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**Hot, hotter, gone? Predicting climate-induced species losses from hot  
African ecosystems**

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## **ABSTRACT**

The Earth's climate warmed by 0.6°C in the 20<sup>th</sup> Century and is expected to become warmer in the next few decades than at any time in the last 40 million years. Not only is the temperature predicted to rise but the frequency and intensity of extreme high-temperature episodes is also expected to increase. Global warming is predicted to threaten more than one million species with extinction by 2050. Determining predictive methods for detecting species vulnerability to climate change is essential in order to minimise biodiversity loss. The ability of a species to persist in an area will depend, in part, on aspects of its physiology which allow it to withstand increases in temperature. If a species repeatedly experiences temperatures which cause it to pass critical physiological thresholds it is unlikely to be able to persist in an area. Determining what these critical thresholds are for individual species requires detailed laboratory-based studies of individuals from populations throughout a species' range. However, the rate of climate change demands that measures are put in place now that will safeguard each species in, if not parts, then all of its range. The objective of this pilot study was to determine whether it was possible to develop a field-based, rapid-assessment technique to assess which bird species may be most vulnerable to rising temperatures and so predict which species (and in approximately what order) may be lost from hot areas as temperatures increase. Field work was conducted in the Kalahari Desert, the area in southern Africa expected to experience the greatest magnitude of warming in the future. Using heat-stress behaviours as a proxy for physiological stress induced by high temperatures, critical temperatures at which each bird species started to experience stress were identified. Body size in birds was found to be a fairly robust indicator for predicting species' vulnerability to increasing temperatures. Larger birds were the most vulnerable to stress at high temperatures. Large birds can therefore be predicted to be the first species that would be lost from this ecosystem under future climate scenarios of increasing temperature.

## **INTRODUCTION**

The Earth's climate warmed by 0.6°C in the 20<sup>th</sup> Century and is expected to become warmer in the next few decades than at any time in the last 40 million years (Christensen et al., 2007). The recent changes are predicted to affect, and in some cases already have, a broad range of organisms across diverse geographical regions

(Parmesan & Yohe, 2003). Global warming is predicted to threaten more than one million species with extinction by 2050 (Thomas et al., 2004). The frequency and duration of extreme weather events such as droughts and floods are predicted to increase, as is the frequency of extremes of temperature (Easterling et al., 2000; Jentsch & Beierkuhnlein, 2008). Although there are uncertainties regarding the prediction of these events (depending on the type of extreme and the region that is considered), predictions for increases in the duration and frequency of temperature extremes are considered the most reliable and likely (Planton et al., 2008). Species will differ in their ability to respond to these changes in climate and their responses will depend on differing aspects of their phenology and physiology, habitat requirements and dispersal characteristics. Species' responses to climate change include adaptation, extinction or range changes (contraction, expansion or whole range shifts). As these changes occur, the composition and functioning of most communities and ecosystems is expected to change (Huntley et al., 2006). It is important to understand the risk that a changing climate will pose to different species so that we can better predict how ecosystems may respond in the future (Welbergen et al., 2008).

Several different methodological approaches have been used to try and predict the potential impact of climate change on biodiversity – the most popular of which use climatic envelope models. These models are aimed at identifying (for any chosen species) the 'envelope' that best describes the limits to its spatial range by either correlating current species distributions with climate variables (climate envelope models) or by ecophysiological models which include a physiological understanding of factors that limit a species' distribution (Dunham & Overall, 1994; Pearson & Dawson, 2003). This approach is centred around ecological niche theory. A species' fundamental ecological niche has been defined as those environmental conditions within which a species can survive and grow (Hutchinson, 1957). A mechanistic understanding of the fundamental niche is important in understanding the basic distribution and abundance of species. However, what is observed and generally used in climatic envelope models is a species' 'realised niche' – the area where the species is found when other factors such as competition, predation and disease are taken into account (Preston et al., 2008). Species may be able to live in certain areas where they are not found now if, for example, certain predators or competitors were to change their distributions. When predicting species' distributions and abundances under novel

circumstances, such as climate change, more confidence can be applied to models based on an understanding of the direct effects of climate on species' physiological tolerance thresholds, because predicting how biotic interactions will change is problematic (Buckley, 2008). Species have been shown to change ranges for many reasons other than climate change (Balbontin et al., 2008; Okes et al., 2008; Hockey & Midgley, in press) including anthropogenic habitat alteration and it therefore becomes important to be able to distinguish climate-induced range changes from range changes driven by other factors.

To determine how physiology might limit a species' range we need to identify and measure key factors that influence an individual's ability to survive in different environments and how these factors interact with the physical environment to influence individual fitness (Kearney & Porter, 2004). Environmental variables that will affect any organism will be those that influence the acquisition of energy (food) required for growth and reproduction and those which allow an organism to avoid entering windows of dangerously high or low body temperatures. In the terrestrial environment these latter variables include radiation, wind, air temperature and humidity (Porter et al., 1973). Environmental stressors which limit a species' distribution may vary in time and space and so deciding on which environmental variables within a species range may affect its fitness is problematic (Helmuth et al., 2005). Further, individuals of the same species will vary in their capacity to deal with environmental variation (McKechnie, 2008).

Birds are particularly responsive to changing environmental conditions and so could potentially be used as bio-indicators of the biological effects of a changing climate (Crick, 2004). Many studies have explored the mechanistic links between climatic conditions and the behaviour, morphology and physiology of individuals, all of which have contributed to a better understanding of how climatic factors influence individual fitness of birds (Root, 1988; Dawson & Whittow, 1999). On a local scale, weather can affect metabolic rates in birds, can influence conditions under which foraging or other essential behaviours are performed and can impact on breeding success (Crick, 2004; Bolger et al., 2005; Gordo, 2007; Robinson et al., 2007). Changes in bird population sizes and distributions and changes in behaviour, such as the onset of breeding and the phenology of migration, have already been attributed to changes in climate (McCarty, 2001; Saether et al., 2004). Under future predicted scenarios, some species may be forced to shift their distributions ten times faster than

during any climate change seen at least since the last ice age (Wormworth & Mallon, 2006).

One meteorological variable to which birds are particularly susceptible is ambient temperature. There is a range of environmental temperatures over which body temperature remains constant for most birds where they do not have to use energy to either lose or maintain body heat (the thermoneutral zone). Temperatures above and below this range both result in increased heat production, which is costly. Below the critical limit an individual must increase its metabolic rate to offset heat loss and above the upper critical limit it must increase its metabolic rate in order to fuel heat dissipating mechanisms. Some bird species have been found to be adversely affected by temperature increases as small as 1°C (Shoo et al., 2005). To understand how birds may respond to changes in climate we need to know how close individuals are to their thermal limits in nature and how they respond to temperature changes (Stillman, 2003).

It has been predicted that Africa is very likely to warm during this century and experience an increase in extreme temperatures, particularly in southern Africa (Kruger & Shongwe, 2004; Christensen et al., 2007). Birds are susceptible to rising temperatures because they are (mostly) diurnal, have high body temperatures and most have high metabolic rates. Only a few make limited use of thermally buffered microsites (Williams et al., 1999). As well as having morphological adaptations such as bald patches, birds respond to high temperatures both behaviourally and physiologically (Wolf, 2000). Behaviourally they can seek shade and perform behaviours that release body heat (Dean et al., 1999). In doing so, however, they have to balance energy and water demands with energy expenditure and water loss. Physiologically, they release excess body heat through evaporative cooling, but dehydration rates increase as evaporative cooling increases (Dawson & Whittow, 1999). In arid areas, where water is in limited supply and ambient temperature reaches a point where the bird cannot maintain this balance, mortality can result. Extreme high-temperature events have caused mass avian mortality in the past (Wolf, 2000). In South Africa, under a climate warming scenario of 1.8-2.0°C, 28-32% (with dispersal) or 33-40% (with no dispersal) of the 951 bird species are predicted to be threatened with extinction (Thomas et al., 2004).

Bioclimatic envelope models have predicted climate-driven range changes for birds in southern Africa. These models have been based primarily on linking current

distributions with associated vegetation types and climate variables (Erasmus et al., 2002). Few of these models have incorporated any knowledge of physiological constraints on species' ranges and acknowledge their limited ability to predict changes without such data (Simmons et al., 2004). However, these data exist for only a limited number of species within each family of birds within southern Africa, such as Alaudidae, Columbidae, Laniidae, Psittacidae and Struthionidae (Soobramoney et al., 2003; Williams & Tieleman, 2005; Burton et al., 2008). Conducting single-species studies of physiological responses of southern African bird species to high temperatures would be a costly and lengthy process and can be fraught with biological inaccuracies due to experimental design (McKechnie, 2008). A more focused approach is first to identify those species which may be more susceptible to high temperatures through a multi-species, field-based behavioural study. A species operating close to its physiological capacity will have limited scope for adapting to changes in the environment (Stillman, 2003). In contrast, a species operating well within its physiological 'comfort zone' will be more capable of responding to environmental fluctuations (Costa & Sinervo, 2004). Because changes in temperature can have multi-faceted effects on an individual, field-based observations may provide a more comprehensive first attempt at identifying lethal temperature thresholds across a broad range of species (Geiser et al., 2007).

