

Elevated temperatures drive fine-scale patterns of habitat use in a savanna bird community[§]

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Many animals use thermally buffered microhabitats, e.g. patches of shade within trees, to avoid temperature extremes. These ‘thermal refugia’ may mediate the impact of climate change on animals. Predicting how species and communities will respond to rising temperatures therefore requires an understanding of the availability of these refugia and how animals use them. We investigated patterns of tree use by birds in the southern Kalahari across different times of day and days of varying maximum air temperature. On ‘hot’ days (>35 °C) birds showed increased preference for trees that provided the greatest density of shade (*Boscia albitrunca*), and this effect was particularly pronounced at the hottest times of day. Comparisons of focal bird species with differing foraging niches revealed interspecific differences in tree use. Two arboreally foraging species showed a similar preference for *B. albitrunca* on both ‘cool’ and ‘hot’ days. In contrast, two ground-foraging species increased their use of *B. albitrunca* trees on hot days, with one species (Scaly-feathered Finch *Sporopipes squamifrons*) changing its behaviour from avoiding to preferring this tree. We discuss the role of *B. albitrunca* trees as thermal refugia and the implications of temperature-driven changes in tree use in the context of rising temperatures due to climate change.

Keywords: Black-chested Prinia, Chestnut-vented Tit-babbler, climate change, heatwave, Kalahari Scrub-Robin, microclimate, microhabitat, microsite, Scaly-feathered Finch, thermal landscape, thermoregulation

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Introduction

As rates of global environmental change accelerate, there is growing interest in understanding the role of behaviour in determining species’ responses to novel environments (Tuomainen and Candolin 2010; Huey et al. 2012; Sih 2013; Wong and Candolin 2014). Rising temperatures due to climate change can present new thermoregulatory challenges, which may be particularly acute for animals living in already hot and arid environments (McKechnie et al. 2012). Many animals use thermally buffered microsites to avoid temperature extremes (e.g. Wolf et al. 1996; Hetem et al. 2012; Briscoe et al. 2014) and, as a result, may be able to reduce their exposure to the direct impacts of rising temperatures (Williams et al. 2008; Kearney et al. 2009; Scheffers et al. 2013). Understanding the links between climatic variation at the macro- and micro-scales and the ways animals use the resulting thermal landscapes will inform predictions of the biological impact of climate change (Sears et al. 2011; Suggitt et al. 2011; Potter et al. 2013).

The thermoregulatory demands an animal experiences when in a particular location within a landscape, depend on

the combined influence of multiple microclimatic variables, such as the air temperature, solar radiation or wind (Porter and Gates 1969; Bakken 1976; Wolf and Walsberg 1996). Physical landscape features, such as trees, can drive variation in these microclimatic variables, for example by providing shade from the sun or shelter from the wind. The way in which animals use the resulting microclimates may determine the degree to which they might be exposed to temperature extremes (Porter et al. 2002; Huey et al. 2012; Sears and Angilletta 2015).

Animals occupying different habitats and ecological niches might be expected to have differing behavioural responses to macro-scale changes in climatic conditions. For animals living in thermally homogenous landscapes, such as within dense forests where closed canopies generate relatively uniform shade, there may be little thermal benefit from moving to alternative microsites (Huey et al. 2009, 2012; Kearney et al. 2009). In a similar manner, for animals living in thermally heterogeneous environments, but carrying out key behaviours such as foraging or courtship in microsites buffered from varying macro-scale conditions, there may

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be little benefit from behavioural adjustments. The greatest shifts in patterns of microsite use in response to elevated temperatures might be expected to occur among animals living in spatially heterogeneous thermal landscapes that use poorly buffered microsites for key behaviours, such as animals that live in savanna landscapes and forage optimally on the ground in open areas.

Birds may be particularly vulnerable to rising temperatures due to climate change (Wolf 2000; McKechnie and Wolf 2010). The majority of species are diurnal and do not use subterranean burrows as thermal refuges, thus they must directly confront high environmental temperatures during the day (Wolf et al. 1996). The small body size of many species confers low thermal inertia, meaning that body temperatures can rise rapidly when exposed to high environmental temperatures. Small body size also limits capacity to store vital resources such as water and water balance may need to be maintained over periods of minutes to hours (McKechnie and Wolf 2010). In such situations, fine-scale behavioural adjustments, for example shifting location to exploit variation in thermal landscapes, could be a critical component of thermoregulatory strategies (Wolf and Walsberg 1996).

