


# Behavioural thermoregulation and climatic range restriction in the globally threatened Ethiopian Bush-crow *Zavattariornis stresemanni*

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Climate may influence the distribution and abundance of a species through a number of demographic and ecological processes, but the proximate drivers of such responses are only recently being identified. The Ethiopian Bush-crow *Zavattariornis stresemanni* is a starling-like corvid that is restricted to a small region of southern Ethiopia. It is classified as Endangered in the IUCN Red List of globally threatened species. Previous work suggested that this range restriction is almost perfectly defined by a climate envelope that is cooler than surrounding areas, but the proximate mechanism remains unexplained. The heavily altered habitats which the species inhabits are widespread across Africa, and recent work has shown that the Bush-crow is behaviourally adaptable and has a catholic diet. We assess whether its enigmatic distribution can be explained by behavioural responses to the higher temperatures that surround its current range. Using environmental niche models and field observations of thermally mediated behaviour, we compare the range restriction and behavioural thermoregulation of the Ethiopian Bush-crow with those of two sympatric control species that are similar in size and ecology, but have much larger ranges that include hotter environments. White-crowned Starling *Lamprotornis albicapillus* and Superb Starling *L. superbus* occupy similar habitats to the Ethiopian Bush-crow and all three frequently forage together. We found that the Bush-crow's range is limited primarily by temperature, with a secondary effect of dry season rainfall, whereas the ranges of the two starling species are better predicted by wet season rainfall alone. Bush-crows exhibited panting behaviour and moved into the shade of trees at significantly lower ambient temperatures than did the starlings, and their food intake declined more steeply with increasing temperature. These results indicate that the limited geographical range of the Bush-crow reflects an inability to cope with higher temperatures. This suggests that a species' response to climate change might not be easily predicted by its ecological generalism, and may represent an inherited debt from its evolutionary history.

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Understanding the factors constraining the geographical ranges of species is often difficult (Warren *et al.* 2001, Pearson & Dawson 2003) because

the occurrence of a species will often depend on the interaction of multiple factors (such as climate, food availability or the presence of competitive species) even at a single range boundary, and limiting factors may vary along different parts of a species' distribution edge (Hersteinsson & MacDonald 1992, Araújo & Luoto 2007, Mason *et al.* 2014). For some species, limited dispersal ability can inhibit occupancy of suitable patches of habitat isolated from the core range (Bibby & Tubbs 1975, Komdeur 1994). For more mobile species, physical or ecological barriers, such as the occurrence of a competitor species, may still prevent suitable habitat patches from being occupied (Gammon & Maurer 2002, Veech *et al.* 2011).

There is clear evidence of physiological limits to bird tolerance of high temperatures experienced within their ranges (Tieleman & Williams 1999, du Plessis *et al.* 2012, Cunningham *et al.* 2013b, Milne *et al.* 2015) and of behavioural mechanisms to avoid daily or seasonal periods of unfavourably high temperature (Kelly *et al.* 2004, Oswald *et al.* 2008, Tieleman *et al.* 2008, Cunningham *et al.* 2015). However, evidence for direct climatic limitation of species ranges due to high temperature remains rare (Thomas 2010). Even if the range of a species is restricted to an area with relatively low temperatures, this restriction may occur because of limited habitat availability, competition from other species or limited dispersal ability. In addition, high temperature may influence the distribution indirectly through the effects on prey, predators or diseases (Newton 2003, Pearce-Higgins & Green 2014, Milne *et al.* 2015).

The restricted range of the Ethiopian Bush-crow *Zavattariornis stresemanni* (henceforth 'Bush-crow') has puzzled ornithologists since the species was first discovered in 1938 (Moltoni 1938, Collar & Stuart 1985). It seems unlikely that its limitation to an area of about 7800 km<sup>2</sup> of seemingly unremarkable acacia woodland and thorn-scrub in southern Ethiopia is explained by habitat availability (Benson 1942, BirdLife International 2016), and the species' generalist diet and wide range of feeding methods make it unlikely that it is geographically constrained by specific dietary needs (Jones *et al.* 2018). However, the possibility that the species might be limited by ambient temperature arose after the range was found to be almost perfectly described by a climate envelope model based on mean annual temperature, temperature seasonality (standard deviation of weekly mean

temperatures) and annual precipitation; mean annual temperature within the range was lower than that in neighbouring areas (Donald *et al.* 2012). Because that study used a single modelling procedure (maximum entropy: Phillips *et al.* 2006) when the choice of modelling technique is a major contributor to variation in species distribution model outputs and projections (Dormann *et al.* 2008, Buisson *et al.* 2010), a further assessment of the evidence is desirable. Furthermore, the proximate mechanisms that underlie the restricted range of the species have not been described. Work on other species has implicated direct or indirect effects of temperature on occurrence rates linked to physiological tolerances (Milne *et al.* 2015) or influences of temperature on habitat, foraging ability or prey abundance (du Plessis *et al.* 2012).

We sought to elucidate the factors that limit the global distribution of the Ethiopian Bush-crow by using several species distribution modelling procedures and a range of candidate bioclimate variables. We also investigated possible mechanisms underlying the restriction of range by measuring Bush-crow behavioural responses to temperature under field conditions. However, because all bird species show behavioural responses to temperature at some level, we considered it essential to compare both the bioclimatic correlates of the boundaries of the global distribution of the Bush-crow and its behavioural responses to temperature with those of ecologically similar species with much less restricted geographical ranges. Our results indicate interspecific differences in the bioclimatic correlates of global range boundaries and in behavioural responses to temperature that are congruent and strongly suggestive of an effect of high temperature in limiting the range of the Bush-crow.

