt, 1995). Ground-foraging birds may make particularly dramatic changes in microsite use in order to manage heat load at high air temperatures (Martin et al., 2015; van de Ven, McKechnie, & Cunningham, 2019), as the exposed microsites on the ground in which these birds forage are typically among the hottest in the landscape (Carroll, Davis, Elmore, Fuhlendorf, & Thacker, 2015; Pattinson & Smit, 2017; Tieleman & Williams, 2002b). Indeed, greater shifts in microsite use at high temperatures have been found for ground-foraging than arboreal-foraging species (Martin et al., 2015).

Resting in shaded microsites may allow individuals to spend time on other necessary activities, such as feather maintenance (Leitão & Mota, 2015; Tieleman & Williams, 2002a), but must also be balanced with foraging, reproductive behaviour and territory maintenance (Cunningham et al., 2015; Funghi, McCowan, Schuett, & Griffith, 2019; Gilman et al., 2008; Martin et al., 2015; Thiollay, 1988; Wiley & Ridley, 2016; Wolf, 2000). Alternatively, individuals can maintain body temperature by reducing daily energy expenditure, and thus reduce metabolic heat production from elevating body temperature above normal levels (Pattinson & Smit, 2017; Visinoni et al., 2015; Weathers & Sullivan, 1989, 1993). However, reducing activity may not always be possible, as birds often need to continue foraging at high temperatures to meet individual energy demands (du Plessis, Martin, Hockey, Cunningham, & Ridley, 2012; van de Ven et al., 2019), and also to meet the additional energy demands of offspring during the breeding season (Clauser & McRae, 2017; Coe, Beck, Chin, Jachowski, & Hopkins, 2015; Cunningham et al., 2015; Edwards, Mitchell, & Ridley, 2015).

A recent meta-analysis on the vulnerability of alpine species to climate change identified a research gap in fine-scale ecological studies of mountain specialist birds (Scridel et al., 2018). The Cape rockjumper, *Chaetops frenatus* (hereafter 'rockjumper') represents one such range-restricted alpine species, inhabiting the upper slopes of the Fynbos mountains in South Africa. Rockjumpers are potential 'climate relicts' due to fragmented ranges probably isolated by past climate shifts (see discussion in Woolbright, Whitham, Gehring, Allan, & Bailey, 2014). For alpine range-restricted specialists such as the rockjumper, use of behavioural buffering may be necessary as they cannot shift their range polewards or upwards into cooler climates (Freeman, Lee-Yaw, Sunday, & Hargreaves, 2018; Gibson, McNeill, de Tores, Wayne, & Yates, 2010; Robin, Gupta, Thatte, & Ramakrishnan, 2015). Rockjumpers are currently experiencing decreasing populations especially in parts of their range that show warming trends (Milne, Cunningham, Lee, & Smit, 2015). Rockjumpers thus provide an ideal model for investigating whether alpine range-restricted species can change their behaviour to mitigate the negative effects of warming temperatures.

In this study, we assessed the relationship between air temperature and rockjumper behaviour, and whether rockjumpers changed their behaviour when using cooler microsites. While the exposed and rocky environment with low vegetation preferred by rockjumpers lacks variation in vegetation structure that would generally provide thermal buffering (Lee & Barnard, 2016), it contains rocks and outcrops providing patches of deep shade throughout the day. We thus hypothesized that daily activity patterns of rockjumpers would be highly temperature and microsite dependent, owing to increasing use of rock shade for behavioural buffering as air temperatures increased. We observed the behaviour of free-living rockjumpers and predicted that as temperatures increased rockjumpers would (1) increase use of rock shade, (2) become less active, (3) reduce foraging, (4) reduce preening and (5) increase heat dissipation (i.e. panting or wing drooping), with significant interactions between microsite and temperature.

METHODS

Field Site and Study Species

Our study took place at Blue Hill Nature Reserve (BHNR), Western Cape, South Africa (33.56S, 23.40E). Habitat at BHNR comprises predominantly fynbos vegetation at elevations between 1000 and 1600 m above sea level, representing ca. 2000 ha of habitat suitable for rockjumpers. While air temperature at BHNR rarely exceeds 35 °C (average, minimum and maximum temperatures throughout our study were 18.4 °C, 1.1 °C and 36.6 °C, respectively), and the area is considered historically climatically stable (Cowling et al., 2015), BHNR is predicted under climate change to periodically experience heatwaves with air temperatures approaching 40 °C in the future (Mucina & Rutherford, 2006).

Rockjumpers are group-living birds, with up to four adult birds occupying territories of 10–20 ha (Holmes, Frauenknecht, & Du Plessis, 2002). As they are predominantly insectivorous, they probably get most of their water from their prey (Bartholomew & Cade, 1963; Fisher, Lindgren, & Dawson, 1972). Indeed, during a study spanning 10 concurrent months at BHNR, rockjumpers were recorded visiting water sources only twice, neither visit resulting in a bird drinking (Lee, Wright, & Barnard, 2017). Rockjumpers spend most of their time foraging on the ground or in low bushes, while also engaging in preening (e.g. feather maintenance), social interactions (e.g. calling to one another while spreading their tail feathers) and defending their territory from other rockjumpers or possible predators by acting as sentinels (Oswald, 2016). Their breeding season extends from early July into January, with most breeding occurring from September to November (Holmes et al., 2002).

Capture and Tagging of Individual Birds

To ensure identification of individual birds within territories, we caught 33 rockjumpers from both focal and adjacent territories ($N = 12$ territories) between October 2014 and September, 2015, using baited snap traps (spring-loaded 30 cm × 30 cm mesh-covered wire frames baited with beetle larvae, Tenebrionoid spp.). Ten birds were caught in October–November 2014, and an additional 23 birds were caught in April–September, 2015. Birds were ringed with aluminium rings (South African Bird Ringing Unit, SAFRING, South Africa) and a unique combination of three colour rings.