In this study we investigated how birds adjusted patterns of microsite use in response to elevated temperatures in the hot arid savanna landscape of the southern Kalahari Desert. This region has recorded strong warming trends since the early 1960s (New et al. 2006; Kruger and Sekele 2012) raising concerns about the impact of climate change on bird communities (Cunningham et al. 2013a). The vegetation in this region is characterised by wide expanses of open ground and grass interspersed with shrubs and trees. Thermal landscapes in such environments are highly heterogeneous with large trees providing islands of shade, within a matrix of exposed ground. These patches of shade are likely a key resource enabling birds to keep body temperatures below lethal limits and reducing the physiological costs of heat dissipation (Wolf and Walsberg 1996). Given that structural differences between tree species affect the amount of shade they provide (Kotzen 2003), we hypothesised that some tree species may be preferred over others as thermal refuges. We predicted that at higher temperatures, birds at our study site would show a greater preference for species of tree that provide the greatest degree of shade. We further hypothesised that the degree to which different bird species adjusted their patterns of behaviour in response to increasing temperature would depend on the ecological niche they occupy. We therefore predicted that species that already forage in relatively exposed locations would show a greater adjustment in their behaviour with

temperature. We compared the degree of shade provided by the two most common tree species at the study site – *Vachellia erioloba* (*Acacia erioloba*; Camelthorn) and *Boscia albitrunca* (Shepherd's tree) – to allow us to predict which tree species should be preferred with increasing temperature. We tested our prediction using direct observations of patterns of tree use by all birds at the study site and subsequently explored interspecific differences between four passerines of similar size, but differing diet and mode of foraging.

Methods

Study site

The study was conducted within semi-arid savanna habitat in the Northern Cape province of South Africa (Tswalu Kalahari Reserve, 27°13' S, 22°22' E). Vegetation at the study site consisted of scattered trees dominated by *Vachellia erioloba* and *Boscia albitrunca*, and to a lesser extent *Terminalia sericea*, *Vachellia haemotoxylon* (*Acacia haemotoxylon*) and *Sengalia mellifera* (*Acacia mellifera*), and the shrubs *Grewia flava* and *Searsia tenuinervis* (*Rhus tenuinervis*) over a sparse grass layer. Trees were generally small, typically not exceeding 5 m in height.

The study was carried out over an austral summer from November 2010 to February 2011. Maximum daily air temperature during the study period ranged from 21.6 °C to 38.7 °C. Mean daily rainfall was 4 ± 9.96 mm d⁻¹. Rain fell sporadically during large thunderstorms separated by dry periods. Periods without rain lasted for up to 12 ± 3 d without rain (mean = 3 d).

Study species

Observational data were collected for all bird species. A full list of all bird species recorded during surveys and sample sizes for each species is provided in Supplementary Table S1. We assessed the effects of temperature at both community-wide and species-specific levels, using four target species: Chestnut-vented Tit-Babbler *Parisoma subcaeruelum*, Black-chested Prinia *Prinia flavicans*, Kalahari Scrub-Robin *Erythropygia paeana* and Scaly-feathered Finch *Sporopipes squamifrons*. These species were selected for the following reasons: (1) they were relatively common, facilitating the collection of adequate sample sizes for independent analyses; (2) they differ in several key aspects, notably their principle modes of foraging behaviour and diets; and (3) they have physical similarities and taxonomic affinities, all being of a similar size and belonging to the avian order Passeriformes (Table 1).

Large trees (defined as greater than or equal to 3.0 m in height) were dominated by two species, *V. erioloba* and

Table 1: A comparison of key physical and ecological traits of the four passerine bird species considered. Information was extracted from species accounts in Hockey et al. (2005)

Trait	Chestnut-vented Tit-Babbler <i>Parisoma subcaeruelum</i>	Black-chested Prinia <i>Prinia flavicans</i>	Kalahari Scrub-Robin <i>Erythropygia paeana</i>	Scaly-feathered finch <i>Sporopipes squamifrons</i>
Mass (g)	15.7	8.9	19.7	11.1
Typical foraging location	Trees	Trees and shrubs	Ground	Ground
Typical dietary components	Arthropods	Arthropods	Arthropods	Seeds, arthropods

B. albitrunca, with other species present in much lower numbers (Table 2). As Ivlev's electivity index performs poorly on small sample sizes, inflating type I errors (Lechowicz 1982), large trees of all other species were treated as a single category.