## METHODS

### Study species

The remarkably close match of the restricted range of the Bush-crow with a climatic gradient indicates the potential of the species as a model for developing our understanding of avian distributional responses to climate and to climate change (Donald *et al.* 2012). However, as all species will show a response to temperature at some level, we think it is essential not to consider the Bush-crow alone, but instead to adopt a comparative approach.

Hence, we tested whether other bird species ecologically similar to the Bush-crow, but with larger global ranges, have global range boundaries less strongly associated with low temperatures than the Bush-crow and show behavioural changes at higher temperature thresholds. Therefore, we assessed the behavioural responses of the Bush-crow to ambient temperature and the influence of climatic covariates on its distribution, and compared them with those of two ecologically similar, sympatric species of similar body proportions which are common throughout the small range of the Bush-crow but whose ranges, while confined to eastern Africa, are far less geographically restricted, namely, the White-crowned Starling *Lamprotornis albicapillus* and Superb Starling *Lamprotornis superbus* (ranges 1 060 000 and 3 030 000 km<sup>2</sup>, respectively: Bird-Life International 2016). The body proportions of the Ethiopian Bush-crow (body length 28 cm) resemble those of larger starlings, including White-crowned and Superb (body lengths 25 and 18 cm, respectively: del Hoyo *et al.* 2009). Indeed, the Bush-crow was formerly classified within the Sturnidae (e.g. Fry *et al.* 2000), although molecular data now confirm that it is a member of the Corvidae, most closely related to the African Piapiac *Ptilostomus afer* and the Central Asian ground-jays *Podoces* spp. (Ericson *et al.* 2005). Like the Bush-crow, both starling species favour open acacia woodland habitat and live in small family groups (Fry *et al.* 2000). All three species typically forage for invertebrates while walking on sparsely vegetated ground, although the starlings also eat small fruits (del Hoyo *et al.* 2009). Within the Bush-crow range, the three species are commonly found foraging together, sometimes in mixed species flocks (Delleleghn 1993, Jones *et al.* 2018), and they sometimes associate to mob raptors and snakes (Bladon *et al.* 2016). This study design allows us to test the null hypothesis that the Bush-crow range is not restricted by high temperature, from which the predicted result would be that all three species alter their behaviour at the same temperature.

### Geographical distribution of the three species

We collated geo-referenced sightings of Bush-crows made by various observers between 2005 and 2011 (Gedeon 2006, Mellanby *et al.* 2008, Donald *et al.* 2012) and added our own recent

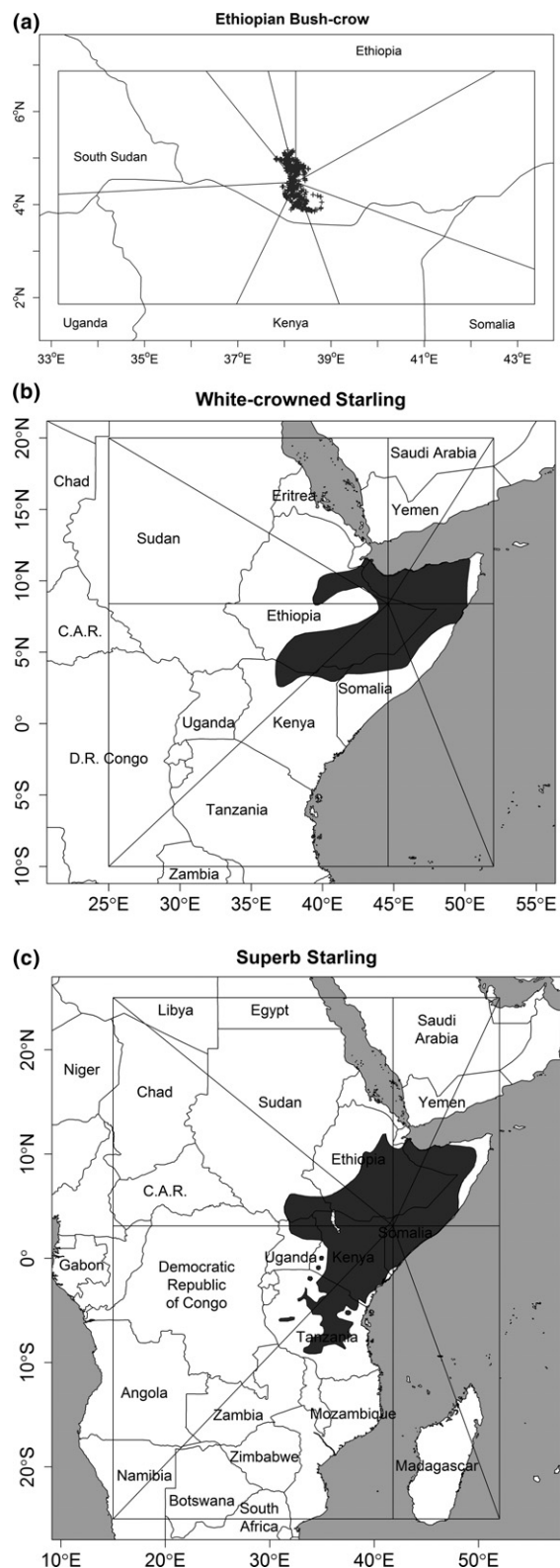
observations of all three species (2012–2015) to produce a dataset of known presences. We compiled locations at which Bush-crows were absent in two ways. First, between 2012 and 2015, we conducted 266 walked transects of 1 km within and outside the known range of the Bush-crow (Donald *et al.* 2012, Bladon *et al.* 2016). The locations of these transects were selected using data on Bush-crow occurrence reported in Donald *et al.* (2012), and this is described in detail in Bladon (2017). Along the 3-km perimeter of 70 equilateral triangles, 210 transects of 1 km were walked at constant pace (mean  $\pm$  standard deviation = 2.55  $\pm$  0.99 km/h), the locations being selected at random within 0.0833  $\times$  0.0833 decimal degree squares located within and around the Bush-crow range and accessible by road or track. A further 56 sections of 1 km were walked at the same pace along one straight transect of 6 km and five straight transects of 10 km which crossed the edge of the Bush-crow range. Bush-crows or their nests were recorded on 102 of these 1-km transects, and were not recorded on the remaining 164. The central point of each 1-km transect on which no birds or nests were recorded was treated as an absence location.