Behavioural data were collected in five rockjumper territories between 23 January, 2015 and 8 March, 2015 ('Cohort 1': $N = 15$ individual birds, 2–4 adults per territory). To aid locating rockjumpers in Cohort 1, five of the adults caught during October–November 2014 (one in each of the five separate territories) were fitted with VHF transmitter tags (2.4 g, < 5.0% average body mass; CTx, Biotrak Ltd., Wareham, U.K.; see below for attachment details). Biotrack tags were programmed to emit radio signals (ca. 150 MHz) for 48 h every 12 days. Behavioural observations on Cohort 1 began in January, 2015, with all ringed and tagged birds still active in their original territory of capture during these observations.

From 12 November, 2015 to 21 January 2016, we continued observations on Cohort 1, as well as collecting observations in an additional five territories ('Cohort 2': $N = 20$ additional individual birds, 2–3 adults per territory). To aid locating rockjumpers in Cohort 2, five of the adults caught in July and August, 2015 were captured and fitted with similar VHF transmitter tags (3.4 g, < 6.5% average body mass; LB-2N, Holohil Systems Ltd., Carp, ON, Canada) programmed to emit continuous radio signals (ca. 150 MHz). Behavioural observations on Cohort 2 began in November, 2015, 2–3 months after being given VHF tags, with all birds still active in their original territory of capture during these observations.

Tags were attached using leg-loop harnesses with tags resting between the wings and antenna pointing toward the rear (Smith, Reitsma, & Marra, 2011; Vandenabeele, Wilson, & Wikelski, 2013). VHF-tagged birds were located during observation sessions using an 8 MHz radio-tracking receiver (SIKA, Biotrack Ltd., U.K.) and flexible three-element Yagi antenna (Lintec Antennas, Worthing, U.K.).

Ethical Note

The baited snap-traps were continuously monitored and so birds never spent > 5 min in a trap before being removed and placed in a holding bag. Eighteen of the 33 ringed birds were ringed and released on location within their territories. The other 15 were captured and transported via cloth bag to an on-site field station at BHNR where they were held in cages (45 × 30 cm and 45 cm high) for 24–48 h as part of a separate study on physiology (see Oswald, Lee, & Smit, 2018a; 2018b). During this 24–48 h period food was provided ad libitum, after which birds were released back at point of capture with no obvious long-term effects (Oswald, Evlambiou, Ribeiro, & Smit, 2018). Transport from site of capture to the field station never took > 1 h and was either via 4 × 4 or bicycle. Our study consisted of behavioural observations where all effort was made to minimize disturbance. Observers remained at 50–200 m from birds except where birds themselves moved closer to observers. While our VHF tags weighed slightly more than the recommended < 5%, continued direct observations of rockjumpers at BHNR have found no visible negative effects, with tag attachments degrading and detaching in most instances after about 6 months; two tags were removed when the birds were recaptured in January and February 2016, respectively. We are further convinced that our VHF tags had minimal negative effects because: (1) for territories we continued to monitor ($N = 7$ territories, $N = 5$ VHF-tagged birds), all five birds were still present and reproductively active in 2017–2018, and (2) a preliminary analysis found no difference in activity levels between VHF-tagged and untagged birds ($Z_{1,2059} = -1.30$, $P = 0.194$; generalized linear mixed-effects model, GLMM, of activity as a function of tagged or untagged with ID and territory as random effects; see below for more details). Bird handling, welfare and observation procedures were approved by the University of Cape Town Animal Ethics Committee (2014/V19/AL; December 2014 to December 2016); the Nelson Mandela University Research Ethics Committee (Animal; A15-SCI-ZOO-007; June 2014 to February 2016) and the Rhodes University Animal Ethics Committee (RU-DZE-2017-10-028; June 2014 to February 2016). Birds were captured with permission from the Western Cape Province: Cape Nature (permit no. AAA041-00565) and ringed with a single-species ringing licence issued to K.N.O. by SAFRING (licence no. 17059).

Behavioural Observations

All observations were collected between 0845 and 1515 SAST. From 23 January to 8 March, 2015, Cohort 1 birds were followed 1 day within each 12-day VHF transmission cycle, with observations collected from a single territory per day. From 12 November, 2015 to 21 January 2016 each territory from Cohorts 1 and 2 was followed 1 day every 2 weeks.

Observational data were collected using teams of two to four persons performing scan samples every 5 min. Owing to the rocky landscape inhabited by rockjumpers, there were often no birds visible at the time of a scan sample. This may have resulted in an underrepresentation of some types of microsite use, as well as periods of inactivity, in our final data set. Data recorded included (1) ordinal date, (2) time of day, (3) territory designation, (4) sex and ID (VHF code, colour ring combination, unmarked with no colour rings or unknown), (5) microsite (sun, rock shade, other, i.e. shade from plants or clouds), (6) overall activity ('active', any movement ≥ 5 s including all behaviours, or 'inactive', no movement ≥ 5 s), (7) breeding stage ('breeding', whether birds were observed nest building, incubating, brooding or provisioning on individual observation days, or 'nonbreeding', no breeding activity observed) and (8) behaviours (see below).

Behaviours included: (1) foraging (erratic movement pattern usually leaning forwards, moving a few steps and stopping, pecking at plants, etc.); (2) panting (bill observed in an open position for ≥ 5 s); and (3) preening (bill placed among feathers for ≥ 5 s). These behaviours were recorded as '1' for presence or '0' for absence. Our distance from birds resulted in an inability to consistently determine whether panting occurred, and so panting was additionally recorded as 'no data' when not able to be determined. While wing drooping (i.e. holding wings away from the body) is a commonly recorded mechanism of heat dissipation among birds (see du Plessis et al., 2012; Edwards et al., 2015; Smit et al., 2013; Smit & McKechnie, 2015; Tieleman & Williams, 2002a), we did not observe it in any observation period.

The data described above were recorded every 5 min with preference for focal VHF-tagged individuals, but were additionally recorded opportunistically for other individuals within the target territory as well as individuals from two adjacent territories. For each instantaneous scan we recorded behaviours for the focal bird up to 10 s and all additional nearby birds up to 20 s, after the 5 min mark. Observations were conducted from 20–200 m away from focal birds to minimize observer disruption, with birds observed using binoculars (8 or 10X magnification) and spotting scopes (20–60X magnification).