Shade density of trees

Shade density provided by *V. erioloba* and *B. albitrunca* was quantified using an LP-80 AccuPAR ceptometer (Decagon Devices, Pullman, WA, USA). The ceptometer is a linear sensor that includes 80 photodiodes, 1 cm apart, and measures radiation in the photosynthetically active radiation waveband (400–700 nm). Average levels of radiation penetrating the canopy were compared against background levels to estimate the leaf area index (LAI). The LAI is typically defined as the total area of leaf tissue per unit ground surface area (Bréda 2003). As we were interested in understanding levels of light penetration rather than leaf area *per se*, we made no adjustments for light intercepted by stems and branches. As a result the index we used is more accurately described as the surface area index (SAI; Bréda 2003) The SAI was measured at 0.5 m intervals between 0.5 m and 2.0 m measured vertically from the top of the tree. Five sensor readings were taken at each height within the canopy totalling 200 point measurements (5 × 80) at each height. The location of each sensor reading was determined haphazardly ensuring that no part of the sensor extended beyond the limit of the canopy and that the same locations were not measured multiple times. Measurements were made on 52 *V. erioloba* and 32 *B. albitrunca* trees ≥3.0 m in height within observation plots (see Behavioural observations).

Temperature data

Air temperature was measured using an on-site weather station (VantagePro 2, Davis Instruments, Hayward, CA, USA) that recorded data at ten-minute intervals throughout the study period. We classified days as 'cool' or 'hot' based on whether maximum daily air temperature (T_{max}) on the day exceeded 35 °C. We used 35 °C as our cut-off as numerous studies of birds have identified this as a threshold that has significance for patterns of behaviour (Ricklefs and Hainsworth 1968; Austin and Miller 1982; Luck 2001; du Plessis et al. 2012; Cunningham et al. 2013b).

Behavioural observations

We identified 12 longitudinal plots within a 12 km by 1.5 km area, which lay on a flat plain covered with arid savanna vegetation, positioned between the rocky Korannaberg

Table 2: Size (height and width of crown; m) of trees in each tree category. The category 'other' trees is made up of *Terminalia sericea* (71 individuals), *Senegalia mellifera* (61), *Vachellia haemotoxylon* (52), *Grewia flava* (38) and *Searsia tenuinervis* (12)

Tree species	n	Height		Width	
		Mean	SD	Mean	SD
<i>Vachellia erioloba</i>	316	3.55	0.55	3.31	1.19
<i>Boscia albitrunca</i>	248	3.72	0.66	3.88	1.29
Other species	234	4.28	1.19	3.26	1.21

mountains and a rolling dune field on Tswalu Kalahari Reserve. Each plot measured 100 m × 800 m and was separated by at least 500 m from the nearest neighbouring plot. Behavioural observations were made during repeated surveys of each plot. Each survey commenced from the centre of the narrow side of each plot and involved walking slowly through the plot from one end to the other looking for birds. Repeat surveys of each plot always started and finished from the same locations. Auditory and especially visual cues were used to locate birds. When a bird was sighted, it was identified and localised at the instant of first detection to plant species and height (to nearest 0.5 m). Birds located on the ground were recorded but this information was not included in analyses. When multiple individuals of the same bird species were observed in different trees, all tree species were recorded as independent observations.

During surveys the observer stopped frequently (every 10–50 m depending on tree density) to scan surrounding vegetation, where necessary using 10 × 42 binoculars. Observers moved through the plot at an average speed of c. 9 ms⁻¹ but speeds varied with the density of vegetation and the number of birds observed. Each survey took approximate 90 min. Vegetation (trees or shrubs) in which the presence or absence of birds could not be determined with certainty was slowly approached until the observer was satisfied that all birds had been detected. The observer then returned to the centre of the plot and continued the survey. Through using this approach we aimed to detect all birds present in the plot and therefore minimise bias due to variation in the detectability of different bird species in different tree species. Observations were made by three observers: ROM and two assistants, R Sutcliffe and D Nkosi. All observers had previous experience of ecological field work in the southern Kalahari and were familiar with the birds and vegetation of the area. Prior to the commencement of field work, a week-long training period was undertaken to ensure that all observers could identify all bird and tree species. Inter-observer consistency in visual estimation of tree height was verified through fortnightly (at minimum) group training exercises involving the direct measurement of tree height.

Each plot was repeatedly surveyed at different times of day and on days differing in maximum daily air temperature (T_{max}). Each plot was only surveyed once on any given day to minimise any effects of disturbance on the behaviour of birds in subsequent surveys. Surveys of each plot, for a given time of day, were timed to be evenly spread throughout the study period and were randomised with respect to T_{max} , within the constraints imposed by the weather. Surveys were conducted during three time periods, 'early morning' (07:30–09:00), 'late morning' (10:30–12:00) and 'mid-afternoon' (13:30–15:00). Air temperatures differed between these periods, being coolest during the early morning and hottest during mid-afternoon (Table 1).

Tree availability

Within each longitudinal plot, six evenly spaced points were surveyed for vegetation. At each point, all plants greater than 0.5 m in height within a 50 m radius were recorded. Distances were measured with a laser range finder (Ranger

LRS-500 6 × 23 Monocular; Vortex Optics, Middleton, WI, USA) and heights and widths visually estimated by ROM.