Second, we repeatedly drove the road network in and around the Bush-crow range between 2008 and 2014 with at least two experienced observers in the vehicle searching for nests (details in Donald *et al.* 2012). Bush-crow nests are large, robust and conspicuous structures, made from thick twigs, often projecting above the canopy of the bush or tree in which they are built, and can last for several years (Benson 1942, Donald *et al.* 2012, Bladon *et al.* 2016). They can be detected at distances of up to 1 km from a moving vehicle (Donald *et al.* 2012, Fig. S1); thus, as most stretches of road were driven several times by different observers, we assumed that stretches of roads with no records of birds or nests on any survey represented Bush-crow absences. We divided the driven road network into 1-km segments, and took the mid-point of each segment without a bird or nest record within 1 km of the route as an absence point; thus all absence points had a precision of 1 km. Combining these methods resulted in 2921 presence points and 1905 absence points. A map of transect centres and centres of road segments with and without Bush-crows is provided in Fig. S2.

The range of values of climatic variables for these presence and absence points was limited

because the Bush-crow is restricted to a small range, and the absence points based on our field-work are distributed within or close to that range. This limits the range of observed values of the bioclimate variables in our analyses and might reduce the accuracy of predictions based on the species distribution models (SDMs) we fitted (Randin *et al.* 2006). To increase the range of bioclimate values used for model building, we selected 3095 additional absence points, constrained to be at least 10 km from any known presence location, at random within the map box shown in Figure 1(a). The extent of the map box was chosen to be the same as that used by Donald *et al.* (2012) for modelling the range of the species. Combining these two types of absence data gave a total of 5000 absence points. Including absences from fieldwork alongside those from further outside the Bush-crow range increased the ability of the model to detect fine-scale, local differences between presence and absence sites.

For the White-crowned and Superb Starlings, we generated presence and absence locations from published range maps (BirdLife International & NatureServe 2015). We converted the polygons to raster format with a 30 arc-second resolution and sampled 5000 cells at random from within the range polygon of each species as presence locations. As absence locations we sampled 10 000 cells, constrained to be on land and at least 100 km from the nearest edge of a range polygon, at random within the map boxes shown in Figure 1(b,c). The extent of the area around the starling species' ranges from which absence points were obtained was chosen to encompass a range of bioclimate variables considerably wider than that within the range polygons, and was necessarily larger than the extent used for the Bush-crow owing to the larger ranges of the starlings.



**Figure 1.** Global range maps for (a) Ethiopian Bush-crow, (b) White-crowned Starling and (c) Superb Starling. For the Bush-crow, co-ordinates of all presence records used to fit the species distribution models are shown. For the two starling species, the ranges are polygons from BirdLife International and NatureServe (2015). The rectangular boxes within each panel bound the areas around the range of each species within which the locations in which the species was absent were sampled for modelling purposes. The lines radiating like spokes from a point within each range show the eight sectors of each map box which were used for cross-validation of the models.

### **Bioclimate variables used for modelling geographical distribution**

Climate data for presence and absence points were downloaded from the WorldClim website (Hijmans *et al.* 2005), which provides values of 19 bioclimate variables that are interpolated and modelled from observations and then averaged over the period 1950–2000 at 30 arc-second resolution. We used five bioclimate variables: maximum temperature of the warmest month (calculated as the mean of the highest monthly means of maximum temperatures recorded each month), temperature seasonality (standard deviation of weekly mean temperatures), annual temperature range, precipitation of the wettest quarter, and precipitation of the driest quarter, chosen to represent climatic extremes which are more likely to drive species distributions than mean values used previously (Donald *et al.* 2012, Cunningham *et al.* 2013a). These five variables were not strongly intercorrelated ( $r \leq 0.72$ ; Table S1).

### **Modelling geographical distribution in relation to bioclimate variables**

We related the geographical distribution of each of the three species to the 1950–2000 mean values of the five bioclimate variables by fitting SDMs to the presence and absence data using the *biomod2* package (Thuiller *et al.* 2009) in R version 3.2.4 (R Core Team 2016). We used six model algorithms and a  $k$ -fold partitioning cross-validation procedure to assess model performance by the area under the curve (AUC) of the receiver operating characteristic (ROC).  $\Delta$ AUC scores for individual variables were obtained by subtracting the  $k$ -fold AUC score for the model without the variable of interest from the  $k$ -fold score for the model with all variables. Full details are given in the Supporting Information.

### **Recording behavioural responses to temperature**

Six study areas at the centre and near the edge of the Bush-crow range were selected for behavioural observation. These sites represented areas at the warm and cool extremes of temperatures recorded during preliminary surveys (Fig. S3). Each site was visited on two pairs of days at least a week apart, between 08:30 and 18:00 h. Within each pair of days, one was spent following Bush-crow groups

and the other following starling groups. Some Bush-crow groups included birds marked individually with colour rings (Jones 2013), but usually a group was identified from its location within the study area, its age composition (juveniles and adults), individual differences in plumage and numbers of birds in the group. Groups sometimes split into smaller foraging units and came together again later, so identification of groups could not be based on group size alone. Data for several different observation periods were available for most groups.