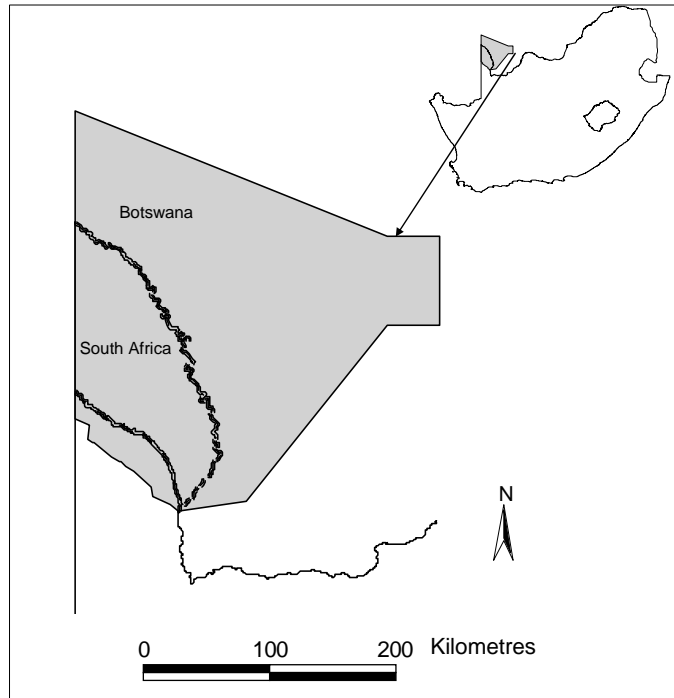
The objective of this pilot study was to determine whether it was possible to develop a field-based, rapid-assessment technique to predict which bird species may be most vulnerable to rising temperatures. The link between stress behaviours and what they mean physiologically has been quantified for a limited number of species (Dawson & Whittow, 1999). Where it has been quantified, direct links have been shown between behaviour and physiology validating the use of behavioural observations as indicators of stress (Withers & Williams, 1990). By calculating how much more time these species will experience stress under future climate scenarios it should be possible to predict which species (and in approximately what order) may be lost from hot areas as temperatures increases.

This study principally tests the hypothesis that small birds will be more sensitive to temperature increases than will larger birds (Simmons et al., 2004). Small birds, which have limited capacity for water storage, are closely coupled with their thermal environment and have a high surface area to volume ratio, making them susceptible to physiological stress brought about by evaporative water loss.

## METHODS

### Study area description

Field work was conducted during November and December 2008 in the South African section of the Kgalagadi Transfrontier Park (situated between 24°15'S and 26°30'S and 20°00'E and 20°45'E). The South African section of the park is approximately 9591 km<sup>2</sup> and is situated in the south-western corner of the Kalahari Desert (Figure 1). The vegetation is Kalahari Thornveld consisting mainly of open *Acacia erioloba* and *Boscia albitrunca* savanna, dominated by *Stipagrostis* grass (Leistner, 1967). Two dry riverbeds, the Nossob and the Auob, run through the Park and flow very infrequently. The climate is temperate and arid. Annual rainfall is unreliable and irregular (200-250 mm) with most rainfall occurring between January and April. There are large temperature fluctuations, both on a daily and seasonal basis, with winter minima of -10.3°C and summer maxima of 45.5°C. Mean daily temperatures range from 34.7°C (maximum) and 19.5°C (minimum) in January to 22.2°C (maximum) and 1.2°C (minimum) in July (Steenkamp et al., 2008).



**Figure 1** Location of the Kgalagadi Transfrontier Park, South Africa. The two dry river beds running through the South African section of the park are represented by thick shaded lines.



The study site was selected because the area has a higher average daily temperature than most other areas within southern Africa, and extreme high temperatures occur relatively frequently (Doolan & Macdonald, 1996). Furthermore, the Kalahari ecosystem will experience the highest level of warming within southern Africa (Moise & Hudson, 2008), therefore species loss is more likely than in cooler, wetter areas of the region (Erasmus et al., 2002). A second reason for the choice of study site relates to simplicity of understanding the possible ecological consequences of species loss. It is considered very unlikely that rising temperatures in the Kalahari will result in an influx of species from elsewhere because there is no source pool of different species inhabiting a hotter area to provide such immigrants.

### **Bird surveys**

Data were collected by one observer using instantaneous sampling transects, point counts and walked surveys. Instantaneous observations and point counts were conducted from within a vehicle along driven transects. Walked surveys were conducted on foot from within rest camps. For each of the three methods, data were recorded for all birds observed except those seen in flight and those showing any change in behaviour due to observer presence. No data were collected during rain. Three data collection methods were used to increase sample size and to test whether the methods had individual sampling biases. For example, instantaneous sampling along driven transects may have biased sampling to conspicuous taxa. Point counts allowed the observer to search for birds within a fixed time period meaning that all birds, including more sedentary species, were likely to be seen. Walked transects allowed the observer to search for birds more thoroughly on foot. For all three survey methods the accompanying data (habitat variables, climatic variables and individual behaviour) were recorded in the same way for each bird seen.

Walked surveys were conducted throughout the day and along no set transect: all observations were instantaneous, collected at the first moment a bird was seen. Instantaneous sampling was conducted from a vehicle driven at 10-20 km/h along transects of variable length between 05h30 and 19h00. Each day a new transect was started and a 500m interval was left between transects. To minimise pseudoreplication, no transect was surveyed more than once and all individual transects were separated by at least 500 m. The vehicle was stopped each time a bird was observed and behaviour and environmental data were recorded immediately.

Along each transect, point counts were conducted at random sites. Each point count lasted five minutes and was preceded by a two-minute period where birds were allowed to habituate to observer presence. Semi-circular point counts were used because the vehicle obstructed the view of one side of the road (cf Fox & Hockey, 2007). The behaviour of every individual bird that was observed during the five-minute period was recorded at the moment the bird was first seen.

### **Bird behaviour**

Behavioural categories were predetermined and not mutually exclusive. Behaviour was categorised into stressed and unstressed behaviours. Unstressed behaviours included foraging, drinking, singing, nest maintenance, dust bathing, adult/juvenile interactions, running, walking, standing and perching. Stress behaviours were panting, wing spreading, gular fluttering, head drooping and ptiloerection. Panting allows air passing through the lungs and air sacs to carry heat away from the body. Wing spreading and ptiloerection increase air circulation over the bird's body. The throat has a generous blood supply and so by flexing the hyoid bone at a rapid rate (gular fluttering – not performed by all birds) heat is released from the area (Bartholomew et al., 1968). Much heat is also lost through bare legs which some species keep cool by deliberately allowing liquid waste to run down them. Some birds also wet their feathers, splash water on themselves for cooling or deliberately dampen their nests or the ground around them (Amat & Masero, 2007). These last three behaviours were considered difficult to observe in the field and so were not included as stressed behaviour types. Similarly, 'seeking shade' was difficult to categorise as stress behaviour because many perching birds would automatically have been put in that category. Rather, birds were simply recorded as being in or out of shade. Drinking behaviour was also recorded but not used in analyses as it is difficult to know whether a species is drinking because it is stressed.

However, to provide some indication of which species were heavily water dependent, water hole observations were conducted. Frequency of observations of a species at a water point was used as a proxy for water dependence. On two separate days, species presence was recorded at waterholes for 5 minutes, 6 times an hour. Observations were conducted between the hours of 06h00 and 16h15. The same environmental variables recorded for individual sightings (see below) were also recorded for water hole observations. Counts were not made as they would have been

biased because it was not possible to count large flocks of highly mobile, skittish birds.

### **Environmental measurements**

Ambient air temperature (accuracy  $\pm 1^\circ\text{C}$ ) and humidity (accuracy  $\pm 3\%$ ) were measured with a shaded, portable, hygro-thermometer dew point meter (BAMR (Pty) Ltd, Claremont, South Africa) which displayed both measurements simultaneously and recorded a daily minimum and maximum for both. Wind speed (km/hr) was determined with a handheld rotating cup anemometer (Deuta Anemowerke, Bergisch, Germany, accuracy:  $\pm 5\%$ ). The manufacturer's calibration for these instruments was relied upon. Cloud cover was estimated by the observer as a percentage. To determine whether there was a significant effect of microsite on environmental variables, measurements of ambient temperature in shade were taken below three species of tree to estimate the extent to which the tree canopy buffered ambient air temperature. Some species of desert trees have been found to reduce solar radiation by up to 87%, and up to 90% in the deepest shade, depending largely on tree architecture. Ground temperature below the canopy can also be reduced by up to 21% (Kotzen, 2003). The same hygro-thermometer dew point meters used for the behavioural observations were used to measure ambient temperatures in shade.

### **Landscape variables**

The study area comprised two main habitats – riverbeds and dunes. The two dry riverbeds are characterised by having many large trees, especially *Acacia erioloba*, *A. heamatoxylon* and *Boscia albitrunca*. Dunes consist of grassy savanna, especially after rain, and also support shrubs and much smaller trees. The geographic coordinates of each observation were collected using a handheld GPS unit (Garmin GPS Map 72). GPS locations were also collected for all water bodies within the Park, including temporary waterholes exceeding 2 m<sup>2</sup> in size. Distance to water of each bird in the database was calculated using the Arcview extension 'Nearest Features' in the geographic information system Arcview 3.3 (Environmental Systems Research Institute., 2002; Jenness, 2004). Trees can modify microclimates by affecting wind speed through the canopy, relative humidity, solar radiation and terrestrial radiation (from the ground). The extent of modification depends on the thickness and characteristics (uniformity) of the tree canopy, the time of day (and so the angle of the

sun) and the soil make up and colour which affects albedo (Kotzen, 2003). A shade category was assigned for each sighting: full sun, ‘structural’ shade (when an individual was observed in the shade of vegetation) and shade provided by clouds (when an individual would have been in full sun except for cloud cover). There are also differences in temperature with height above ground (Brown et al., 1994). If birds were observed in a tree, the height (m) at which they were perched was estimated.