Statistical analysis

Differences in the 'shadiness' of *B. albitrunca* and *V. erioloba* trees were analysed using general linear models fitted with maximum likelihood using the 'glm' function within the R statistical environment (R Core Team 2013). We explored how SAI varied within and between tree species by fitting a series of nested models, which included tree species, distance from the top of tree or canopy edge, and the interaction of these two terms as fixed effects. The fit of these models was evaluated using AIC and we report the effect size of each explanatory variable, confidence interval, Wald statistic and associated *p*-value.

To analyse differences in patterns of tree use by birds between cool and hot days we used two approaches. First, we used chi-square goodness-of-fit tests to evaluate the hypothesis that patterns of tree use by birds were non-random with respect to temperature (cool or hot days). Separate tests were applied to each time of day (early morning, late morning and mid-afternoon) for all bird species combined and then repeated for subsets of these data for each of our four focal species (see Study species) separately. The alternative hypothesis was accepted if the *p*-value was <0.05.

If differences were detected, further investigations were conducted by calculating Ivlev's electivity indices (*E*; Ivlev 1961). Ivlev's electivity index evaluates patterns of use relative to availability within the environment, by applying the following equation:

$$E_i = (r_i - P_i)/(r_i + P_i)$$

where, r_i = proportion of observations of each bird in tree species i , and P_i = proportion of trees available of tree species i within the environment. *E* values range from -1 to 1, with positive values indicating preference and negative values indicating avoidance. In addition, 95% confidence intervals were calculated following Strauss (1979). The hypothesis that a particular tree species was preferred or avoided was accepted if confidence intervals for *E* did not include zero.

For the purposes of interspecific comparisons we calculated *E* for all four focal species during mid-afternoon on hot and cool days.

Results

Tree shadiness

The SAI, a measure of the amount of radiation intercepted by the canopy, showed a marginally non-significant tendency to increase more rapidly with vertical distance from the top of the canopy in *B. albitrunca* compared with *V. erioloba* (est. = 0.25, CI = -0.02 to 0.52, $t = 1.83$, $p = 0.069$, $n = 52$ *V. erioloba* and 32 *B. albitrunca*; Figure 1). When the interaction term (Tree species*Vertical distance) was removed from the model, SAI was greater in *B. albitrunca* than in *V. erioloba* (est._{*b,al*} = 0.29, CI = 0.02 to 0.56, $t = 3.91$, $p < 0.001$), indicating that *B. albitrunca* generally provided a greater level of shade. Overall the degree of shade

increased rapidly with distance from the top of the canopy (est. = 0.94, CI = 0.80 to 1.07, $t = 13.7$, $p < 0.001$).

Patterns of tree use by birds

For observations of all bird species combined, patterns of tree use differed between hot and cool days during all three periods of the day investigated (Table 3, Figure 2). The degree of difference was smallest during the early morning period when temperatures were lowest (Table 4) and greatest during the mid-afternoon period when temperatures were highest.

These findings were supported by examination of Ivlev's electivity indices (Figure 2). During the early morning period, on cool days, the bird community as a whole showed no strong preferences for, or aversions to, any tree species. Under these conditions, birds used trees in proportion to their availability. However, on hot days when maximum temperatures were 2.7 °C warmer than on cool days during the early morning period (Table 3), birds showed a small preference for *B. albitrunca* trees ($E = 0.13$, CI = 0.019 to 0.24) and corresponding aversion to *V. erioloba* trees ($E = -0.16$, CI = -0.24 to -0.09). No preference or aversion to other trees was evident during the early morning. During the late morning, on cool days, there was a small, but significant, preference for *B. albitrunca* trees ($E = 0.09$, CI = 0.03 to 0.16) and aversion to other trees ($E = -0.09$, CI = -0.14 to -0.04) with no preference or aversion to *V. erioloba* trees. On hot days, when maximum temperatures during the late morning were 4.0 °C warmer than on cool days (Table 3), birds showed a stronger

