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Seasonal behavioral responses of an arid-zone passerine in a hot environment

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ABSTRACT

Many arid-zone animals have to forage under extremely hot conditions to maintain water and energy balance. The effect of high air temperatures (T_{air}) on the behavioral patterns of small endothermic animals—characterized by their high energy and water demands—will provide a valuable framework for understanding species vulnerability to climate warming. We determined the seasonal behavioral responses to changes in T_{air} in a ~ 10-g arid-zone passerine, the rufous-eared warbler (*Malcorus pectoralis*), in the Karoo semi-desert, South Africa. Rufous-eared warblers showed significant temperature-dependence in their behavior in summer, but not in winter. During summer, the warblers frequently experienced T_{air} exceeding 40 °C in the shade. For all observations < 26 °C compared to > 36 °C, the warblers showed reductions in preening (40% decrease), foraging effort (56% decrease), and foraging success (15% decrease), as well as a significant increase in time spent engaged in evaporative cooling behavior. Moreover, as T_{air} increased the warblers shifted increasingly off the ground and out of the full sun, into microsites in the shade (131% increase) and in shrubs (23% increase). In this regard, behavior varied seasonally, with the time spent in the shade 23% higher, and foraging effort 28% higher, in summer compared to winter across a range of moderate T_{air} (15–30 °C). Our findings emphasize the link between behavior and temperature in small birds inhabiting hot, arid environments, as well as the importance of understanding these responses for predicting biologically meaningful responses (and hence, vulnerability) of arid-zone avian communities to climactic shifts.

1. Introduction

Differences in behavior can be expressed at numerous spatial and temporal scales – from large seasonal changes such as migration, to small, rapid changes within seconds of each other during an organism's active phase [1,2]. One of the foremost drivers of variation in behavioral phenotypes is climate, which exerts a strong influence on resource availability and thermoregulatory demands [3–5].

This relationship between climate and behavior is vital for energy and water balance, from the scale of daily survival, to lifetime reproductive output [6,7]. This is perhaps most pronounced in arid-zones, where animals face high temperatures and, generally, a severe lack of water [4,8]. The primary challenge in these habitats is centered on heat flux [7,9,10]; animals have to acquire enough food and water to survive and reproduce, whilst regulating their heat gain and loss [11–13]. The role that behavior plays in coping with this challenge is often demonstrated in ectotherms, in which thermoregulation is primarily achieved through behavioral adjustments [14]. In contrast, endotherms generally regulate heat flux largely through physiological responses [15]. However, for endotherms in arid-zones, behavior can also greatly affect the physiological costs of regulating heat flux [10].

Birds are model endotherms to demonstrate this, as behavior is a critical and conspicuous component of their thermoregulation; partly facilitating their occupation of hot, arid-zones [16,17]. Moreover, unlike many small species of mammal, birds are largely diurnal and generally do not make use of burrows or other similar thermal refuges during the heat of the day ([18,19], but see also [20]). They are therefore subjected to high environmental temperatures during their active phase, creating trade-offs between activity, heat load, and hydration [15,21].

In small birds, the consequences of these trade-offs are severe, because of their low thermal inertia, high body temperature (T_b), limited capacity for energy and water storage, and high rates of mass-specific water loss [3,22]. Moreover, when air temperature (T_{air}) exceeds T_b, a crucial method for birds to dissipate heat and avoid lethal hyperthermia is evaporative water loss (EWL) [12,23,24]. This puts small birds at risk of dehydration at high T_{air}[9], which has important implications for foraging decisions. Foraging creates metabolic heat, and often requires

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entering the hottest microsites in the landscape [15]. Therefore, at high T_{air} birds can either reduce foraging effort and limit activity to the shade in exchange for low risk of lethal hyperthermia, or maintain foraging effort in hot microsites, incurring a high risk of lethal hyperthermia and high water demands [20]. Small, arid-zone birds that employ the latter strategy are therefore naturally risk-prone, potentially suffering long-term survival and reproductive consequences as a result [16,25]. Indeed, studies on Kalahari Desert birds of southern Africa have shown that high T_{air} cause reduced foraging efficiency, and ultimately cause mass loss [25] or reduced provisioning rates to young [16].

Given the potential fitness consequences of behavioral trade-offs at high temperatures, it has become important to identify how birds have adapted to hot, arid environments, and how they are likely to respond to climate warming [19,26]. We investigated the seasonal behavior patterns of a wild population of rufous-eared warblers (*Malcorus pectoralis,* Order: Passeriformes, Family: Cisticolidae; hereafter warblers); this 9-g arid-zone passerine is semi-terrestrial, typically foraging and breeding close to the ground, and may therefore be exposed to extreme changes in operative temperatures (T_e, defined as the integrated thermal environment experienced by an animal [16]). We predicted that seasonal changes in temperature would drive behavioral changes, and we expected that higher temperatures would increase the thermoregulatory costs associated with foraging, particularly at or near the ground where T_e are highest. Specifically, we hypothesized 1) that the warblers would show greater temperature-dependence in their behavioral patterns during summer compared to winter; alternatively we hypothesized that a lack of seasonal change in the temperature-dependence of their behavior may indicate improved heat tolerance during summer in the warblers [2,27]. We further predicted that seasonal variation in absolute foraging efforts would be related to seasonal water and/or energy demands in the warblers, and therefore 2) hypothesized that higher absolute foraging efforts in summer (i.e. more risk prone to heat stress) would indicate that the warblers were more likely to experience deficits in water and/or energy balance during the hot summer season compared to cooler winter months.