## **Analyses**

### *Statistical analyses*

Binomial generalised linear mixed effects models were used to link species’ responses to environmental variables. The procedure lmer was used (add-on package lme4) with fit by Laplace approximations in R 2.7.1 (R Development Core Team, 2008). Mixed-effects models are capable of performing analyses when multiple random factors affect data simultaneously and when data follow a non-normal binomial distribution (Quene & van den Bergh, 2008). Discrete and categorical factors can be combined in a single model. Fitting such models by maximum likelihood involves integrating over these random effects. In general, these integrals cannot be expressed in analytical form. R does not associate a *P*-value with the deviance because in these types of models the *P*-value is only an approximation. The response variable was binomial because data were categorised into ‘stressed’ or ‘non-stressed’ behaviour. The Akaike Information Criterion (AIC) is a measure of goodness of fit which takes the number of fitted parameters into account and was used to compare models (Anderson et al., 2000). Before choosing which environmental variables could be included in the model, all variables were examined to test for autocorrelation using STATISTICA 8 (StatSoft Inc., 2007). There was a strong correlation between temperature and wind speed, shade category and cloud so the latter three factors were excluded from the analyses. Temperature, humidity, and method were entered as fixed factors – with temperature as a covariate factor. Species and body mass were entered as random effects. The model including species as a random effect effectively controls for phylogeny by allowing the effect of species to be tested. For both body mass and species random effect models extra models were run. These extra models were run to examine the effect of method, humidity, distance from water and height of a species in a tree on behavioural response. An average body mass (g) was derived by taking an

average for both males and females combined (Hockey et al., 2005). All random effects models were compared with a mean (no random effects) model to determine whether within-species variation or body mass was the better predictor of response. The model with the lowest AIC value is the model that best describes the data. GenStat 11.1 (VSN International., 2008) was used to derive Wald Statistics for the best model to determine the importance of the fixed factors in the model (Zar, 1999).

### *Species' response scales*

To investigate further how stress responses between species differed, it was necessary to break down the two response factors used for the generalised linear mixed effects models (stressed and unstressed) into more detailed categories. Because it was not possible to quantify the physiological implications of the various behaviours, a categorical scale of behavioural response, representing escalating reactions to stress, was derived for all species. A ranking based on behaviour type, whether the behaviour was performed in the shade or the sun and the lowest ambient temperature at which the behaviour was observed was obtained for all species observed more than 50 times ( $n = 22$ ). Species observed fewer times would have biased the ranking because not all species were observed performing all behaviours and not all species were observed across the full range of temperatures experienced during the study. The sequence in which behaviours were observed in response to escalating temperatures was ranked (1, 2, 3....) and an average rank was calculated across all the species. The categorical scale included 11 behaviours, 5 of which were classified as stress responses. Unstressed responses were categorised as 1=sedentary in full sun, 2 = active in shade, 3 = sedentary in shade, 4 = active in full sun, 5 = walking in shade and 6 = walking in sun. Stressed responses included 7 = panting in shade, 8 = panting in sun, 9 = head drooping in sun, 10 = panting and gular fluttering in the sun and 11 = panting and gular fluttering in the shade. It is important to note that this ranking relates only to the sequence of behaviours: the temperatures at which different behaviours were initiated varied between species. Wing-spreading was excluded from the final analyses because of the difficulty in determining the reason for wing-spreading (for example, to rid the individual of parasites vs cooling behaviour) on the advice of expert opinion.

### *Determining which species experience stress first as temperatures increase*

Temperature ranges (minimum, median and maximum) over which ranked behaviours were performed were established for each species. The median value was taken as an average to minimise the effect of outliers. For each species, the lowest temperature at which they were observed stressed was determined. Assuming that birds observed stressed at lower ambient temperatures were most vulnerable to high temperatures, species were ordered from the most vulnerable to the least vulnerable species. Mann-Whitney U and Kruskal-Wallis tests were used to test relationships between the temperatures at which birds become stressed and possible predictive factors (Zar, 1999).

### *Individual responses to high temperatures*

The lowest temperatures at which stress-related behaviours occur indicate which species may be vulnerable to high temperatures but it is also important to understand how high temperatures may compound physiological stress by affecting other behaviours. To determine whether the activity budgets of different species differed at high temperatures, the proportion of sightings in which each species was seen performing different behaviours was calculated over a range of temperatures. All species observed more than 50 times (n=22) were used in this analysis. Activity budgets were determined for temperatures ranges of 30-35°C, 36-40°C and  $\geq 41^\circ\text{C}$ . Observations below 30°C were not included as no individuals were visibly stressed below this temperature. Activity budgets were based on the same categories that were used for the ranked stress scale and included five categories: proportion of time spent stressed, proportion of time spent active in the sun, proportion of time spent active in the shade, proportion of time spent sedentary in the sun and proportion of time spent sedentary in the shade.

### *Climate prediction data*

Species' range data and appropriate-scale climate predictions are not currently available for all the species observed during the study. However, to gain some perspective on which species are likely to leave the Kalahari area first based on the temperature thresholds identified in this study, each species was assessed in a future scenario of increased temperature. Global Climate Models (GCMs) are the best tools available for making climate-change projections, but these differ in the predictions

they make at a regional scale (Christensen et al., 2007). GCMs predict temperature changes in average global temperature. However, these are generally not useful at the regional or local scale because the underlying data used to generate the information are often highly aggregated (Meadows, 2006). Much recent work on climate change modelling has focused on downscaling these global models to a regional focus. Empirical downscaled models for a number of GCMs are available for Africa and provide meteorological station-level responses to global climate (Climate Systems Analysis Group, 2006). Namibia has only limited climate data and so the nearest reliable weather station to the study site is Vanzylsrus, South Africa, which lies 180 km to the south-east of the study site. The downscaled version of the GCM *csiro\_mk3\_5* was used for current and future projections (Climate Systems Analysis Group, 2006). This model was chosen for its capacity to represent climatic variables for Africa (Meadows, 2006). Future scenarios (A2 SRES) for this area were available from 2046 to 2065. Daily data do exist but future projections are not as reliable and so monthly climate data were used for both current and future climate conditions. The increase in temperature predicted for the Kalahari was estimated by comparing future scenarios (2046) of monthly temperature with baseline data (an average of temperatures from 1950 to 2001).

To create a physiological model for how an increase in temperature may impact a species' distribution normally requires a complex suite of data (Dunham & Overall, 1994). From the stress thresholds derived in this study it was only possible to estimate on a monthly basis whether a species is likely to spend time stressed. Two measures were used to estimate this. The average daily maximum temperature ( $TM_{av}$ ) provides a conservative estimate (because it is based on averages) of monthly maximum temperature. The maximum monthly temperature represents the highest temperature occurring within a month ( $TM_{max}$ ). The lowest temperature at which a species became stressed was used to determine for the values of  $TM_{av}$  and  $TM_{max}$  how many months a year a species would enter stress situations in the future relative to the present. This could only be determined for species which demonstrated stress behaviour.

## RESULTS

### Weather conditions

Weather was variable during the study period with ambient temperature during some observation periods not exceeding 28°C. The weather conditions reported here are those that were encountered during observation periods only; they do not represent daily fluctuations. Rainfall was variable, with two nights receiving over 17 mm of rain. Some days had cloud cover 100% of the time which reduced the heat reflection from the ground.

	Unit	Mean $\pm$ SD	Range	N
T <sub>a,min</sub>	°C	29.9 $\pm$ 6.5	12.2-40.5	40
T <sub>a,max</sub>	°C	40.3 $\pm$ 4.6	27.6-47.6	40
H <sub>a,min</sub>	%	21 $\pm$ 3.7	20-39	40
H <sub>a,max</sub>	%	29 $\pm$ 11.6	20-60	40
Ws	m/s	0.12 $\pm$ 0.3	0-2.7	5723
Cloud cover	%	36.2 $\pm$ 31.2	0-100	5723

**Table 1** Weather conditions experienced during observation periods for the duration of the study. T<sub>a,min</sub> = daily minimum ambient temperature; T<sub>a,max</sub> = daily maximum ambient temperature; H<sub>a,min</sub> = daily minimum humidity; H<sub>a,max</sub> = daily maximum humidity; Ws = wind speed; Cc = Cloud cover.

### Species observations

A total of 5723 birds of 91 species were observed (instantaneous = 3885, point counts = 1176 and transects = 662). Not all species were observed using every method and not all species were seen over the full range of temperatures experienced (Appendix 1). Body mass ranged from 7.9 g for the smallest bird (Yellow-bellied Eremomela *Eremomela icteropygialis*) to 68.7 kg for the largest bird (Common Ostrich *Struthio camelus*). Number of observations per species ranged from 1-655.

### Predicting heat stress response

All models that included body mass as a random factor were better predictors of stress response at high temperatures than models that included exactly the same variables as fixed factors but included species as random factors (Table 2). The best model for determining heat stress response included temperature and body mass as covariates



and temperature, species, humidity and sampling method as fixed factors ( $AIC_c = 2303$ ). However, two other models had  $AIC_c$  values within 2  $AIC_c$  units of the best fit model. One model included the same factors as the best model but included tree height ( $AIC_c = 2304$ ) and the second did not include method as a fixed factor, only temperature and body mass as covariates and temperature, species and humidity as fixed factors ( $AIC_c = 2305$ ). A model with a  $\Delta AIC_c$  value of less than 2 between it and the best model is thought to be a good model given the data (Zar, 1999). Method (Wald statistic = 1.86,  $P < 0.173$ ) was not found to be a significant predictor of heat stress. This meant that all observations collected by different sampling methods to be used for further analyses. Humidity (Wald statistic = 6.50,  $P < 0.011$ ), temperature (Wald statistic = 139.26,  $P < 0.001$ ) and species (Wald statistic = 178.72,  $P < 0.001$ ) all significantly determined whether individuals experienced heat stress.