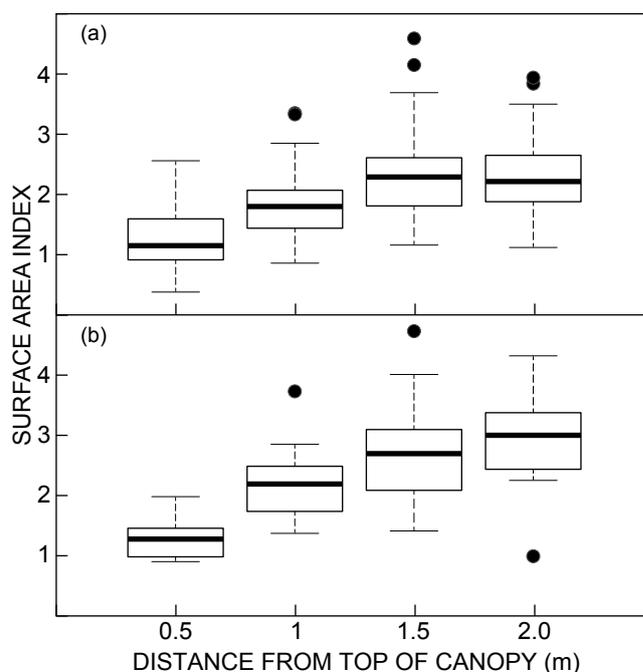


Figure 1: 'Shadiness' (surface area index; SAI) of focal tree species as a function of distance from the top of the canopy in (a) *Vachellia erioloba* and (b) *Boscia albitrunca*. Note that SAI is greater in *B. albitrunca*, particularly at greater distances from the top of the canopy

Table 3: Results of chi-square tests comparing patterns of tree use on hot ($T_{\max} > 35\text{ }^{\circ}\text{C}$) and cool days ($T_{\max} < 35\text{ }^{\circ}\text{C}$) at different times of day by birds in the southern Kalahari. Values of $p < 0.05$ (in bold) indicate significant differences in patterns of tree use between hot and cool days for a given species (or group of species) at a given time of day

Bird species	Time of day	Cool vs hot			
		n	χ^2	df	p
All species (combined data)	Early morning (07:30–09:00)	1 636	8.88	2	0.012
	Late morning (10:30–12:00)	1 518	30.62	2	<0.001
	Mid-afternoon (13:30–15:00)	1 341	108.21	2	<0.001
Chestnut-vented Tit-Babbler	Early morning (07:30–09:00)	76	1.76	2	0.41
	Late morning (10:30–12:00)	89	0.91	2	0.63
	Mid-afternoon (13:30–15:00)	66	2.48	2	0.29
Black-chested Prinia	Early morning (07:30–09:00)	86	0.50	2	0.78
	Late morning (10:30–12:00)	95	5.47	2	0.065
	Mid-afternoon (13:30–15:00)	110	3.09	2	0.21
Kalahari Scrub-Robin	Early morning (07:30–09:00)	139	2.21	2	0.33
	Late morning (10:30–12:00)	137	3.02	2	0.22
	Mid-afternoon (13:30–15:00)	97	12.35	2	0.002
Scaly-feathered Finch	Early morning (07:30–09:00)	162	2.33	2	0.31
	Late morning (10:30–12:00)	138	12.71	2	0.002
	Mid-afternoon (13:30–15:00)	148	19.88	2	<0.001

preference for *B. albitrunca* trees ($E = 0.26$, $CI = 0.16$ to 0.36) and aversion to other trees ($E = -0.34$, $CI = -0.29$ to -0.40). During the mid-afternoon the overall pattern of preference was similar to that seen during the late morning period, but magnified. On hot days, when temperatures were $4.69\text{ }^{\circ}\text{C}$ warmer (Table 3), and consistently greater than $35\text{ }^{\circ}\text{C}$, birds showed the strongest preferences for *B. albitrunca* trees ($E = 0.40$, $CI = 0.31$ to 0.48) and aversion to other trees ($E = -0.54$, $CI = -0.51$ to -0.57). A weak, but significant, aversion to *V. erioloba* trees also occurred ($E = -0.11$, $CI = -0.17$ to -0.05).

Comparisons of tree use by focal bird species

Neither of the arboreal gleaning species, Chestnut-vented Tit-Babblers and Black-chested Prinias, showed a change in patterns of tree use as a function of T_{\max} during any period of the day (Table 4). Both species, showed strong preferences for *B. albitrunca* trees and aversions to other trees during mid-afternoon on both cool as well as hot days (Figure 3). This contrasted with the patterns observed in predominantly ground-foraging species, Kalahari Scrub-Robins and Scaly-feathered Finches, which both adjusted their behaviour as a function of T_{\max} , although to differing degrees. Scaly-feathered Finches showed the most dramatic change in behaviour with T_{\max} , with differing patterns of tree use during both the late morning and mid-afternoon periods (Table 1). On cool days during the mid-afternoon, Scaly-feathered Finches showed a weak but significant preference for *V. erioloba* trees and an aversion to *B. albitrunca* trees. On hot days, however, they no longer preferred *V. erioloba* trees switching instead to preferring *B. albitrunca* trees, and avoiding other trees (Figure 3). Kalahari Scrub-Robins only showed a preference for *B. albitrunca* during the mid-afternoon (Figure 3).