Two types of behavioural study were conducted, alternately, throughout the day on the focal species. In one type of study, to assess the use of shade by the birds, focal individuals were observed using binoculars from a distance of 10–15 m for protracted periods ('follows'). The start and end time of each follow were recorded. At 1-min intervals, measured on a timer, the position (in sun, in shade or neither because of cloud cover) of the focal bird was recorded, following a similar procedure to that of Altmann (1974). If the focal bird was lost from view, a new bird from the same group was chosen (and recorded as such) for the next sample. If the group was lost from view for two consecutive samples, a new follow was started when the group was relocated.

In the second study, foraging adults were approached to a distance of 5–10 m (at which none of the species showed signs of disturbance such as alarm calling or retreating from the observer) and one bird was selected at random and watched continuously through binoculars for as long as contact could be maintained ('watches'). Observations were dictated into a digital voice recorder and transcribed later. The number and success of all foraging attempts (where the bird was seen to peck at a bush or the ground, dig with its beak, turn over an object or chase a flying insect) were recorded along with the occurrence and duration of panting behaviour (open bill and/or gular fluttering), typical of evaporative heat loss (Tieleman & Williams 1999). This was converted to a proportion of each watch spent panting. Recordings were paused if the bird was not visible (for example if it walked behind a bush) and note was taken of any periods where the bird ceased foraging. In all, 100 watches of Ethiopian Bush-crows were completed (total time = 390 min; minimum/mean/maximum = 0.4/3.9/26.2 min) along with 30 watches of White-crowned Starlings (total time = 103 min; minimum/mean/maximum = 0.5/3.4/10.7 min) and 50 watches of Superb Starlings

(total time = 207 min; minimum/mean/maximum = 0.5/4.1/29.7 min).

At the start of each observation day, two iButton ThermoChron<sup>®</sup> (Maxim Integrated, DS1921G-F5) were deployed in the study area, one in constant shade from a bush or tree, and the other constantly unshaded (therefore in full sunlight unless cloud cover was present). The units were glued to golf tees pressed into the soil to lift them 2 cm off the ground. This was to measure air temperature near to ground level, comparable to the temperature where the birds were foraging. Although the absolute temperature recorded by a metal iButton unit cannot be expected to match that experienced by a foraging bird (Bramer *et al.* 2018), we were interested in the differences among the three species in behavioural responses to changes in temperature rather than the absolute values at which they occurred. Temperature was recorded at 1-min intervals on the two iButtons throughout the observation periods. The mean temperature for the iButton in full sunlight and that for the iButton in the shade were calculated for each observation period. iButtons were calibrated prior to the study by recording temperatures simultaneously in controlled conditions. A two-way ANOVA was fitted to model the temperatures recorded by each unit at each time. The difference between the average predicted temperature of each unit and the lowest predicted temperature across all units was subtracted from each recorded field temperature on the unit to calibrate the data.

### Analysis of proportion of time spent panting

Visual inspection of scatter plots indicated that it was not straightforward to analyse the data using ordinary least squares regression with the proportion of the watch spent panting ( $P_{\text{pant}}$ ) as the dependent variable and temperature in full sunlight or time of day as the independent variable. This was because (1) many values of  $P_{\text{pant}}$  were zero or one, (2) values of  $P_{\text{pant}}$  between zero and one were widely scattered for a given value of temperature or time of day and (3) residual variation in  $P_{\text{pant}}$  was non-normal and appeared to vary with temperature and time of day in a way that could not easily be dealt with by standard transformations of  $P_{\text{pant}}$  such as logit, Box-Cox or arcsine square root (Fig. S4).

These problems resemble those addressed by the statistical model of avian primary feather moult

(Underhill & Zucchini 1988). Therefore, an equivalent model to that used by Underhill and Zucchini for their Type 2 data was fitted, with  $P_{\text{pant}}$  being taken to be equivalent to primary moult score, and temperature in full sunlight or time of day being taken to be equivalent to calendar date. Hence, the model for temperature had three parameters: (1) the mean temperature at which individual birds began to show some panting behaviour ( $P_{\text{pant}} > 0$ ), (2) the difference between the temperature at which an individual began to show panting behaviour and that at which it pants throughout the watch (this difference is taken to be the same for all individuals) and (3) the standard deviation of the temperature at which individual birds began to show some panting behaviour. For the effect of time of day, we wished to allow for the probable effect to be hump-shaped, as suggested by inspection of scatter diagrams. We therefore calculated the quantity  $v = t + qt^2$ , where  $t$  is the time of day at which the observation was made and  $q$  is the quadratic coefficient. We fitted the models as described above for temperature, but with the mean, difference and standard deviation all being estimated for the transformation of time of day  $v$ , rather than temperature. Underhill–Zucchini models were fitted by using the NONLIN module of SYSTAT 5.01 (Wilkinson 1990) to identify the values of the mean, difference and standard deviation and, for the time of day models, the quadratic parameter  $q$ , at which the likelihood of the data was maximized. Model variants were fitted with all possible combinations of each of the parameters being the same or different among the three species and with either temperature or time of day as the independent variable (Table S2). The sample size, residual deviances and numbers of fitted parameters of these models were used to calculate the corrected Akaike information criterion ( $AIC_c$ ) and  $AIC_c$  weights for each model, following Burnham and Anderson (2002). We used predicted mean  $P_{\text{pant}}$  values for each of a range of temperatures for each species from the model with the lowest  $AIC_c$  value to represent the relationship between  $P_{\text{pant}}$  and ambient temperature.