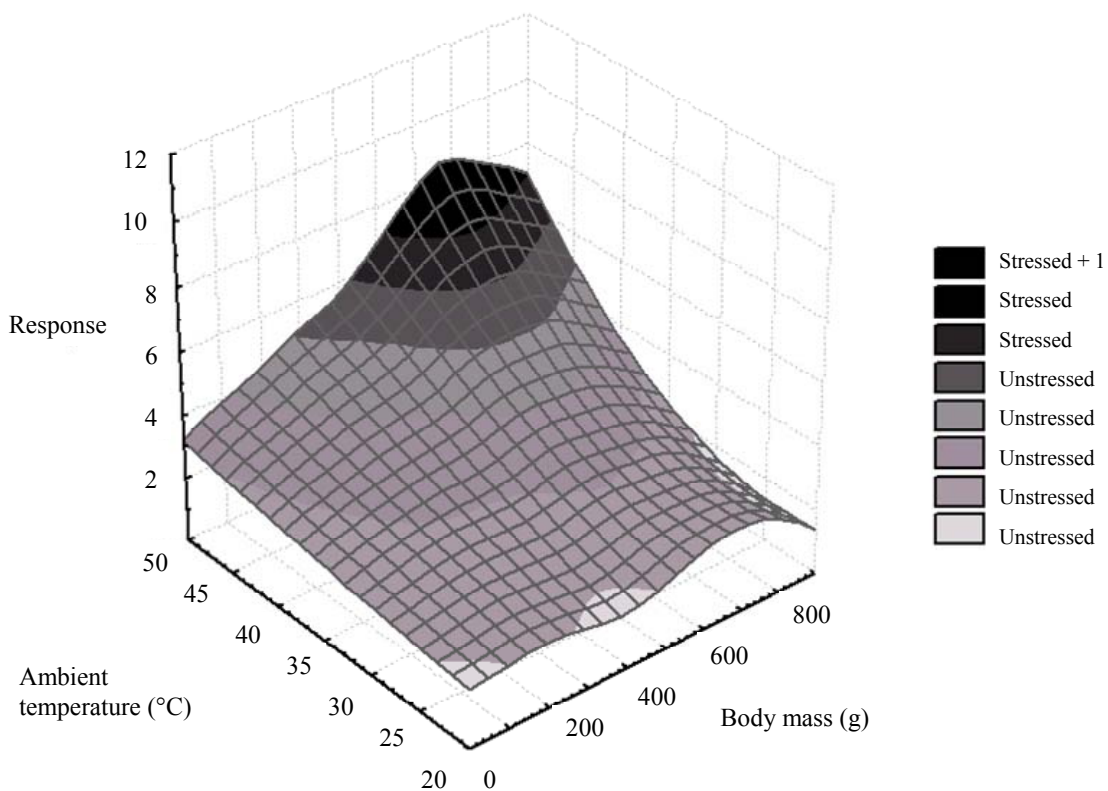
Models	AIC <sub>c</sub>
<i>St</i> Temperature + Species + Humidity + Method + Distance + Tree height (Random: Temperature: Body mass)	2641
<i>St</i> Temperature + Species + Humidity + Method + Tree height (Random: Temperature: Body mass)	2304
<i>St</i> Temperature + Species + Humidity + Method + Distance (Random: Temperature: Body mass)	2628
<i>St</i> Temperature + Species + Humidity + Distance (Random: Temperature: Body mass)	2615
<i>St</i> Temperature + Species + Humidity + Tree height (Random: Temperature: Body mass)	2306
<i>St</i> Temperature + Species + Humidity + Method (Random: Temperature: Body mass)	2303
<i>St</i> Temperature + Species + Method + Distance (Random: Temperature: Body mass)	2631
<i>St</i> Temperature + Species + Method + Tree height (Random: Temperature: Body mass)	2309
<i>St</i> Temperature + Species + Humidity (Random: Temperature: Body mass)	2305
<i>St</i> Temperature + Species + Method (Random: Temperature: Body mass)	2308
<i>St</i> Temperature + Species + Distance (Random: Temperature: Body mass)	2617
<i>St</i> Temperature + Species + Tree height (Random: Temperature: Body mass)	2310
<i>St</i> Temperature + Body mass + Humidity + Method + Distance + Tree height (Random: Temperature: Species)	2514
<i>St</i> Temperature + Body mass + Humidity + Method + Tree height (Random: Temperature: Species)	2513
<i>St</i> Temperature + Body mass + Humidity + Method + Distance (Random: Temperature: Species)	2514
<i>St</i> Temperature + Body mass + Humidity + Distance (Random: Temperature: Species)	2512
<i>St</i> Temperature + Body mass + Humidity + Tree height (Random: Temperature: Species)	2511
<i>St</i> Temperature + Body mass + Humidity + Method (Random: Temperature: Species)	2513
<i>St</i> Temperature + Body mass + Method + Distance (Random: Temperature: Species)	2516
<i>St</i> Temperature + Body mass + Method + Tree height (Random: Temperature: Species)	2514
<i>St</i> Temperature + Body mass + Humidity (Random: Temperature: Species)	2510
<i>St</i> Temperature + Body mass + Method (Random: Temperature: Species)	2514
<i>St</i> Temperature + Body mass + Distance (Random: Temperature: Species)	2513
<i>St</i> Temperature + Body mass + Tree height (Random: Temperature: Species)	2512

**Table 2** Summary of model (*St*) selection results for the predictors of heat-stress response in different species. Factors in the model included temperature (°C), species, body mass (g) of each species, humidity (%), sampling method (instantaneous, point-count or transect), distance (m) to water and height (m) of the bird in a tree (if the species was observed in a tree or 0 if it was observed on the ground).

### Body mass as a predictor of temperature-related stress response

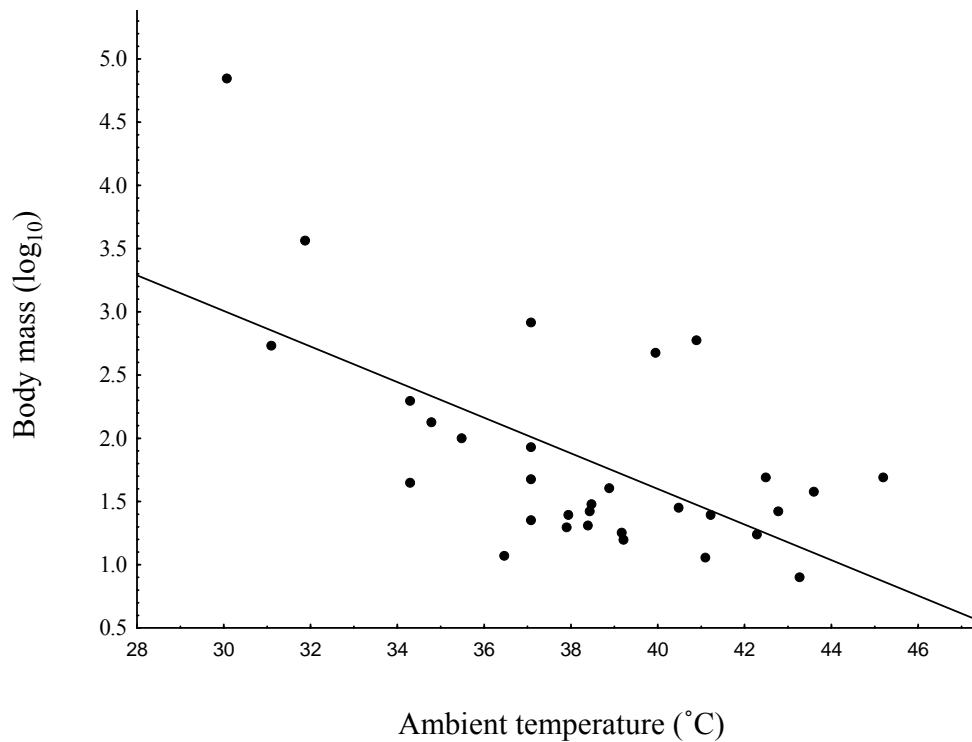
A distance-weighted, least-squares procedure was used to fit a 3-D surface function to a 3D scatter plot in STATISTICA 8, to reveal the relationship between temperature, body mass and the 11 behavioural response categories (McLain, 1974). The plot was adjusted to contain positive values and the fit procedure meant that although the overall visual pattern is the same, the response variables appear to only reach 9. Only data from birds weighing less than 1000 g ( $n = 85$  species) were used in the surface plot because interpolating between large gaps in mass would have produced an unrealistic representation of the data.

Larger birds not only display a greater range of stress behaviours than smaller birds but as body mass increases birds are more likely to become stressed at lower temperatures (Figure 2). This is contrary to the original hypothesis and, at face value, unexpected in terms of physiological predictions.



**Figure 2** A three-dimensional plane reflecting the interplay between body mass, ambient temperature and behavioural response derived for birds weighing < 1000 g. Behavioural response is categorised into unstressed responses (1=sedentary in full sun, 2 = active in shade, 3 = sedentary in shade, 4 = active in full sun, 5 = walking in shade and 6 = walking in sun) and stressed responses (7 = panting in shade, 8 = panting in sun and 9 = head drooping in sun) and stressed response + 1 (10 = panting and gular fluttering in the sun and 11 = panting and gular fluttering in the shade).