Discussion

Our study showed that arid savanna birds increasingly used dense shaded microhabitats within *B. albitrunca* trees

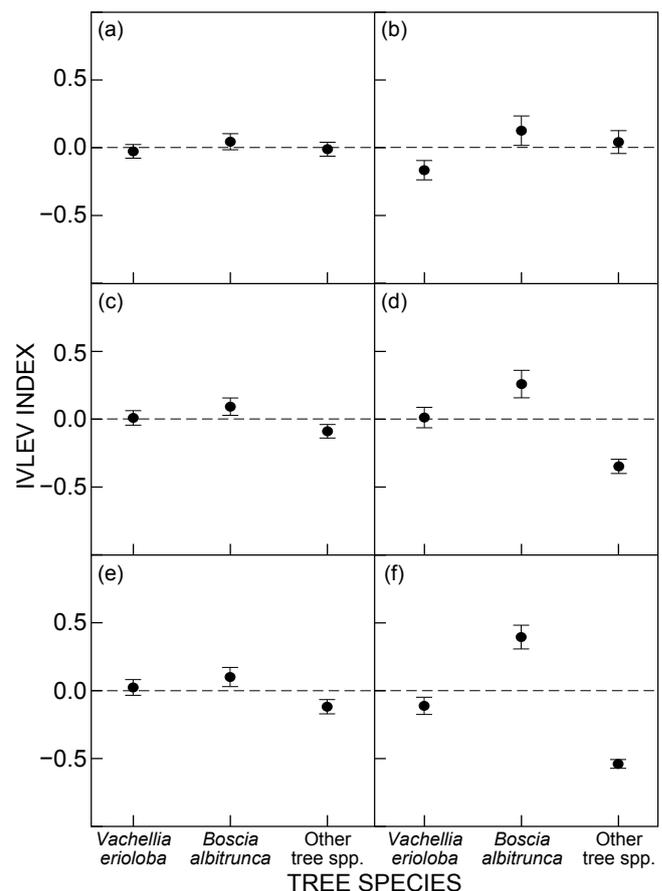


Figure 2: Changing patterns of tree use by a bird community in the southern Kalahari at different times of day and on days differing in maximum temperature. Observations of all bird species are combined. First row: early morning (07:30–09:00) on (a) cool days, (b) hot days; second row: late morning (10:30–12:00) on (c) cool days, (d) hot days; third row: mid-afternoon (13:30–15:00) on (e) cool days, (f) hot days. Ivlev index values >0 indicate preference, <0 indicate avoidance

in preference to other tree types at high air temperatures. This pattern was evident at all times of day we investigated but was particularly pronounced during the mid-afternoon when air temperatures were highest. However, when bird species were considered individually, we found considerable interspecific differences in tree preference patterns. Two arboreal gleaning species, Chestnut-vented Tit-Babbler and Black-chested Prinia, showed strong preferences for *B. albitrunca* trees on cool days and did not change tree use on hot days. In contrast, two predominantly ground-foraging species, Scaly-feathered Finch and Kalahari Scrub-Robin, showed no preferences for any tree species on cool days, but a strong preference for *B. albitrunca* on hot days.

The degree of exposure to solar radiation can have a large influence on the heat load experienced by small animals such as birds (Walsberg and Wolf 1995; Wolf et al. 2000). In hot, arid areas such as the southern Kalahari Desert during summer, patches of shade created by large trees may thus be a critical resource. The degree of shade provided, and hence the thermal benefits conferred on birds, can differ between trees (Brown and Gillespie 1995; Kotzen 2003). *Boscia albitrunca* trees are often considered to provide dense shade (Alias and Milton 2003) but to our knowledge the density of shade of different trees in the Kalahari has not been previously quantified. Our study represents the first empirical demonstration that *B. albitrunca* provides a more shady environment than *V. erioloba*, at least among trees of architecture typical of our study site.

Quantifying microclimates on scales relevant to individual organisms is a major challenge in thermal biology (Angilletta 2009; Bakken and Angilletta 2014). Using a linear sensor comprising multiple closely spaced photodiodes, we were able to efficiently measure the level of radiation penetrating through tree canopies to a large number of points in close proximity to each other. Thus, our measure of shadiness (SAI) captured not only the intensity of radiation but also the density of substrates that intercept radiation (i.e. foliage and branches) at the scale of the entire canopy. We believe measurements on the scale measured here are likely important from the perspective of small birds moving within the canopies of trees (e.g. to forage) as short-term exposure to sunflecks may rapidly increase the heat loads they experience (Wolf and Walsberg 1996). However, under certain circumstances (e.g. during extreme heatwaves where all activity is curtailed) measurements of microclimates at much finer scales (e.g. Wolf et al. 1996) may be more relevant.