Temperature

Air temperature data (T_{air}) were collected every 30 min by a VantageVue weather station at BHNR ('weather station'; Davis Instruments Corp., Hayward, CA, U.S.A.). The weather station was placed ca. 2 m above the ground at 1030 m above sea level, 500–5000 m from observed rockjumper territories.

To estimate temperature variation at the microsite level within the landscape, on observation days during our second round of observations (November, 2015–January 2016), 'black bulb' thermometers were deployed and collected within the focal observed territory on that specific day (ca. 0830–1530 SAST; see below for details). Black bulbs were constructed from two copper hemispheres (diameter 30 mm, thickness 0.9 mm); in each black bulb, one iButton (model DS1921G-F5 ± 0.1 °C, Fairbridge Technologies, Sandton, South Africa) was secured to an iButton retainer (model DS9098P-TRW+, Fairbridge Technologies) placed inside the two hemispheres, which were then glued together as a sphere and painted matte black.

Black bulbs integrate ambient temperature, solar radiation and wind effects to approximate the conditions experienced across different locations (Campbell & Norman, 2012; Cunningham et al., 2015). However, as studies have shown using black bulbs as a proxy for operative temperature can have multiple issues (see Bakken, 1992; Bakken, Santee, & Erskine, 1985), we used black bulbs solely as an indication of potential variation in thermal conditions between microsites within the rockjumpers' environment. On each day of black bulb deployment, before beginning observations we secured three replicate black bulbs within the observed territory in each of two microsite types (three in 'rock shade', i.e. under the rock in full shade, and three in 'sun', i.e. on the rock surface in direct sun), and collected the black bulbs at the end of the day's observations. Black bulb data were collected from 10 territories on 18 days. Owing to logger failure, data were collected in triplicate on 11 observation days, but in duplicate on 7 observation days.

Analyses

Rockjumper behaviour

As one of our main objectives was to examine how microsite choice affects behaviour, we used only observations for which birds were visible ($N = 2862$ scan samples) and then only observations when microsite was sun or rock shade ($N = 2059$ scan samples), omitting instances of 'other' (plant or cloud shade; $N = 803$ scan samples; 28%). As Fynbos vegetation is sparse, thermal conditions within plant shade could vary, which meant we were not able to reliably ascertain whether or not any particular patch of plant shade constituted a true 'thermal refuge'. Similarly, cloud shade is temporally unpredictable, and cloudy weather alters the thermal landscape wholesale, rendering comparisons between different microsites less meaningful. Therefore, these data were excluded. For panting analysis, we only included instances where panting was recorded as '1' or '0' ($N = 958$ scan samples). We used weather station T_{air} data as the 'temperature' predictor variable in all analyses, and time of day ('time') was rounded to the nearest 30 min to better align with T_{air}.

We created GLMMs using package lme4 (Bates, Maechler, Bolker, & Walker, 2015; https://CRAN.R-project.org/package=lme4) with binomial error distribution and rockjumper individual ID and territory as random effects to explore rockjumper behaviour and microsite use data. To understand the influence of microsite use, T_{air}, time, sex and breeding stage on activity, foraging, panting and preening we fitted binomial GLMMs with a log link function as follows.

$$\text{behaviour}_{i,j,k^*} \sim \text{binomial}\,(N, \pi_{ijk})$$

$$E(\text{behaviour}_{ijk}) = N \times \pi_{ijk} \text{ and } \text{var}(\text{behaviour}_{ijk}) = \pi_{ijk} \times (1 - \pi_{ijk})$$

$$\text{logit}(\pi_{ijk}) = \text{microsite} + \text{sex} + \text{breeding} + \text{microsite} \times T_{air} + \text{time} + \text{microsite} \times \text{sex} + \text{microsite(scaled)} \times \text{breeding(scaled)}$$

$$\text{ID}_i \sim N\,(0, \sigma^2_{\text{ID}})$$

$$\text{territory}_j \sim N\,(0, \sigma^2_{\text{territory}})$$

where i is the number of IDs, j is the number of territories and k is the number of observations.

Following Afshartous and Preston (2011) we transformed categorical variables into numeric sum-to-zero variables [sex (1 female, -1 male), breeding stage (1 breeding, -1 not breeding), microsite (1 sun, -1 rock shade)]. To aid convergence for activity, microsite was retained as a standard categorical variable. Continuous variables (T_{air}, time) were centred and scaled using the standard scale function in R. The coefficient output thus represents the contribution of variables relative to each other. We discuss competing models within 2 AICc of the top model (where AICc is the Akaike information criterion corrected for small sample size), with model selection carried out using the package MuMIn (Barton, 2018; https://CRAN.R-project.org/package=MuMIn), and statistical output using lmerTest (Kuznetsova, Brockhoff, & Christensen, 2015; https://CRAN.R-project.org/package=lmerTest). Parameters are discussed based on the magnitude of their coefficients and their occurrence in the set of top models.

See the Supplementary material for the raw data and Appendix Tables A1–A8 for competing model outputs as well as model coefficient summaries. Multicollinearity of variables in the final models was explored using the vif function for the car package (Fox & Weisberg, 2019; https://CRAN.R-project.org/package=car), with values < 2.5 in all cases.

Overall microsite use

To explore whether rockjumpers were found more often in rock shade as air temperature increased, we created a GLMM fitting microsite as a function of the potential predictor variable, T_{air}, along with random effects of ID and territory, and a binomial error distribution.

Black bulb temperatures

To assess whether black bulbs recorded different temperatures depending on microsite placement, and to confirm that 'rock shade' microsites were indeed thermally buffered compared to 'sun' microsites, we fitted data to a generalized additive mixed-effects model using gamm4 (Wood, Scheipl, & Wood, 2017; https://CRAN.R-project.org/package=gamm4). We additionally included air temperature data (T_{air}) from the weather station for comparison with temperature recorded by the black bulbs. Our model explored whether recorded temperature was explained by location (sun, rock shade, weather station) or time of day, adding territory and date as random effects ($N = 10$ territories, 18 days).