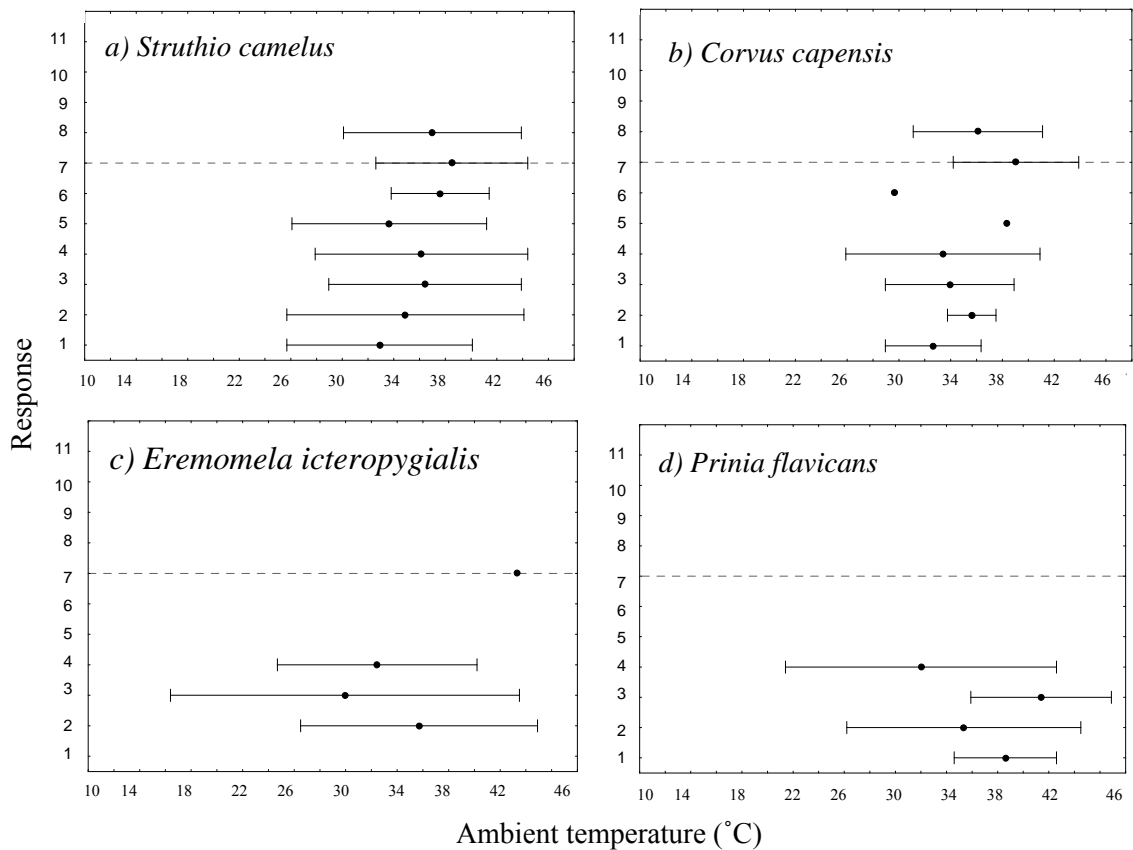
Although the data do not fit a linear pattern closely, larger birds initiated stress-related behaviours at lower temperatures (N=55,  $P < 0.0002$ ,  $r^2 = 0.3832$  for log-transformed mass data, Figure 3).



**Figure 3** The relationship between body mass ( $\log_{10}$  g) and the temperature ( $^{\circ}\text{C}$ ) at which a bird was first observed stressed. This analyses included only species which were observed  $> 30$  times – this was to avoid outlying species which may only been observed once at one temperature from biasing the results. Species which were never observed stressed could not be used in this analysis.

Common Ostriches, weighing an average of 68.7 kg, sometimes became stressed at temperatures as low as  $30.1^{\circ}\text{C}$  (Figure 4a). Other large birds that became stressed at relatively low temperatures included Cape Crows (*Corvus capensis* – 537 g) at  $31.1^{\circ}\text{C}$  (Figure 4b) and Giant Eagle-Owls (*Bubo lacteus* – 2045 g). By contrast, the smallest species seen in the study, Yellow-bellied Eremomela, was only observed stressed twice, at  $43.3^{\circ}\text{C}$  (Figure 4c). Neither Black-chested Prinias (*Prinia flavicans* - 8.8g) nor Rufous-eared Warblers (*Malcorus pectoralis* - 10.1 g) were seen demonstrating stress behaviours even though they were observed at temperatures as high as  $46.9^{\circ}\text{C}$  and  $43.5^{\circ}\text{C}$  respectively (Figure 4d). Not only were small species less likely to become stressed at lower temperatures but they were also active at higher temperatures (Appendix 2). Assuming that reduced activity at high temperatures may

be affecting life-history traits, a change in non-stressed behaviour at high temperatures can help understand which birds may be more vulnerable to rising temperatures. Yellow-bellied Eremomelas were the most frequently observed species active in the sun at temperatures  $\geq 41^\circ\text{C}$ . Of all the species, Black-chested Prinias, Scaly-feathered Finches (*Sporopipes squamifrons* – 11.1g) and Chestnut-vented Tit-Babblers (*Parisoma subcaerulum* – 15.7 g) were observed most commonly active in the shade (60%, 44% and 78% respectively) over  $\geq 41^\circ\text{C}$ ). Only 3% of Common Ostriches and 8% of Cape Crows were seen active in the shade at temperatures  $\geq 41^\circ\text{C}$ . In fact, 63%, 72% and 68% of Common Ostriches and 38%, 61% and 100% of Cape Crows were stressed at 30-35°C, 36-40°C and  $\geq 41^\circ\text{C}$  respectively (Appendix 2).



**Figure 4** Temperature ranges (minimum, maximum and median °C) over which four different species (a-d) demonstrated different types of behaviour. A categorised behavioural scale was devised with categories relating to certain behaviour types: 1 = sedentary in full sun; 2 = active in shade; 3 = sedentary in shade; 4 = active in full sun; 5 = walking in the shade; 6 = walking in full sun; 7 = panting in shade; 8 = panting in sun; 9 = head drooping in full sun; 10 = panting and gular fluttering in the sun and 11 = panting and gular fluttering in the shade. Behaviours on and above the dashed line (response = 7) all represent stress behaviours.

### **How does water-dependence influence temperature-related stress response?**

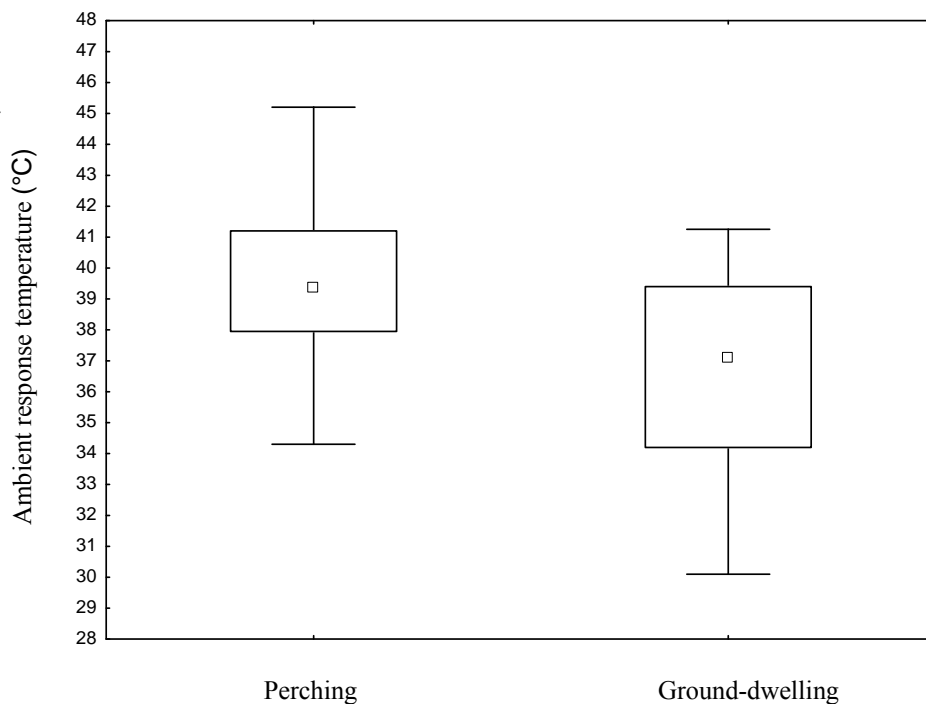
Only 20 species were observed drinking at the waterhole. None of the very smallest species recorded during the study were observed drinking. The smallest birds observed drinking at the waterholes were Black-throated Canary (*Crithagra atrogularis* – 12.7 g) and Yellow Canary (*C. flaviventris* – 17.5 g): these species had earliest stress temperatures of 41.1°C and 39.2°C respectively. The most frequently observed species at the waterholes were Namaqua Doves (*Oena capensis* - 39.9 g), Cape Turtle-Doves (*Streptopelia capicola* - 130.3 g) and Red-headed Finches (*Amadina erythrocephalus* – 11.5 g). Namaqua Doves first became stressed at higher temperatures (38.9°C) than Cape Turtle-Doves (34.8°C) and are regarded as desert-adapted bird species (Schleucher et al., 1991). The distance at which each species was seen from water was not a significant predictor of vulnerability to high temperatures in the models (AIC<sub>c</sub> = 2617, when body mass was entered as a random factor, Table 2). The mean earliest stressed response for all species observed at waterholes was 38.9°C (n = 14 for those species that had an earliest stress response temperature) compared with 38.1°C (n = 39) for birds that were never observed at water troughs.