Consistent with our prediction, the bird community, when considered as a population of birds of multiple species, showed an increased preference for shadier *B. albitrunca* trees on hotter days. The effect of temperature was greatest

at the hottest time of day, further consistent with the hypothesis that changes in behaviour were driven by selection for these trees as thermal refuges. This finding suggests that the shade provided by *B. albitrunca* trees could be a keystone resource for birds on hot days and may play an important role in mitigating the effects of rising temperatures due to climate change on birds. *Boscia albitrunca* trees are currently protected in South Africa. Protected status was granted on the basis that these trees provide browse to

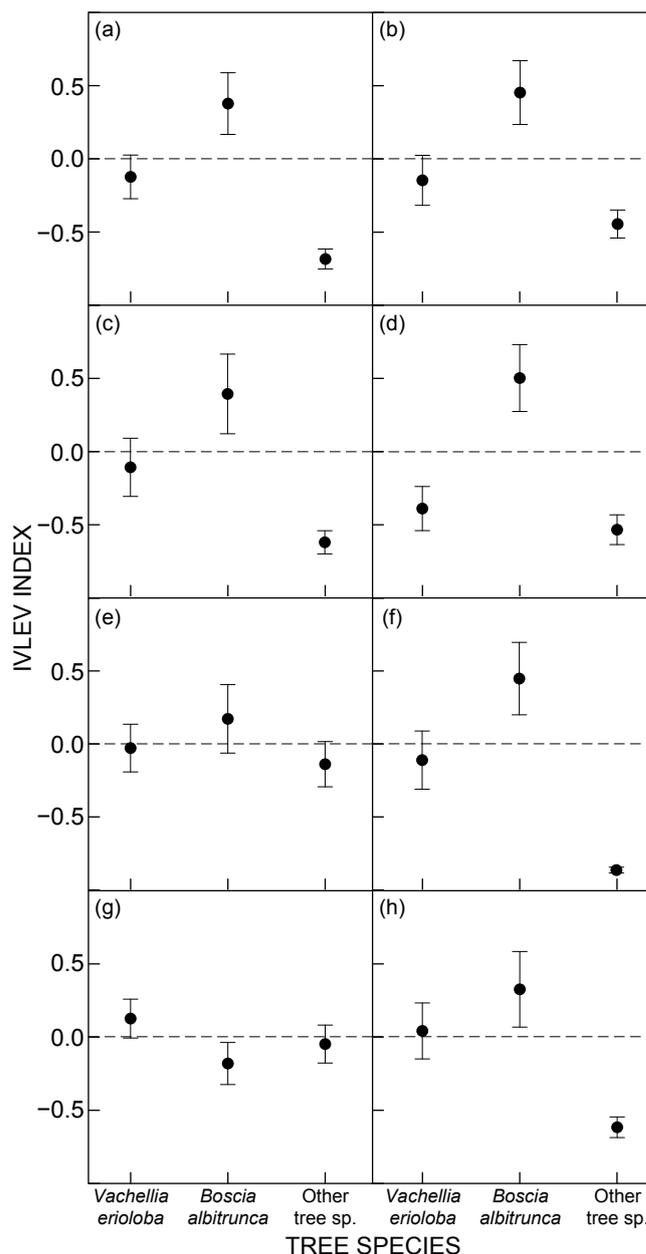


Table 4: Air temperature ($^{\circ}\text{C}$) during the three observation periods on cool and hot days

Time of day	Cool ($T_{\text{max}} < 35^{\circ}\text{C}$)			Hot ($T_{\text{max}} > 35^{\circ}\text{C}$)		
	n	Mean	SD	n	Mean	SD
Early morning (07:30–09:00)	42	25.67	2.18	12	28.35	1.58
Late morning (10:30–12:00)	38	29.30	2.09	12	33.31	1.23
Mid-afternoon (13:30–15:00)	27	31.47	2.53	13	36.16	1.06

Figure 3: Comparison of patterns of tree use during the hottest period of the day (mid-afternoon, 13:30–15:00) on cool and hot days. First row, Chestnut-vented Tit-Babbler on (a) cool days and (b) hot days; second row, Black-chested Prinia on (c) cool days and (d) hot days; third row, Kalahari Scrub-Robin on (e) cool days and (f) hot days; and fourth row, Scaly-feathered Finch on (g) cool days and (h) hot days

livestock and game, and shade, food and shelter to other animals, including invertebrates and birds (Alias and Milton 2003). Our data supports the case for the protection of this species from threats, including the cutting of branches for browse and low recruitment due to the loss of other large trees, which provide microsites for *B. albitrunca* seed germination (Dean et al. 1999). Our study was carried out in a protected area where no removal of native trees occurs. However, elsewhere the cutting of entire crowns as fodder supplement during severe droughts reportedly transforms trees into flat, multistemmed shrubs (van der Walt and Le Riche 1999). The degree to which these transformed trees provide the thermal refuges needed by birds is unknown. Caution must be taken when making inferences to areas outside the study area regarding the relative importance of thermal environments provided by *B. albitrunca* compared with other tree species. The architecture of trees can vary considerably due to a number of biotic and abiotic factors, and can have profound consequences on the shade they provide (Brown and Gillespie 1995).