All analyses were performed in the R statistical environment version 3.5.3 (R Core Team, 2019) using RStudio version 1.1.463 (R Studio Team, 2016).

RESULTS

Microsite Use

The probability of recording a rockjumper in rock shade was higher with increasing T_{air} (logistic regression estimate = 0.68, 95% confidence interval, CI, 0.55–0.81, $Z_{2059} = 10.29$, $P < 0.001$); rock shade was cooler than sites in the sun (see Microsite Temperature results below).

Activity

Rockjumper activity was best explained by microsite use, with activity recorded more often in the sun than rock shade (top model coefficient estimate = 4.45, 95% CI 3.7–5.3; Table A2); these results were seen across all six of the top competing models (refer to Table A1 for competing models and Table A2 for model coefficients). All models also indicated the probability of a bird being recorded as active decreased throughout the day (coefficient estimate = -0.40, CI -0.67 – -0.10; Table A2). Activity was also generally lower when breeding (coefficient estimate = -0.64, CI -1.08 – -0.18; Table A2). A decrease in activity at higher T_{air} was observed, but this response was of low amplitude and not significant (coefficient estimate = -0.23, CI -0.51 – 0.04; Table A2). Interactions were mostly not included in the competing models, and generally not significant when included.

Foraging

The probability of observing a rockjumper foraging depended most strongly on microsite use, being lower in rock shade (top model coefficient estimate = 0.37, 95% CI 0.24–0.49; Table A4) and with females reducing their foraging to a larger degree than males between microsites (coefficient estimate = 0.21, 95% CI 0.00–0.32; Table A4, inset Fig. 1); these effects were observed in both competing models within 2 AICc of the top model (refer to Table A3 for competing models and Table A4 for model coefficients). Breeding birds also had a lower probability of being recorded as foraging (coefficient estimate = -0.24, 95% CI -0.40 – -0.05; Table A4), with some evidence that this was microsite dependent (coefficient estimate = 0.14, 95% CI 0.02–0.25; Table A4). The probability of observing a bird foraging also decreased with increasing air temperature (coefficient estimate = -0.17, 95% CI -0.29 – -0.05; Table A4), again with evidence that this was microsite dependent (coefficient estimate = 0.13, 95% CI 0.01–0.25; Table A4, Fig. 1).

Preening

The probability of observing a rockjumper preening was most dependent on breeding stage and the interaction of microsite and T_{air}, being lower when birds were breeding (top model coefficient estimate = -0.42, 95% CI 0.72–0.13; Table A6, inset Fig. 2), and decreasing at higher T_{air} in the sun (coefficient estimate = -0.30, 95% CI -0.49 – -0.10; Table A6, Fig. 2); these effects were observed in all competing models within 2 AICc of the top model ($N = 5$; refer to Table A5 for competing models and Table A6 for model coefficients). In most competing models ($N = 4$) females were also less often observed preening than males (coefficient estimate = -0.24, 95% CI -0.51 – 0.02; Table A6). A decrease in preening was observed in sun, at higher T_{air} and as the day progressed, but these responses were of low amplitude and not significant (sun: coefficient estimate = -0.10, CI -0.31 – 0.12; T_{air}: coefficient estimate = -0.03, CI -0.23 – 0.17; time: coefficient estimate = -0.14, CI -0.29 – 0.01; Table A6). The interactions of microsite and breeding, and microsite and sex, were included in few competing models ($N = 2$, $N = 1$, respectively), but were not significant.

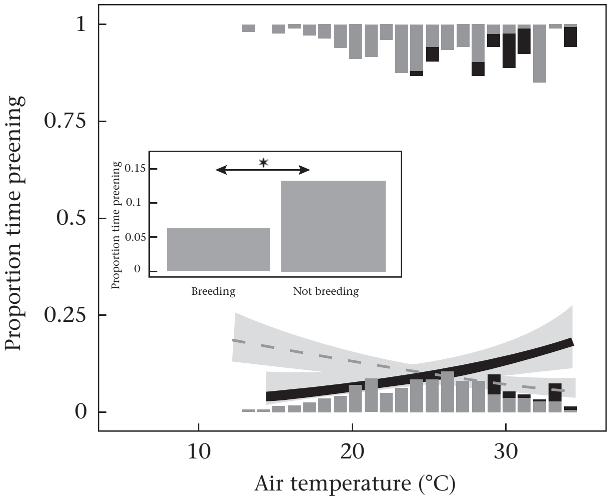

Figure 2. Preening by Cape rockjumpers (0 = not preening, 1 = preening) based on microsite ('rock shade': black, solid line; 'sun': grey, dashed line) across a range of air temperatures (°C). Model fit is a GLMM with binomial error structure, logistic regression and shaded 95% confidence intervals, with histograms indicating relative number of observations based on bar length, and microsite. Inset: bar graphs showing proportion of observations Cape rockjumpers spent preening when breeding or not breeding. *$P < 0.05$.

Panting

The probability of observing a rockjumper panting was most dependent on breeding stage and the interaction of temperature and microsite, being higher when birds were breeding (top model coefficient estimate = 1.14, 95% CI 0.51–1.86; Table A8, inset Fig. 3), increasing at higher T_{air} (coefficient estimate = 0.82, 95% CI 0.18–1.62; Table A8) and increasing more at higher T_{air} when in the sun (coefficient estimate = 0.88, 95% CI 0.19–1.51; Table A8, Fig. 3);

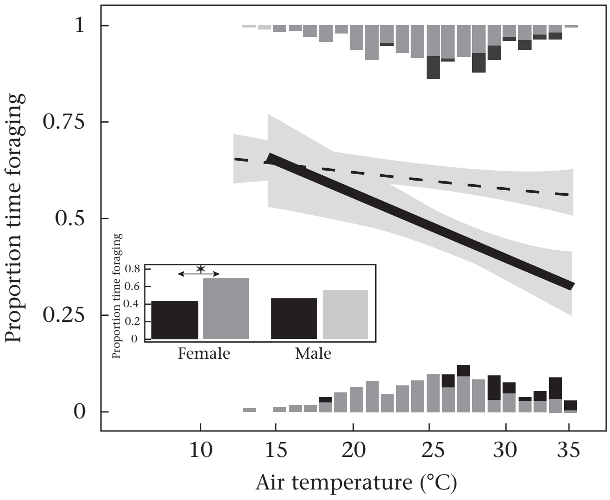

Figure 1. Foraging by Cape rockjumpers (0 = not foraging, 1 = foraging) based on microsite ('rock shade': black, solid line; 'sun': grey, dashed line) across a range of air temperatures (°C). Model fit is a GLMM with binomial error structure, logistic regression and shaded 95% confidence intervals, with histograms indicating relative number of observations based on bar length, and microsite. Inset: bar graphs showing proportion of behavioural observations females and males spent foraging in sun (grey) or rock shade (black). *$P < 0.05$.