### **Terrestrial vs arboreal birds: do their temperature-related stress responses differ?**

Ground-dwelling birds were significantly more likely to become heat stressed at lower temperatures than perching bird species (Figure 5, Mann-Whitney U = 156;  $P < 0.01$ ). Five of the seven species that became stressed at the lowest temperatures were ground-dwellers. Ground-dwelling birds are also less active at high temperature than perching birds of similar weights. Crowned Lapwings (*Vanellus coronatus* – 195 g) were first observed stressed at 34.3°C, were sedentary in the shade in over 85% of observations at temperatures  $\geq 41^\circ\text{C}$  and were stressed in all other observations (15%) above this temperature. Pink-billed Larks (*Spizocorys conirostris* – 14.3 g) first became stressed at 37.1°C and at higher temperatures were always sedentary in the shade. By comparison, arboreal Chestnut-vented Tit-Babblers (15.7 g) first became stressed at 39.3°C but were active in the shade in over 78% of observations above  $\geq 41^\circ\text{C}$ . Shade temperatures within canopies varied but shade temperatures under large *Acacia erioloba* were on average 5.7°C below ambient temperature (4.4°C below ambient temperature under smaller canopied trees). Average shade temperature under *Acacia heamatoxylon* was 2.4°C below ambient temperature. Ground birds may

experience higher environmental temperatures even when in the shade because of radiation.

Four species, all ground-dwellers, were confined to the dunes - Black-headed Heron (*Ardea melanocephala*), Cape Clapper Lark (*Mirafra apiata*), Stark's Lark (*S. starki*) and Red-crested Korhaan (*Lophotis ruficrista*). By contrast, 37 species were confined to river beds. Ground-dwelling birds made up 25% of species in the riverbeds and 33% of species in the dunes. However, in terms of individuals observed, ground-dwelling birds made up 30% of birds in the dunes versus only 11% in the riverbeds. If ground-dwellers are the most susceptible to rising temperatures, then the dunes may lose a disproportionately large number of birds under a scenario of increasing temperatures.

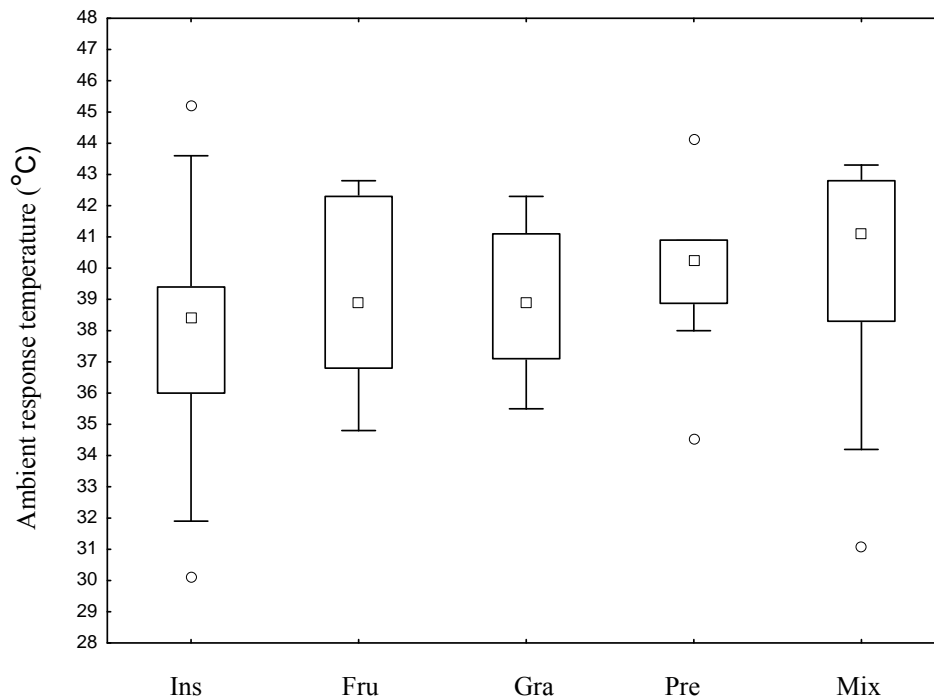


**Figure 5** The lowest mean ambient temperature (°C) at which ground-dwelling bird species and perching species were observed exhibiting stress.

### **Dietary guild as a predictor of temperature-related stress response**

If species that are vulnerable to rising temperatures are a non-random subset of the functional guilds represented among Kalahari birds, their loss from the system has potential ecological repercussions. Functional guild in this case refers to dietary guild. There was, however, no significance in temperatures at which species in different

dietary guilds became stressed (Kruskal-Wallis  $K = 3.36$ ,  $P < 0.5$ ; Figure 6). However, members of some dietary guilds had wider tolerances to high temperatures: this may increase their resilience to changing conditions (Figure 6). Overall, however, the average temperatures at which members of different guilds first exhibited stress varied by only  $2.2^{\circ}\text{C}$ . Omnivores ( $n = 9$  species) appeared the most tolerant of high temperatures: on average, these first became stressed at  $40.4^{\circ}\text{C}$ . At the other end of the scale were the insectivores ( $n = 25$ , the most species-rich guild), which became stressed at the lowest mean temperature ( $38.2^{\circ}\text{C}$ ).



**Figure 6** The mean temperature ( $^{\circ}\text{C}$ ) and range at which species in different dietary guilds first exhibit a heat stress response. Ins = Insectivores, Fru = Frugivores, Gra = Granivores, Pre = Predators and Mix = Mixed feeders (omnivores).

### Which species are most likely to be adversely affected by future climate change?

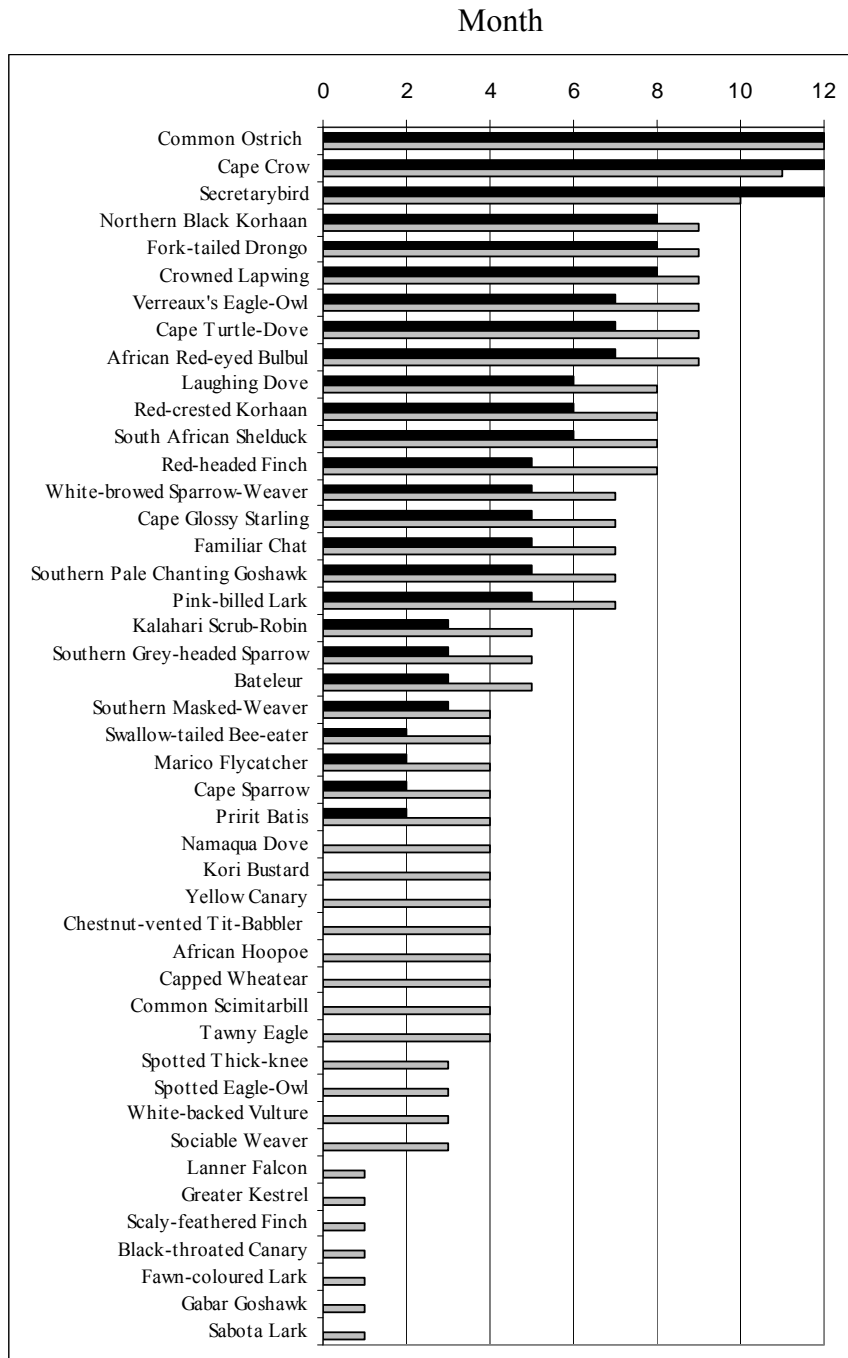
Future climate scenarios predict a  $1.1^{\circ}\text{C}$  rise in  $\text{TM}_{\text{av}}$  and a  $1.5^{\circ}\text{C}$  rise in  $\text{TM}_{\text{max}}$ , by 2046, although it is important to note these monthly values are averages (Table 3). The increase in projected  $\text{TM}_{\text{av}}$  for different months ranges from  $0.6^{\circ}\text{C}$  in October to  $3.8^{\circ}\text{C}$  in April. The increase in  $\text{TM}_{\text{max}}$  ranges between  $0.1^{\circ}\text{C}$  for December and  $3.7^{\circ}\text{C}$  for July, but with increases of  $2.3$ - $3.1^{\circ}\text{C}$  at the height of summer (January and February).