### Analysis of proportion of time spent in the shade

Individual focal observations during which the bird was in sunlight were scored as zero and those where it was in shade were scored as one. These

data were modelled as a binary response variable in a logistic regression. Focal observations that occurred under cloud cover were excluded. Temperature recorded in full sunlight, species, group type (adult only or family group with juveniles) and time of day were fitted as predictor variables, along with each two-way interaction involving either temperature or time of day, and the squares of these two variables, to give quadratic effects. Group identity was fitted as a random effect and, because over-dispersion remained, a random effect of observation period was nested within it (du Plessis *et al.* 2012). Individual identity could not be used as a random factor because not all birds were colour-marked. The model assumptions were checked and were satisfied. Model selection was carried out by backwards stepwise selection, with the removal of each term tested using a likelihood-ratio test. A minimal adequate model was obtained, in which all remaining terms were significant according to likelihood-ratio tests (Crawley 2005).

### Analysis of food intake rate

Food intake rate was modelled using Poisson regression in which the count of items ingested during a watch was the dependent variable, and the natural logarithm of the amount of time spent foraging (in minutes) during the watch was included in the model as an offset. This is equivalent to modelling the number of items ingested per minute as the dependent variable. The independent variables in the regression were temperature in full sunlight, species and time of day, along with each two-way interaction and the squares of temperature and time of day to give quadratic effects. Group identity was modelled as a random effect, with a random effect of observation period nested within it, as the data were over-dispersed. The model assumptions were checked and were satisfied.

## RESULTS

### Geographical distribution

For the Bush-crow SDM, the boosted regression tree (BRT) algorithm performed best, according to the AUC *k*-fold cross-validation test (AUC = 0.824). When the bioclimate variables were deleted in turn from this model, maximum temperature of the warmest month (0.022) and

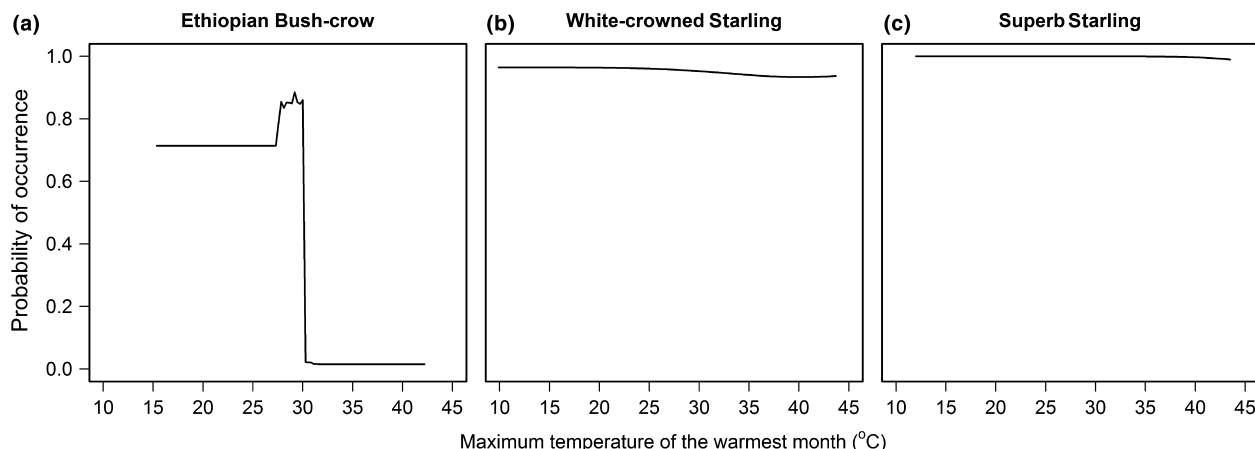
precipitation of the driest quarter (0.018) had the highest  $\Delta$ AUC scores. Plots of modelled probability of occurrence against covariates indicated a steep threshold at 30 °C for maximum temperature of the warmest month, above which Bush-crows did not occur (Fig. 2). The second most important variable, dry season precipitation, also showed a narrow peak in predicted Bush-crow occurrence, around 30 mm (Fig. S5).

For the White-crowned Starling SDM, the generalized linear model (GLM) performed best according to the AUC *k*-fold cross-validation test (AUC = 0.920). When the bioclimate variables were deleted in turn, precipitation of the wettest quarter had the highest  $\Delta$ AUC score (0.237). For the Superb Starling SDM, multiple adaptive regression splines (MARS) were the best performing algorithm (AUC = 0.971) and precipitation of the wettest quarter again had the highest  $\Delta$ AUC score (0.142).

$\Delta$ AUC scores for each variable for the best model for each species were standardized by dividing each score by the sum of the scores for all five variables in the models. The standardized maximum temperature and dry season precipitation scores were much higher for the Bush-crow than for the two starlings, for which the wet season precipitation score was higher (Fig. 3). The importance of wet season precipitation to the starlings was also indicated by the response plots, which showed a sharp decline in probability of occurrence when wet season precipitation exceeded 400 mm (White-crowned Starling) and 500 mm (Superb Starling; Fig. S6). While the Bush-crow showed a sharp decline in probability of occurrence when temperatures exceeded 30 °C, White-crowned Starlings exhibited only a slight decline in probability of occurrence at temperatures greater than 38–40 °C, and there was no indication of any effect of temperature for the Superb Starling (Fig. 2).