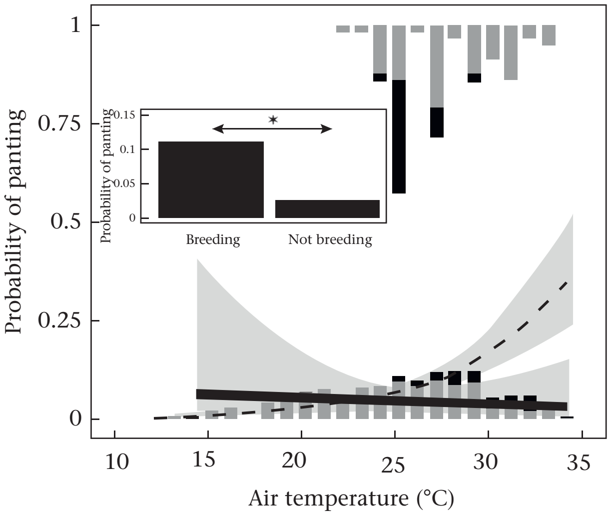

Figure 3. Panting by Cape rockjumpers (0 = not panting, 1 = panting) based on microsite ('rock shade': black, solid line; 'sun': grey, dashed line) across a range of air temperatures (°C). Model fit is a GLMM with binomial error structure, logistic regression and shaded 95% confidence intervals, with histograms indicating relative number of observations based on bar length, and microsite. Inset: bar graph showing proportion of observations Cape rockjumpers spent panting when breeding or not breeding. *$P < 0.05$.

these results were included in both competing models (refer to Table A7 for competing models and Table A8 for model coefficients). Panting depended on time of day in one competing model, where birds were observed panting more often as the day progressed, but the effect was of low amplitude and not significant.

Microsite Temperature

Recorded temperatures (°C) were significantly affected by location, with black bulbs in sun recording temperatures on average 11.8 ± 1.6 °C higher than those recorded by the weather station, and 13.4 °C higher than black bulbs in rock shade (coefficient estimate = 13.4 ± 0.2, 95% CI 13.1–13.7 °C, $Z_{6128} = 86.78$, $P < 0.001$), with recorded temperature at all locations increasing throughout the day (coefficient estimate = 1.78 ± 0.05, 95% CI 1.68–1.87, $Z = 37.76$, $P < 0.001$; Fig. 4).

DISCUSSION

Overall, rockjumpers were observed increasingly more often in rock shade as T_{air} increased, providing evidence of the potential for behavioural buffering (sensu Huey et al., 2012) as a mechanism for dealing with high T_{air} in this alpine species. Both T_{air} and microsite appeared in all top model sets for the behaviours we investigated (panting, preening, foraging and active/inactive), although T_{air} significantly predicted variation in only two behaviours (foraging and panting). Higher T_{air} was associated with reductions in activity and foraging, with the effect of T_{air} on preening and panting possibly mitigated by microsite use. Preening decreased, and panting increased, only in sun-exposed microsites, suggesting that seeking rock shade might buffer birds from impacts of temperature on these behaviours. Birds decreased levels of both activity and foraging while they were in rock shade. This suggests that while any potential direct impact of temperature is mediated by the change in microsite use, seeking shade might involve a trade-off against foraging or maintaining activity levels. Long-term negative consequences of increasing T_{air} could therefore be mediated by such trade-offs if these threaten the ability of birds to maintain energy and/or water balance. Breeding stage was also a significant predictor variable for all behaviours, and the impact of breeding on behaviour was significantly modified by microsite use for foraging, preening and panting. The only behaviour for which we found a strong sex-based effect was the interaction of sex and microsite for foraging: females foraged more than males and this extra foraging was done in the sun. Males also preened more than females. It thus seems that, overall, birds may be able to mitigate the direct effects of high T_{air} through behavioural buffering, that is, by making use of cooler microsites.

Interacting Effects of Temperature and Microsite Use

Our main purpose in placing black bulbs was to examine whether significant temperature variation existed between areas in full sun and those in rock shade, by placing black bulbs in microsites where birds had previously been seen. Although our black bulb temperature data do not directly represent the operative temperatures experienced by the birds, these data nevertheless indicate that shaded microsites available within rockjumper habitat are cooler than areas of direct sunlight (Fig. 4). Rockjumpers made clear use of cooler microsites as T_{air} increased, but they continued to maintain foraging in sun while decreasing foraging in rock shade (Fig. 1). We propose four possible explanations for this observation: (1) food availability in sun is higher than in rock shade, forcing birds to maintain foraging in sun at the expense of thermoregulation; alternatively (2) food availability in sun is higher than in rock shade, and so birds are able to obtain water from their diet which would offset water loss from panting; (3) birds sought areas with reduced thermoregulatory demands at the expense of overall energy intake when making use of cooler microsites (a foraging–thermoregulation trade-off); or (4) food availability does not differ between sun and rock shade, but birds were more often observed foraging in sun simply because, on average, a greater area of their territories is in sun than in rock shade. Unfortunately, in this study we were unable to determine food availability per microsite, and so the potential implications of foraging in sun versus rock shade at high T_{air} remain unclear.