	T <sub>mav b</sub>	T <sub>mav f</sub>	T <sub>mav dif</sub>	TM <sub>av max b</sub>	TM <sub>av max f</sub>	TM <sub>av max dif</sub>
Jan	29.7	30.5	0.7	38.4	40.6	2.3
Feb	30.7	33.3	2.6	38.9	42.0	3.1
Mar	30.5	31.5	1.0	38.9	39.8	0.9
Apr	27.4	31.2	3.8	37.3	40.9	3.5
May	23.9	25.7	1.8	33.5	35.1	1.5
Jun	22.9	24.1	1.1	33.4	31.1	-2.3
Jul	23.0	24.2	1.2	33.1	36.8	3.7
Aug	22.9	24.3	1.4	33.1	31.8	-1.3
Sep	23.7	23.4	-0.3	34.3	32.5	-1.8
Oct	26.1	26.7	0.6	35.5	37.2	1.8
Nov	28.0	29.9	1.9	36.4	38.1	1.7
Dec	28.9	31.6	2.7	37.7	37.8	0.1

**Table 3** Baseline (b) and future (f) scenarios of average maximum monthly temperature (TM<sub>av</sub>, °C) and the maximum monthly temperature (TM<sub>ma</sub>, °C). dif = temperature change (°C) between now and 2046.

The number of months in which a species would experience stress could only be determined for the 56 species in which stress behaviour was observed. Under future TM<sub>av</sub> conditions, Secretarybirds (*Sagittarius serpentarius*), Common Ostriches and Cape Crows will experience stressful conditions for at least some of the time in every month of the year (Figure 7). Under future TM<sub>max</sub> predictions, temperature increases would push 53 species into temperature windows where they would experience levels of heat stress greater than those they experience at present (Appendix 1). Most species will experience an extra one (n = 11 species) or two (n = 18 species) months during which they periodically enter a stressed state. Some species will experience an extra three (n = 5 species) or four (n = 8 species) months during which they will be stressed for some of the time. More than 40% of species - all those that enter stressed states at temperatures below 37.1°C - will experience stressful conditions during at least six months of the year (Figure 7, Appendix 1).



**Figure 7** Number of months in which each species seen stressed during observations would endure temperatures ( $TM_{max}$ ) above which they would become stressed for current (black) and future (grey) scenarios of temperature change. Species in the lower half of the table (from Namaqua Dove) apparently experience no stress under current conditions even though they did display stress behaviour during this study. The reason for this is that these stressed behaviours were only observed at temperatures above the average  $TM_{max}$  for the past 51 years which was used as the baseline for comparisons with a future climate scenario (in 2046).

## **DISCUSSION**

### **Assessing vulnerability to climate change**

Determining predictive methods for detecting species' vulnerability to climate change is essential in order to minimise biodiversity loss. Most attempts to date have been based on assessing vulnerability of single species or running large-scale models of species' distributions to assess where changes in climate will have the largest impact (Hilbert et al., 2004). Assessing threats to single species will be of limited use to policy makers who have to make decisions at the regional and national scale that must take into account multiple species and ecosystems. On the other hand, large-scale models may find patterns but not necessarily understand the mechanisms underlying them (Helmuth et al., 2005). Recent assessments have focused on trying to define biological characteristics that make a species vulnerable to climate change in order to make rapid, multi-taxon assessments of vulnerability (Jiguet et al., 2007; Foden et al., 2008). These include traits such as specialised niche requirements, narrow environmental tolerances, and poor dispersal abilities. However, validation of these traits as predictors of vulnerability will need to be verified for most species and in some cases this may only happen once a species has already been adversely affected by changing climate. Many of these traits are found in species that are already (and perhaps naturally) threatened or rare. Although population size and trend are the best correlates of extinction risk, it is important to identify susceptible species which are widespread or common and although not currently threatened, may be at risk from novel conditions imposed by climate change (Julliard et al., 2004; Hulme, 2005). Methods that can predict a species' vulnerability through biological knowledge, i.e. ones that do not have to be verified because the impacts of climate change are already known, will be by far the most useful for decision makers and conservation planners. This pilot study investigated whether it was possible to assess which bird species may be most vulnerable to rising temperatures in the Kalahari Desert using a rapid, field-based assessment technique.

Body size in birds was found to be a fairly robust indicator for predicting species' vulnerability to increasing temperatures. Large birds became heat stressed at significantly lower temperatures than smaller birds. Large birds can therefore be predicted to be the first species that would be lost from this ecosystem. This finding is in direct contrast to that which was predicted based on physiological theory and

highlights the importance of empirical investigations when trying to predict the impacts of climate change. Relationships between body mass and physiological adjustments to temperature have been found to be less than convincing when based on purely laboratory-derived data (McKechnie, 2008). Not only does experimental design become a compounding factor but data for larger birds (> 30 g) are also limited.

### **Body size and vulnerability to high temperatures in birds**

There are several possible explanations of why larger birds become stressed at lower temperatures. Firstly, access to microsites may play an important role in conserving water loss in small bird species and therefore reducing stress (Wolf & Walsberg, 1996a). Although smaller birds may be more susceptible to mass-specific evaporative water loss they may be able to reduce the rate of such loss by seeking shade. Trees in the Kalahari lowered temperatures under canopies by between 2.4-5.0°C when compared with ambient temperature. In other hot areas, small birds (5-7 g) have been shown to choose specific microsites within shaded canopies, which can result in water savings of up to 50-67% (Wolf et al., 1996; Wolf & Walsberg, 1996b). Microsites have also been shown to play a role in thermoregulation by larger birds, with species showing less heat stress when shaded microsites were available (Barrows, 1981). In the Spotted Owl (*Strix occidentalis*), selection of cooler nesting sites resulted in a 40-90% decrease in the number of days per year in which continuous gular fluttering was required. However, as body size increases the numbers of available microsites in hot environments that are cooler than the surroundings become increasingly limited. In southern African ecosystems both Spike-heeled Larks (*Cherosomanes albofasciata*) and Anteating Chats (*Myrmecocichla formicivora*) use underground burrows of fossorial mammals to escape from high temperatures (Williams et al., 1999). This is not an option available to larger birds.

Secondly, larger birds may not be able to rid themselves of excess heat as efficiently as smaller species. The original hypothesis of the study was that because smaller birds have a high surface to volume area, water loss by evaporative cooling would be limited by their ability to replenish water and as a result they would be the birds most stressed at high temperatures. Although larger birds may not be restrained by water they may be restrained by their ability to shed heat because of their smaller surface area to volume ratios and concomitantly lower evaporation rates. If they

cannot evaporate water fast enough, their heat load will build up and they may experience hyperthermia at relatively low temperatures. For example, a relatively large bird, the Yellow-billed Magpie (*Pica nuttalli* – 159 g), has limited capacity for evaporative cooling at high temperatures, with death sometimes occurring at temperatures as low as 40°C, despite the fact that these birds have relatively low basal metabolic rates (Hayworth & Weathers, 1984). A study of several raptor species, including Tawny Eagles (*Aquila rapax*), found that they had lower thermal conductance than expected for birds of that size living in hot environments (Wasser, 1986). In contrast some small birds, such as Diamond Doves (*Geopelia cuneata*) in Australia, can dispel more than 100% of their metabolic heat at temperatures as high as 44°C (Schleucher et al., 1991).

Thirdly, some small bird species were observed foraging in shade at relatively high ambient temperatures. Other studies have shown that as temperatures increase, small birds select cooler foraging sites but this nonetheless allows them to continue to forage at relatively high temperatures (Ricklefs & Hainsworth, 1968). Larger bird species, such as raptors and species that feed on the ground may have reduced access to shaded foraging sites, forcing them to choose between abandoning foraging or foraging in the sun.

The use of three different sampling methods in this study was an attempt to avoid bias towards sampling species with relatively high detectability. However, it is still possible that unobtrusive, less mobile species were not seen as often as other species. This is especially true of species which may have been seeking shade in thick vegetation. However, the vegetation of the Kalahari is quite sparse and so this bias, if present, was likely to have been small.

### **Ground-dwelling as an additional indicator of vulnerability to high temperatures**

Ambient temperatures are highest directly above the ground because of reflection of heat (Kotzen, 2003). In this study, ground-dwelling birds experienced more heat stress than perching species of similar size: elsewhere, ground-nesting birds have been shown to be negatively affected by climate changes such as increasing temperatures and higher humidity (Oparin, 2008). Large, ground-dwelling birds must find large trees under which to shade at high ambient temperatures: these may not always be readily available.