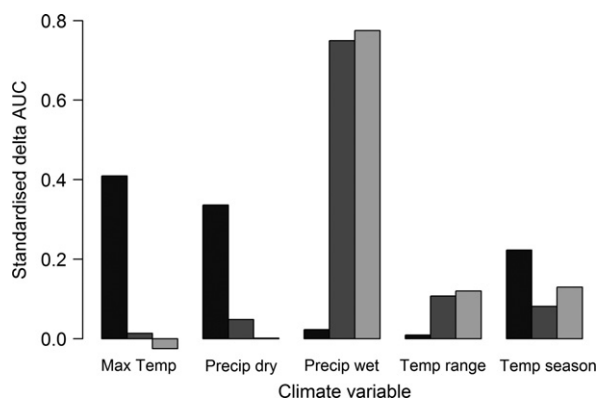
### Proportion of time spent panting in relation to temperature and time of day

Models describing the relationship between the proportion of time spent panting and temperature in full sunlight at the time of the observation performed much better than those using time of day as the independent variable (Table S2). The model with the lowest AIC<sub>c</sub> value was that with species-specific means and standard deviations of the



**Figure 2.** The relationship of modelled partial probability of occurrence of (a) Ethiopian Bush-crow, (b) White-crowned Starling and (c) Superb Starling to maximum temperature of the warmest month. All other bioclimate variables are held constant. Curves show the predicted response determined using the model algorithm that gave the highest AUC value for each species in a  $k$ -fold cross-validation test. Equivalent plots for all five bioclimate variables and all model algorithms are presented in Figs S5 and S6.

temperature at the start of panting, and with a constant difference between mean temperatures at the start of panting and when panting became continuous (i.e. no individual species effect; Model 6; Table S2). There was significant variation among the three species in the relationship between the proportion of time spent panting and temperature. A likelihood-ratio test found a significant



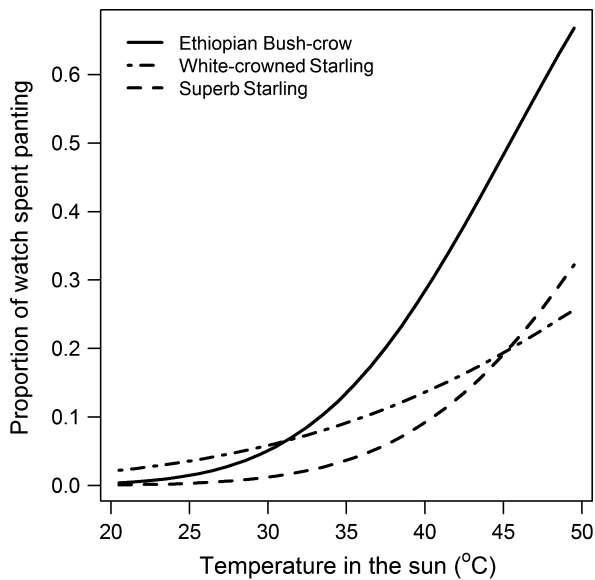
**Figure 3.** Comparison of the relative importance of five bioclimate variables in models describing the geographical range of the Ethiopian Bush-crow and two sympatric starling species. Standardized  $\Delta$ AUC scores from the model fitted using the algorithm giving the best fit for each species for the Ethiopian Bush-crow (black), White-crowned Starling (mid-grey) and Superb Starling (light grey).  $\Delta$ AUC scores were obtained by subtracting the  $k$ -fold AUC score for the model without the variable of interest from the  $k$ -fold score for the model with all variables. Scores were standardized by dividing each one by the sum of all five scores for the species.

difference in residual deviance between the Underhill–Zucchini model with the three parameters assumed to be the same for all species (Model 1) and that in which each species had a different value for all parameters (Model 8) ( $\chi^2_6 = 16.26$ ,  $P = 0.012$ ). Curves showing expected mean values of the proportion of time spent panting in relation to temperature indicated that Bush-crows showed a more rapid rise in the proportion of time spent panting with increasing temperature than did either of the two starling species (Fig. 4).

### Proportion of time spent in the shade in relation to temperature in full sunlight

All species increased the amount of time spent in the shade as temperature in full sunlight increased. The temperature at which Bush-crows spent half of their time in the shade (early morning (10:21 h) = 38.8 °C, late afternoon (17:30 h) = 31.9 °C) was lower than the equivalent temperature for the White-crowned (early morning (10:21 h) = 40.4 °C, late afternoon (17:30 h) = 37.7 °C) and Superb Starlings (early morning (10:21 h) = 45.0 °C, late afternoon (17:30 h) = 35.4 °C). Bush-crows spent more time in the shade than either starling species at temperatures below 40 °C, although White-crowned Starlings increased the amount of time spent in the shade more rapidly at temperatures over 35 °C (likelihood-ratio test;  $\chi^2_2 = 6.44$ ,  $P = 0.040$ ). At a given temperature, all species spent more time in the





**Figure 4.** Proportion of time spent panting by Ethiopian Bush-crows (solid line), White-crowned Starlings (dot-dashed line) and Superb Starlings (dashed line) in relation to temperature near the ground surface in sunlit areas. Curves show expected mean proportions from the model with the lowest AIC<sub>c</sub> (Model 6; Tables S2 and S3).

shade later in the day ( $\chi^2_1 = 4.51$ ,  $P = 0.034$ ), and there was no effect of the presence of juveniles on time spent in the shade by adult birds ( $\chi^2_1 = 0.09$ ,  $P = 0.763$ ; Fig. 5, Table S4). The mean temperature in full sunlight during our observations was