Nonbreeding rockjumpers were significantly more likely to be observed preening than breeding birds (inset Fig. 2). As in killdeer, *Charadrius vociferus,* for which preening was most likely to occur just before laying (Brunton, 1988), preening just before breeding may help rockjumpers obtain or retain mates for the upcoming breeding season by enhancing the plumage (Leitão & Mota, 2015; Zampiga, Hoi, & Pilastro, 2004). Use of rock shade also allowed birds to maintain levels of preening even at high T_{air} and appeared to reduce their evaporative cooling requirements (i.e. panting; see below).

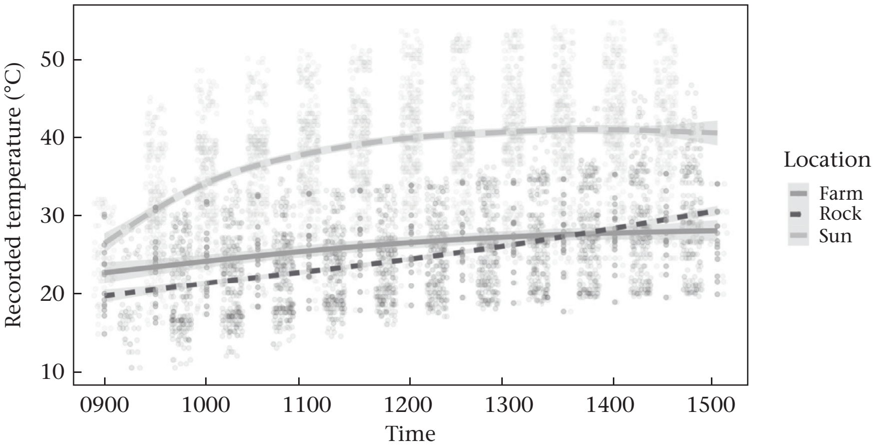

Figure 4. Temperature (°C) recorded by the weather station (farm) and by black bulbs placed in full sun (sun) or full shade (rock) from 0900 to 1500 hours SAST ($N = 18$ days) from November, 2015 to January 2016 at Blue Hill Nature Reserve, Western Cape, South Africa. Data points have been rounded for clearer visualization (jitter set to $\alpha = 0.1$); model fit is a generalized additive model with shaded 95% confidence intervals.

Rockjumpers began panting at T_{air} as low as 20.8 °C when in the sun, which is very low compared to studies on other Southern African passerines, in which birds generally began panting at temperatures above 25 °C (du Plessis et al., 2012; Pattinson & Smit, 2017; Smit et al., 2013; Smit et al., 2016). However, the previous studies were all on arid zone birds, and panting may occur at lower temperatures for birds in cooler environments; panting has been demonstrated at similarly low T_{air} in other alpine (albeit nonpasserine) birds such as white-tailed ptarmigan, *Lagopus leucura* (Johnson, 1968). Rockjumpers were rarely recorded panting when in rock shade, even on hot days (Fig. 3).

Whereas the probability of an adult rockjumper panting at any given T_{air} (up to 35.3 °C) was never greater than 33.33% during our study, concurrently observed juvenile rockjumpers panted whenever T_{air} was above 28.1 °C ($N = 16$ observations of four individuals; Ostwald, Smit, Lee & Cunningham, n.d.). Recent studies on physiological responses to heat in rockjumpers found that despite adults showing no obvious physiological stress at high temperatures (Oswald, Lee, & Smit, 2018b), juveniles may face higher overall water and energy demands than adults due to increased rates of both metabolism and evaporative water loss (Oswald et al., 2018a). Additionally, breeding rockjumpers were significantly more likely to pant than nonbreeding birds (inset Fig. 3), even more so in sun than rock shade, possibly due to changes in metabolism or increased intensity of activity when breeding, which can carry high energetic demands resulting in increased metabolic rates and thus increased requirement for evaporative cooling (Weathers & Sullivan, 1993; Zhang, King, Harmon, Eyster, & Swanson, 2015).

Conclusions

Our results show that rockjumpers use cooler microsites at higher temperatures, resulting in less need to use evaporative water loss to maintain their body temperature, and providing further evidence that microsite use may allow endotherms to conserve water and energy at high temperatures (Williams et al., 1995; Williams & Tieleman, 2005; Xie et al., 2017). While we were unable to directly link the observed behavioural changes to changes in fitness, other studies showing behavioural changes at high temperatures document downstream costs of these in terms of reduced provisioning behaviour, chick growth and adult mass maintenance (Cunningham, Martin, Hojem, & Hockey, 2013; du Plessis et al., 2012). As birds with restricted alpine breeding distributions are likely to be more negatively impacted by climate change than other species (Scridel et al., 2018), the impact of behavioural thermoregulatory responses on overall fitness in range-restricted species with shrinking habitats remains an important avenue for further study.

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Supplementary data

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Appendix

Table A1
Competing model summary table for top models (Δ2 AICc; $N = 6$) explaining activity

Model	*df*	logLik	AICc	ΔAICc	Weight
Activity ~ **microsite*breeding** + T_{air} + **time**	8	-279.098	574.3		0.282
Activity ~ **microsite*breeding** + **time**	7	-280.468	575.0	0.72	0.197
Activity ~ **microsite*breeding** + T_{air} + **time** + microsite*sex	10	-277.636	575.4	1.11	0.162
Activity ~ **microsite** + **breeding** + T_{air} + **time**	7	-280.798	575.7	1.39	0.141
Activity ~ **microsite** + **breeding** + **time**	6	-282.025	576.1	1.82	0.113
Activity ~ **microsite*breeding** + microsite*T_{air} + **time**	9	-279.085	576.3	1.99	0.104
Activity ~ microsite*breeding + T_{air} + time +sex[1]	9	-279.565	577.2	2.02	

Activity as a function of the interaction between microsite (‘sun’ or ‘rock shade’) and air temperature (T_{air}), the interaction between microsite and breeding stage (‘breeding’ or ‘nonbreeding’), time of day and the interaction of microsite and sex (‘male’ or ‘female’). Significant predictors ($P < 0.05$) are in bold.

[1] Next top model > 2 AICc added for comparison of model fit.