2. Methods and materials

2.1. Study species

The rufous-eared warbler (*Malcorus pectoralis*, Order: Passeriformes, Family: Cisticolidae) is the only species in the genus *Malcorus* and is endemic to Southern Africa. Individuals will maintain territories year-round, and pairs or small family groups will remain resident in an area throughout the year [28]. They are primarily insectivorous, feeding mostly on small beetles, but they do opportunistically consume small fruits and succulent plant material [29]. They forage close to the ground, energetically searching for food on the ground (often fully exposed to sun) and within or on top of small shrubs (< 1 m) within their Karoo and Succulent Karoo habitat.

2.2. Study site

The study site was a farm, Hopedale, which is situated west of the town Steytlerville (33°20′ S, 24°20′ E; altitude ~480 meters above - sea level). The landscape was dominated by ~1 m tall non-succulent shrubs, *Lycium cinereum*, interspersed among bare ground and shorter shrubs, *Pentzia incana*, *Ruschia* spp., and *Leipoldtia schultzei*. *Pappea capensis* trees (~ 2 m tall) occurred intermittently throughout the landscape (Appendix 1). Between 1900 and 2000, Steytlerville had an annual rainfall of ~240 mm, with no significant pattern of change [30]. Long-term temperature data are not available for Steytlerville. However, temperature patterns in the rest of South Africa have shown annual increases in both average and maximum temperatures to be almost ubiquitous across the country [31,32]. Data for this study was collected between 10 June and 10 August 2015 (Austral winter), and between 2 January and 2 March 2016 (Austral summer).

2.3. Temperature measurements

A custom-made weather station was placed 2 m off the ground at the field site (GPS: 33°22′41.0″ S, 24°11′21.1″ E) to record air temperature (T_{air}). This weather station consisted of a solar radiation screen, made of four layers of bowl-shaped, white, Perspex slats stacked horizontally with 3 cm gaps between them. These had a 5 cm diameter Perspex tube running vertically through their center, with an iButton™ (Model DS 1922 L ± 0.1 °C, Fairbridge Technologies, Sandton, South Africa) suspended in the center. The Perspex tube had 0.5 cm diameter holes at regular intervals in between the layers of slats to allow air flow.

To measure temperature variation at the microsite level within the landscape we secured seven black bulb thermometers on and inside a *Lycium cinereum* shrub. The black bulbs were constructed from two hemispheres of copper with a diameter of 30 mm and thickness of 0.9 mm. One iButton (model DS1921G-F5 ± 0.1 °C) was secured to an iButton retainer (model DS9098P-TRW +) that was placed inside the two hemispheres, soldered together as a sphere. The copper spheres were painted matt black [33]. A *L. cinereum* shrub was chosen as it was both dominant in the landscape, and frequently used by the warblers throughout the day. Black bulbs were secured (using copper wire) in triplicate 1 cm and ~20 cm off the ground, north, south, and in the middle of the shrub, respectively, and the last bulb was secured on top of the shrub ~1 m off the ground (Appendix 1). Black bulbs measure three of the four factors that may impact an animal's thermal balance; namely radiant heat exchange, dry-bulb temperature, and convective heat exchange [34]. Black bulbs therefore give a better approximation of the thermal environment an animal might experience than would be possible from only measuring T_{air}[16,35]. However, compared to the various methods of measuring operative temperature (T_e), black bulbs face several issues (see [33,36,37] for discussion). As a result, our use of black bulbs was not to measure T_e. Rather, we used black bulb temperature (T_{bb}) as an indication of the variation in environmental temperature among different microsites and between seasons [38–40]. Both the black bulbs and the weather station recorded temperatures every 10 min throughout the day.

2.4. Behavioral observations

In total, 29 and 35 territories (typically roughly 150 m^2 in size) were identified in winter and summer, respectively. The center of each was recorded using a GPS (Etrex H, Garmin, Taiwan). To conduct focal observations, a territory was searched on foot to find the birds either visually or by call. One bird in the pair/family group would be randomly selected for the focal observation. The observer was usually 5–15 m away from the bird, with a maximum distance of ~25 m. Within this range the observer was confident the behavior of the warblers could be accurately determined. No data was recorded if the bird was obviously affected by the observer's presence (i.e., began alarm calling at, or was flushed by the observer) during observations.

Focal observations lasted up to 20 min. Every 1–2 min (depending on how easily observable the bird was) of the 20 min focal a note was logged, including various aspects of the bird's microsite and behavior. Microsite characteristics included exposure to the sun (i.e. full sun or shade), and position relative to vegetation (i.e. open ground, or edge, within or on top of shrubs). The relative wind speed was also recorded. This was a subjective estimate of wind speed on a scale with four levels: none, slight, moderate, and strong. Although wind was not objectively measured by a device, all estimates were made by the same observer. This made us confident that the relative differences in wind speed were consistent throughout each season, and therefore useful for analyses including relative wind speed as a factor.

We recorded the dominant behavior/s the bird engaged in during

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