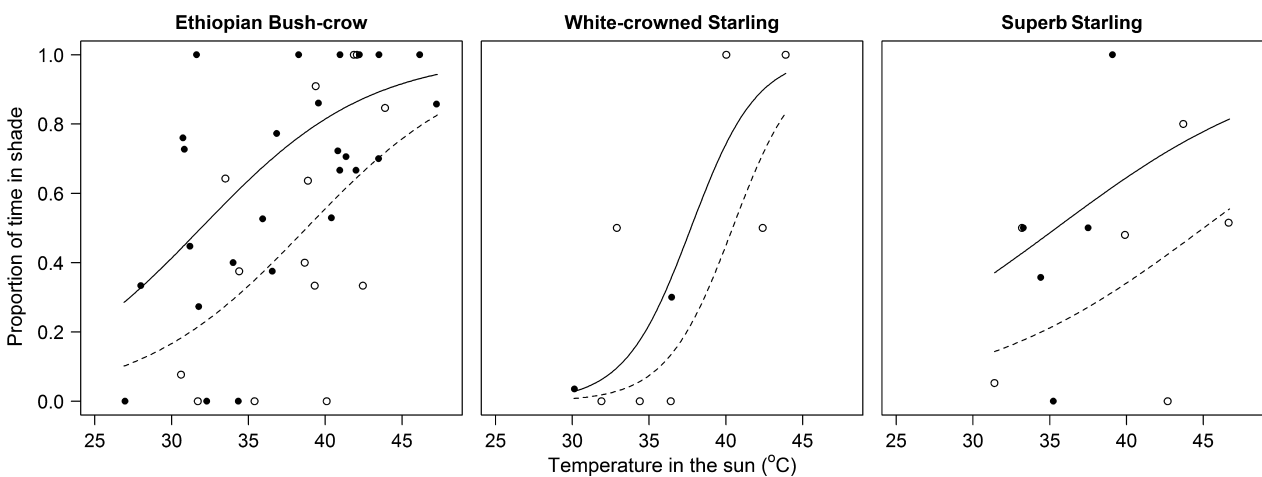
11.2 °C higher than in the shade ( $t_{99} = 18.00$ ,  $P < 0.001$ ).

### Food intake rate in relation to temperature

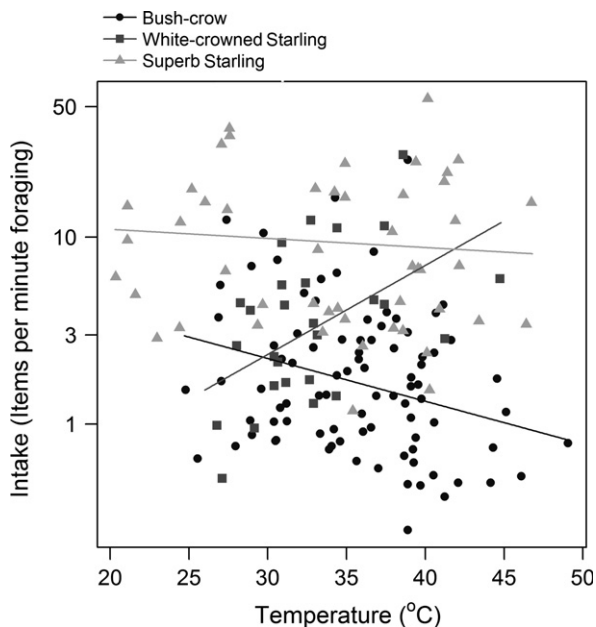
The food intake rate of Bush-crows declined with increasing temperature, whereas it increased with temperature in White-crowned Starlings and was not significantly affected by temperature in Superb Starlings (Fig. 6; Table S5). There was a significant temperature-by-species interaction term ( $\chi^2_2 = 10.64$ ,  $P = 0.005$ ), indicating that the relationship of intake rate to temperature differed significantly among species. There was no significant effect of time of day on the rate of food intake ( $\chi^2_1 = 1.49$ ,  $P = 0.222$ ).

### DISCUSSION

Previous studies have demonstrated associations between climatic patterns and the geographical distributions of many bird species (e.g. Huntley *et al.* 2007, Cunningham *et al.* 2016) and between changes in modelled climate suitability and population trends (e.g. Stephens *et al.* 2016). Others have demonstrated the impact that local temperature fluctuations can have on individuals, in terms of behavioural strategies, food intake rates and condition (du Plessis *et al.* 2012, Cunningham *et al.* 2015, 2017). We combined these two approaches



**Figure 5.** Relationship of the proportion of time spent in the shade to temperature in full sunlight for the Ethiopian Bush-crow, White-crowned Starling and Superb Starling. Points show data from individual follows conducted before (open) and after (filled) the median time of all follows (13:42 h). Dashed lines show predicted proportions for the middle of the earliest morning follow (10:21 h); solid lines show predicted proportions for the middle of the latest afternoon follow (17:30 h).



**Figure 6.** Relationship of food intake rate (items consumed per minute foraging) to temperature for the Ethiopian Bush-crow (black circles), White-crowned Starling (mid-grey squares) and Superb Starling (light grey triangles). Points show data from individual watches. Lines show predicted values from the model. The response is presented on a log-scale.

to demonstrate the fine-scale thermal mechanisms driving broad-scale population responses to climate in the Ethiopian Bush-crow. An inability to cope with high temperatures without expending substantial energy and time on behavioural thermoregulation has been suggested as a range-limiting characteristic in other species (Cunningham *et al.* 2013b, 2015, Milne *et al.* 2015).

The restricted global range of the Ethiopian Bush-crow is well described by a climate envelope model based predominantly on maximum temperature of the warmest month, with a secondary effect of dry season precipitation. Bush-crows occur in areas that are cooler and receive less dry season rainfall than surrounding regions. This result, produced from six model algorithms, is similar to that using only the maximum entropy model (Donald *et al.* 2012) but supports it more rigorously by using more presence observations, transect-based absence records, a wider suite of modelling techniques and *k*-fold cross-validation (Huntley *et al.* 2007, Dormann *et al.* 2008, Buisson *et al.* 2010). The same suite of modelling techniques indicates that the ranges of the two sympatric starling species are limited primarily by

wet season precipitation rather than by temperature.