Table A2
Model coefficient summary table for top models (all models within Δ2 AICc; $N = 6$) explaining activity

Model	Response variable	Estimate	SE	*Z*	Pr (>|z|)
Activity ~ microsite*breeding + T_{air} + time	Intercept	1.38	0.36	3.80	**< 0.001**
	Breeding	-0.64	0.23	-2.80	**< 0.01**
	Sun	4.45	0.39	11.50	**< 0.001**
	T_{air}	-0.23	0.14	-1.64	0.100
	Time	-0.40	0.14	-2.81	**< 0.01**
	Breeding*sun	0.73	0.38	1.91	0.056
Activity ~ microsite*breeding + time	Intercept	1.30	0.36	3.63	**< 0.001**
	Breeding	-0.63	0.23	-2.81	**< 0.01**
	Sun	4.54	0.38	11.86	**< 0.001**
	Time	-0.45	0.14	-3.27	**< 0.01**
	Breeding*sun	0.69	0.38	1.83	0.068
Activity ~ microsite*breeding + T_{air} + time + microsite*sex	Intercept	1.36	0.37	3.72	**< 0.001**
	Breeding	-0.64	0.23	-2.81	**< 0.001**
	Sun	4.85	0.56	8.72	**< 0.001**
	T_{air}	-0.24	0.14	-1.70	0.089
	Time	-0.40	0.14	-2.77	**< 0.01**
	Female	-0.07	0.15	-0.45	0.652
	Breeding*sun	0.78	0.38	2.05	**0.043**
	Sun*sex	0.81	0.55	1.48	0.139
Activity ~ microsite + breeding + T_{air} + time	Intercept	1.36	0.37	3.71	**< 0.001**
	Breeding	-0.53	0.22	-2.36	**< 0.05**
	Sun	4.65	0.39	11.98	**< 0.001**
	T_{air}	-0.22	0.14	-1.56	0.120
	Time	-0.39	0.14	-2.76	**< 0.01**
Activity ~ microsite + breeding time	Intercept	1.30	0.36	3.55	**< 0.001**
	Breeding	-0.53	0.22	-2.40	**0.016**
	Sun	4.73	0.37	12.24	**< 0.001**
	Time	-0.44	0.14	-3.20	**< 0.01**
Activity ~ microsite*breeding + microsite*T_{air} + time	Intercept	1.37	0.36	3.78	**< 0.001**
	Breeding	-0.64	0.23	-2.80	**< 0.01**
	Sun	4.46	0.41	11.09	**< 0.001**
	T_{air}	-0.22	0.15	-1.54	0.125
	Time	-0.40	0.14	-2.80	**< 0.01**
	Breeding*sun	0.73	0.38	1.92	0.055
	T_{air}*sun	-0.07	0.44	-0.16	0.871

Activity as a function of the interaction between microsite (‘sun’ or ‘rock shade’) and air temperature (T_{air}), the interaction between microsite and breeding stage (‘breeding’ or ‘nonbreeding’), time of day and the interaction of microsite and sex (‘male’ or ‘female’). Significant predictors ($P < 0.05$) are in bold.

Table A3
Competing model summary table for top models (Δ2 AICc; $N = 2$) explaining foraging

Model	*df*	logLik	AICc	ΔAICc	Weight
Foraging ~ **microsite*breeding** + **microsite*T_{air}** + **microsite*sex**	10	-1335.010	2690.1		0.659
Foraging ~ **microsite*breeding** + **microsite*T_{air}** + time + **microsite*sex**	11	-1334.659	2691.4	1.32	0.341
Foraging ~ microsite*breeding + T_{air} sex[1]	9	-1337.211	2692.5	2.38	

Foraging as a function of the interaction between microsite (‘sun’ or ‘rock shade’) and air temperature (T_{air}), the interaction between microsite and breeding stage (‘breeding’ or ‘nonbreeding’), time of day and the interaction of microsite and sex (‘male’ or ‘female’). Significant predictors ($P < 0.05$) are in bold.

[1] Next top model > 2 AICc added for comparison of model fit.

Table A4
Model coefficient summary table for top models (all models within Δ2 AICc; $N = 2$) explaining foraging

Model	Response variable	Estimate	SE	*Z*	Pr (>|z|)
Foraging ~ microsite*breeding + microsite*T_{air} + microsite*sex	Intercept	-0.18	0.12	1.53	0.127
	Breeding	-0.24	0.09	-2.71	**< 0.01**
	Sun	0.37	0.06	5.65	**< 0.001**
	T_{air}	-0.17	0.06	-2.76	**< 0.01**
	Female	0.14	0.08	1.83	0.068
	Breeding*sun	0.14	0.06	2.33	**0.020**
	T_{air}*sun	0.13	0.06	2.08	**0.037**
	T_{air}*female	0.21	0.06	3.61	**< 0.001**
Foraging ~ microsite*breeding + microsite*T_{air} + time + microsite*sex	Intercept	0.17	0.12	1.47	0.143
	Breeding	-0.24	0.09	-2.71	**< 0.01**
	Sun	0.37	0.06	5.71	**< 0.001**
	T_{air}	-0.18	0.06	-2.87	**< 0.01**
	Time	0.04	0.05	0.84	0.402
	Female	0.14	0.08	1.77	0.077
	Breeding*sun	0.14	0.06	2.32	**0.020**
	T_{air}*sun	0.12	0.06	2.04	**0.041**
	T_{air}*female	0.21	0.06	3.65	**< 0.001**

Foraging as a function of the interaction between microsite (‘sun’ or ‘rock shade’) and air temperature (T_{air}), the interaction between microsite and breeding stage (‘breeding’ or ‘nonbreeding’), time of day and the interaction of microsite and sex (‘male’ or ‘female’). Significant predictors ($P < 0.05$) are in bold.