Not all bird species we studied responded in a similar manner to elevated temperatures, suggesting birds vary in their capacity or need to adjust behaviour as temperatures increase. Species that already showed strong preferences for *B. albitrunca* trees on cooler days (Chestnut-vented Tit-Babblers and Black-chested Prinias) did not adjust their patterns of behaviour on hotter days. The preference for *B. albitrunca* trees by these species could be explained by their diet and foraging mode. Both are insectivorous arboreal gleaners. Due to the density of their foliage, *B. albitrunca* trees may provide prime foraging sites with a high density of arthropod prey, compared with the other large trees considered in this study. However, no data on differences in arthropod prey availability between these trees were collected. Given that Chestnut-vented Tit-Babblers and Black-chested Prinias already showed preferences for using *B. albitrunca* on cooler days, they may derive little benefit from adjusting patterns of tree use at higher temperatures.

In contrast, species that primarily forage on the ground (Scaly-feathered Finches and Kalahari Scrub-Robins) showed significant temperature-driven adjustments in their behaviour. Both of these bird species preferred *B. albitrunca* trees only during the hottest times of day on hot days. These birds probably use trees mainly for activities other than foraging, e.g. for communication and vigilance. These are activities for which different tree species likely perform equally well. This may explain why, during cooler periods, these birds use trees in proportion to their availability. The denser shade provided by *B. albitrunca* may only become relevant to these birds as a desired resource during periods of elevated temperature.

The degree to which the greater shift in behaviour observed in ground-foraging species reflects greater vulnerability to elevated temperatures is unclear. Assessing vulnerability requires a detailed understanding of the fitness implications of changes in the way animals use the landscape (Kearney 2013). Patterns of microsite use reflect the resolution of trade-offs between the physiological costs of thermoregulation and other costs and benefits of occupying particular microsites, e.g. opportunity for territorial

defence, predator avoidance or foraging (Santee and Bakken 1987; Carrascal et al. 2001; Tieleman and Williams 2002; Levy et al. 2012). Changing patterns of microsite use at elevated temperatures might therefore reflect either high physiological costs of occupying a particular microsite, or low costs of switching to a new one. For example, a bird that is able to meet all of its energy and water requirements while foraging in the cooler hours of the day may show a pronounced change in microsite use during hotter periods with negligible fitness costs (Tieleman and Williams 2002). In contrast, a bird may continue foraging in a hot microsite despite high physiological costs, in order to meet energy or water demands. Elevated temperatures might have severe fitness consequences in such instances, which are not reflected in changes in patterns of microsite use.

Unravelling the implications of changing patterns of microsite use in response to temperature therefore requires a detailed consideration of the activities carried out within those microsites. For example, Cunningham et al. (2015) showed that for Common Fiscals *Lanius collaris*, an ambush predator that hunts from exposed perches, shifting to shaded perches on hotter days resulted in a reduction in foraging success. This potentially explains reductions in nestling provisioning rates on hotter days and reductions in nestling growth during hotter periods (Cunningham et al. 2013).

Our study demonstrates how birds adjust their behaviour in response to hot weather, increasingly seeking out the shadiest large trees in the landscape. These trees may be critical thermal refuges for birds, and become increasingly important as temperatures rise as a result of human-induced climate change. This study provides an initial step towards understanding the role of behaviour in mediating the impacts of climate change on birds in the arid savanna landscapes of the southern Kalahari. Robust predictions of how bird communities will be affected by rising temperatures need an improved understanding of the fitness implications of adjustments in patterns of microsite use. Our data suggest that different bird species will be affected to varying degrees and a fruitful approach might be to focus detailed investigations on a subset of species of varying physical characteristics (e.g. body size) and ecological niches (e.g. diet). This approach could be used to identify general rules about which species will be most affected by rising temperatures. If the realism of predictions for the impact of climate change on species and ecosystems is to be improved, we need more empirical investigations of natural systems that integrate measurements of behaviour and physiology in the context of variable thermal landscapes (Angilletta and Sears 2011).

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