All three species spent more time exhibiting thermoregulatory behaviour (panting and taking cover in shade) when the temperature was high. Moving to the shade is a means of behavioural thermoregulation (Cunningham *et al.* 2015), with the temperature close to the ground being an average of 11.2 °C lower in the shade than in full sunlight in our study. However, Bush-crows began to pant and moved to the shade at significantly lower temperatures than did either of the less temperature-restricted starling species. This suggests that Bush-crows are physiologically more influenced by high temperature than the two starlings, and therefore that they start to feel physiological stress at lower temperatures. This may explain why maximum temperature described the range of the Bush-crow so accurately, while not doing so for the extensive ranges of the starlings. Assessing the direct physiological responses of the Bush-crow to increases in temperature (for example to determine the metabolic responses of the species to, and rates of evaporative water loss at, different temperatures) offers an important avenue for future research to understand how and when the species might respond to climate change (Tieleman & Williams 1999, Kearney & Porter 2009, Thompson *et al.* 2015). Case studies of the physiological determinants of species ranges along environmental gradients in the tropics are rare but are important for increasing our understanding of the range limitations of species (Londoño *et al.* 2017).

The additional time spent panting and in the shade by the Bush-crow than by the starlings at high temperatures might have no effect on survival or breeding success if these could be compensated for by higher foraging success. However, the food intake rate of the Bush-crow declined markedly with increasing temperature, whereas it remained stable in Superb Starlings and increased in White-crowned Starlings. A reduction in foraging ability with increasing temperature, especially when combined with increased physiological costs of thermoregulation (Tieleman & Williams 1999), might lead to an inability of Bush-crows to maintain condition, and ultimately to survive, in areas where temperatures are high for a substantial proportion of time. Recent work on several species of arid zone birds has indicated that critical temperature thresholds exist ( $T_{crit}$ ; Cunningham *et al.* 2013a) above which foraging efficiency (du Plessis *et al.*

2012) and nestling growth (Cunningham *et al.* 2013b) are affected. Further work should aim to identify the presence of such critical thresholds in the Bush-crow, which may allow more detailed mechanistic models of the potential range of the species to be built (Kearney & Porter 2009).

The temperatures measured in our behavioural studies cannot be directly compared with those from the data layers used in the SDMs. Whereas the SDM data layers come from interpolated weather station and satellite data (Hijmans *et al.* 2005), which generally measure ambient air temperature in the shade (Bramer *et al.* 2018) and are averaged over decades, our field data were instantaneous recordings collected on metal iButton units left close to the ground in continuously exposed and shaded locations, designed to better represent where the birds were foraging. This would lead to very different temperatures being recorded for a given area during the same time period. However, our conclusions do not depend on direct comparisons between temperatures measured during the behavioural study with those from weather stations or satellites. Instead we show, at two different scales, that the Ethiopian Bush-crow responds to lower temperature thresholds than do either of the two sympatric, but more widely ranging, starling species.

The Ethiopian Bush-crow is classified as Endangered in the IUCN Red List because of a recent reduction in population size driven by habitat alteration, and a possible susceptibility to climate change (BirdLife International 2016). Our results suggest that increased ambient temperatures associated with future climatic change are likely to pose a significant threat. The mean temperature in Ethiopia increased by 1.3 °C between 1960 and 2006, and further substantial increases are projected by 2050 (the 50th percentile prediction of mid-range scenario (RCP4.5) model runs is an increase of 1.3, and 1.8 °C for high-range scenarios (RCP8.5); IPCC, 2014). Species with narrow climatic tolerances are predicted to be at the greatest risk of extinction (e.g. Huntley & Barnard 2012) and it will be important to use SDMs to assess how the projected changes in climate in Ethiopia described above are likely to affect the future prospects of the Ethiopian Bush-crow.

We found that the effects of high temperatures on Ethiopian Bush-crow behaviour were considerably more pronounced than those for two sympatric starling species in the same habitat. This

mirrors the differences in the global distributions of the three species, which for the starlings are largely determined by rainfall, whereas for the Bush-crow it is determined by temperature. Our results demonstrate that apparent adaptability (Gedeon 2006) and ecological generalism (Collar & Stuart 1985, Jones *et al.* 2018) are not sufficient to protect species against the threat of climate change if their evolutionary past has bequeathed them an underlying physiology which is unable to cope with rising temperatures.

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

**Table S1.** Pairwise correlation coefficients for the five bioclimatic variables chosen for distribution modelling.

**Table S2.** Comparison of Underhill–Zucchini models of the panting behaviour of Ethiopian Bush-crows, White-crowned Starlings and Superb Starlings.

**Table S3.** Maximum-likelihood estimates of parameters of the Underhill–Zucchini model of panting behaviour with asymptotic standard errors.

**Table S4.** Analysis of variance tables for models of the proportion of time spent in the shade by the Ethiopian Bush-crow, White-crowned Starling and Superb Starling.

**Table S5.** Analysis of variance tables for models of the food intake rate of the Ethiopian Bush-crow, White-crowned Starling and Superb Starling.

**Figure S1.** Bush-crow nests positioned at the top of tall acacia trees demonstrating their detectability from a slow-moving vehicle.

**Figure S2.** Bush-crow presence and absence locations used in species distribution modelling.

**Figure S3.** The location of study sites used to record Ethiopian Bush-crow, White-crowned Starling and Superb Starling behaviour.

**Figure S4.** Relationship of the proportion of time spent panting to temperature in full sunlight for the Ethiopian Bush-crow, White-crowned Starling and Superb Starling.

**Figure S5.** Response of partial probability of occurrence of Ethiopian Bush-crow to each bioclimatic variable.

**Figure S6.** Predicted response of partial probability of occurrence to each bioclimatic variable for (A) White-crowned Starling and (B) Superb Starling.