Table A5
Competing model summary table for top models (Δ2 AICc; $N = 5$) explaining preening

Model	*df*	logLik	AICc	ΔAICc	Weight
Preening ~ **breeding** + **microsite*T_{air}** + **sex** + time	9	-651.06	1320.2		0.308
Preening ~ **breeding** + **microsite*T_{air}** + microsite*sex + time	10	-650.14	1320.4	0.17	0.283
Preening ~ **breeding** + **microsite*T_{air}** + microsite***sex**	8	-652.71	1321.5	1.28	0.162
Preening ~ **breeding** + **microsite*T_{air}** + **sex** + time	9	-651.91	1321.9	1.70	0.132
Preening ~ microsite***breeding** + **microsite*T_{air}** + **sex** + time	10	-651.03	1322.2	1.96	0.116
Preening ~ microsite*breeding + microsite*T_{air} + microsite*sex + time[1]	11	-650.172	1322.5	2.18	

Preening as a function of the interaction between microsite (‘sun’ or ‘rock shade’) and air temperature (T_{air}), the interaction between microsite and breeding stage (‘breeding’ or ‘nonbreeding’), time of day and the interaction of microsite and sex (‘male’ or ‘female’). Significant predictors ($P < 0.05$) are in bold.

[1] Next top model > 2 AICc added for comparison of model fit.

Table A6
Model coefficient summary table for top models (all models within Δ2 AICc; $N = 5$) explaining preening

Model	Response variable	Estimate	SE	*Z*	Pr (>|z|)
Preening ~ breeding + microsite*T_{air} + sex + time	Intercept	-2.63	0.24	-10.84	**< 0.001**
	breeding	-0.42	0.15	-2.89	**< 0.01**
	sun	-0.10	0.11	-0.92	0.360
	T_{air}	-0.03	0.10	-0.30	0.765
	time	-0.14	0.08	-1.80	0.072
	female	-0.24	0.12	-1.97	**0.048**
	T_{air}*sun	-0.30	0.10	-2.96	**< 0.01**
Preening ~ breeding + microsite*T_{air} + microsite*sex + time	Intercept	-2.62	0.24	-10.80	**< 0.001**
	breeding	-0.41	0.15	-2.84	**< 0.01**
	sun	-0.13	0.11	-1.17	0.243
	T_{air}	-0.03	0.10	-0.30	0.766
	time	-0.15	0.08	-1.89	0.059
	female	-0.18	0.13	-1.41	0.160
	T_{air}*sun	-0.29	0.10	-2.97	**< 0.01**
	female*sun	-0.12	0.09	-1.38	0.168
Preening ~ breeding + microsite*T_{air} + microsite*sex	Intercept	-2.65	0.25	-10.81	**< 0.001**
	breeding	-0.42	0.14	-2.91	**< 0.01**
	sun	-0.08	0.11	-0.78	0.439
	T_{air}	-0.06	0.10	-0.56	0.578
	female	-0.26	0.13	-2.06	**0.040**
	T_{air}*sun	-0.30	0.10	-3.02	**< 0.01**
Preening ~ breeding + microsite*T_{air} + sex + time	Intercept	-2.65	0.25	-10.80	**< 0.001**
	breeding	-0.42	0.15	-2.87	**< 0.01**
	sun	-0.11	0.11	-0.99	0.322
	T_{air}	-0.06	0.10	-0.56	0.574
	female	-0.21	0.14	-1.54	0.123
	T_{air}*sun	-0.30	0.10	-3.03	**< 0.01**
	female*sun	-0.12	0.09	-1.28	0.199
Preening ~ microsite*breeding + microsite*T_{air} + time	Intercept	-2.64	0.24	-10.85	**< 0.001**
	breeding	-0.43	0.15	-2.84	**< 0.01**
	sun	-0.09	0.12	-0.72	0.471
	T_{air}	-0.03	0.10	-0.30	0.762
	time	-0.14	0.08	-1.82	0.069
	female	-0.24	0.12	-1.98	**0.048**
	female*sun	0.03	0.11	0.25	0.799
	T_{air}*sun	-0.29	0.10	-2.94	**< 0.01**

Preening as a function of the interaction between microsite (‘sun’ or ‘rock shade’) and air temperature (T_{air}), the interaction between microsite and breeding stage (‘breeding’ or ‘nonbreeding’), time of day and the interaction of microsite and sex (‘male’ or ‘female’). Significant predictors ($P < 0.05$) are in bold.

Table A7
Competing model summary table for top model (Δ2 AICc; $N = 2$) explaining panting, with next best model for comparison

Model	*df*	logLik	AICc	AICc	Weight
Panting ~ **breeding** + **microsite*T_{air}**	7	-166.366	346.8		0.717
Panting ~ **breeding** + **microsite*T_{air}** + time	8	-166.317	348.8	1.86	0.283
Panting ~ breeding + microsite*T_{air} + sex[1]	8	-166.356	348.9	2.01	

Panting as a function of the interaction between microsite (‘sun’ or ‘rock shade’) and air temperature (T_{air}), the interaction between microsite and breeding stage (‘breeding’ or ‘nonbreeding’), time of day and the interaction of microsite and sex (‘male’ or ‘female’). Significant predictors ($P < 0.05$) are in bold.

[1] Next top model > 2 AICc added for comparison of model fit.

Table A8
Model coefficient summary table for top model (all models within Δ2 AICc; $N = 2$) explaining panting

Model	Response variable	Estimate	SE	*Z*	Pr (>|z|)
Panting ~ **breeding** + **microsite*T_{air}**	Intercept	-4.60	0.75	-6.16	**< 0.001**
	breeding	1.14	0.34	3.35	**< 0.001**
	sun	0.21	0.27	0.76	0.448
	T_{air}	0.82	0.36	2.28	**0.023**
	T_{air}*sun	0.88	0.33	2.64	**< 0.01**
Panting ~ **breeding** + **microsite*T_{air}** + time	Intercept	-4.58	0.74	-6.32	**< 0.001**
	breeding	1.13	0.34	3.31	**< 0.001**
	sun	0.21	0.27	0.78	0.438
	T_{air}	0.78	0.38	2.08	**0.038**
	T_{air}*sun	0.87	0.33	2.63	**< 0.01**
	time	0.07	0.23	0.32	0.753

Panting as a function of the interaction between microsite (‘sun’ or ‘rock shade’) and air temperature (T_{air}), the interaction between microsite and breeding stage (‘breeding’ or ‘nonbreeding’), time of day and the interaction of microsite and sex (‘male’ or ‘female’). Significant predictors ($P < 0.05$) are in bold.