### **Increasing temperatures: what will they mean for the bird species assemblage of the Kalahari?**

Increases in ambient temperature may cause local extinctions of species in an area through direct mortality or by affecting life-history attributes such as breeding success. Although the physiological implications of what stressed behaviour means for each species remain unknown in this study, predictions can be made based on the assumption that heat-stress behaviour means that high temperatures are having a negative physiological effect. Those species that demonstrate stress at the lowest temperatures are the species most likely to be adversely affected by high temperatures. In addition, those species that will experience the greatest increases in the amount of time during which they are stressed may also be particularly vulnerable to changes in climate (because stress effects can be assumed to be cumulative). Based on the findings of this study, large birds which experience such changes, for example Kori Bustards (*Ardeotis kori*) and Tawny Eagles, may be more vulnerable than smaller birds.

Because birds are mobile, it can be predicted that they will respond more rapidly to climate change than more sessile or non-volant species. However, they will only be able to emigrate from an area if there is a suitable receiving area. Bird populations on the more mesic periphery of the Kalahari undertake mass movements from drier areas to the wetter areas when it is very hot, abandoning their territories in the process (Herremans, 2004). If these populations are already adept at avoiding adverse conditions then the Kalahari may lose species at a rapid rate. In anticipation of such future conditions it may be important to maintain or increase habitat connectivity between these arid zones areas and more mesic areas (Hulme, 2005).

Predictions of future climate conditions always have an element of uncertainty in terms of both the magnitude and character of changing conditions, especially when scaled down to a regional level (Huntley et al., 2006). The climate predictions used in this study are based on ambient temperatures which are often regarded as a minimum index of environmental temperatures (Wolf et al., 1996). If this is the case, then it is likely that the number of months in which each species is predicted to spend time stressed under future predictions should be regarded as the minimum.

### **Is there potential for adaptation to high temperatures?**

When trying to gauge the impact of climate change on individual species, the possibility of adaptation to novel conditions should always be considered. Many desert birds have physiological and behavioural adaptations that allow them to survive at high temperatures. Desert birds have been shown to have not only unique physiological adaptations such as reduced metabolic rates, but also life-history attributes such as small clutch sizes in comparison to birds living in more mesic environments (Williams & Tieleman, 2005). However, not all desert-living birds have such metabolic adaptations (Tieleman & Williams, 2000; Gabriel, 2005; Williams & Tieleman, 2005; Burton et al., 2008). Basal metabolic rate has been shown to be a highly flexible physiological trait that can be adjusted over short time scales in response to changes in temperature and phenotypic plasticity needs to be taken into account when comparing how species react to environmental variation (McKechnie, 2008). If species can adapt to novel local conditions by behavioural or physiological means, they may not be lost from an area. However, whether it is possible for all species to adapt as circumstances change is debatable, especially in the case of species which may already be living close to the upper limit of their physiological tolerances. Some marine species that have evolved to withstand high maximum temperatures have limited capacity to cope with changes outside those high ranges (Tomanek, 2008). This suggests that species close to their thermal limits, such as larger and ground-dwelling birds, may not be able to acclimate if temperatures increase. Small birds, with short generation times, may be able to adapt to changes in climate much faster than longer-lived, larger birds (Harte et al., 2004). This lends support to the prediction that large birds will be the first to disappear from hot ecosystems. To assess which species may have evolved physiological phenotypic plasticity and therefore be able to predict which species may be able to adapt it would be necessary to repeat this study along gradients (such as aridity gradients) and in different populations (Williams & Tieleman, 2002; Soobramoney et al., 2003; Cavieres & Sabat, 2008). It is important to note, however, that although some adaptation may be possible, birds are very unlikely to be able to adapt to extreme events (e.g. Wolf, 2000).

High temperatures can affect individuals in ways that were not taken into account in this study. For example, high temperatures may force birds to make choices that favour limiting stress to themselves at the expense of reproductive

success. Hoopoe Larks (*Alaemon alaudipes*) favour nesting sites that decrease the risk of predation to themselves early in the breeding season but as temperatures increase through the season they select sites that are more thermally buffered but place the birds at greater risk of predation (Tieleman et al., 2008). These are long-lived birds that favour survival in any one year over breeding success. There is also evidence that increases in day-to-day variation in temperature can influence reproductive success (Pendlebury et al., 2004).

### **Birds and climate**

Climate variables other than temperature and humidity are predicted to change in the Kalahari, including rainfall (Moise & Hudson, 2008). It is therefore important to note that high temperatures will not act in isolation in forcing species from the area. Drought is a recurring event in the Kalahari and has a marked effect on trees and shrubs which maintain the savanna ecosystem. In the Kalahari, bird breeding populations drop by 37-81% in droughts (Herremans, 2004). Similar patterns have been observed elsewhere: in California, a record drought in 2002 caused a 97% decrease in arid-land breeding birds (Bolger et al., 2005).

Although small birds in this study were predicted to have the greatest resilience to increasing temperatures, they may be susceptible to drought. The most numerous bird observed in this study, the Scaly-feathered Finch, is only a seasonal visitor to the drier parts of the Kalahari ecosystem and leaves in droughts (Herremans, 2004). Larger birds may be better at adapting to drought than smaller species because they have lower mass-specific metabolic rates and can carry larger fat reserves (Simmons et al., 2004). Other studies have predicted that if annual rainfall remains unchanged but increases in variability it could result in the extinction of certain raptors in the southern Kalahari (Wichmann et al., 2003).

Many studies that use climate to predict range shifts assume that climate is the overriding mechanism currently limiting the abundance and distribution of species (the basis of climatic envelope modelling). Evidence of localised extinctions and range shifts along climatic gradients in response to changes in climate is supported across a wide range of taxa (Thomas & Lennon, 1999; Warren et al., 2001; Shoo et al., 2005). However, interactions between species, such as interspecific competition, also play a role in determining species' ranges. However, these biotic interactions will not prevent a species' response to increasing temperature. Indeed, local extinctions in



one area (perhaps due to climate change) may allow the expansion of less thermally vulnerable species whose ranges previously were limited by, for example, interspecific competition.

### **Predicting impacts of climate change on species' abundances and distributions**

Predicting which species will be adversely affected by climate change is a complex process, but more often than not the data required to make the most accurate predictions are unavailable for the vast majority of species. It is unlikely in many cases that this information will ever become available and so predictions of different species' responses to climate change make do with available data. In the face of rapidly changing climates, it is necessary and urgent to make reliable predictions for as many species as possible. The most accurate predictions will be those that take the individual biology of a species into account. This study is a first attempt at trying to determine the vulnerability of a multi-species assemblage to a single climatic variable, namely temperature. Not only were the most vulnerable birds identified, but body size was identified as a fairly robust proxy for vulnerability to increased temperatures in bird species. Although most of the species observed in the study are not currently threatened, it will be important to identify those areas from which they may be lost in the future because of increasing temperatures. Ensuring that they are adequately protected in more mesic areas of their range will help in securing the long-term persistence of these species under future climate conditions.

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**Appendix 1** List of bird species seen during the study with the ambient temperature (°C) ranges (minima and maxima) within which they were observed. Body mass (g) and temperature (°C) at which each species was first observed demonstrating stress behaviour is given for each species. Not all species were observed demonstrating stress behaviour. T<sub>a r mi</sub> = Ambient temperature range minima, T<sub>a r ma</sub> = Ambient temperature range maxima, St<sub>min</sub> = temperature at which stress behaviour was first observed.

Species	Scientific name	Body mass (g)	T <sub>a r mi</sub> (°C)	T <sub>a r ma</sub> (°C)	St <sub>min</sub> (°C)
Acacia Pied Barbet	<i>Tricholaema leucomelas</i>	32.2	35.0	42.1	42.1
African Hoopoe	<i>Upupa africana</i>	53.1	32.4	40.8	39.4
African Red-eyed Bulbul	<i>Pynonotus nigricans</i>	30.8	26.5	45.6	34.9
Anteater Chat	<i>Myrmecocichla formicivora</i>	47.6	20.4	43.6	42.5
Ashy Tit	<i>Parus cinerascens</i>	20.4	33.6	43.8	
Bateleur	<i>Terathops eucaudatus</i>	2240.0	38.0	40.5	38
Black-chested Prinia	<i>Prinia flavicans</i>	8.9	26.4	46.9	
Black-chested Snake-Eagle	<i>Circaetus pectoralis</i>	1500.0	22.5	41.3	
Black-headed Heron	<i>Ardea melanocephala</i>	1440.0	30.9		
Black-shouldered Kite	<i>Elanus caeruleus</i>	247.8	30.3	40.6	
Black-throated Canary	<i>Crithagra atrogularis</i>	12.7	36.9	41.1	41.1
Booted Eagle	<i>Aquila pennatus</i>	842.0	40.7		
Burchell's Starling	<i>Lamprotornis australis</i>	122.0	23.6	40.4	
Cape Clapper Lark	<i>Mirafra apiata</i>	27.0	39.1		
Cape Crow	<i>Corvus capensis</i>	537.0	25.9	43.9	31.1
Cape Glossy Starling	<i>L. nitens</i>	82.5	14.3	41.4	37.1
Cape Sparrow	<i>Passer melanurus</i>	29.5	17.0	45.6	38.5
Cape Turtle-dove	<i>Streptopelia capicola</i>	130.3	13.9	46.9	34.8
Capped Wheatear	<i>Oenanthe pileata</i>	25.5	29.0	44.8	39.4
Cardinal Woodpecker	<i>Dendropicos fuscescens</i>	31.0	38.7	42.9	
Cattle Egret	<i>Bubulcus ibis</i>	373.5	33.9	33.9	
Chat Flycatcher	<i>Bradornis infuscatus</i>	37.0	30.2	43.6	43.6
Chestnut-vented Tit-Babbler	<i>Parisoma subcaeruelum</i>	15.7	17.5	45.6	39.25
Common Fiscal	<i>Lanius collaris</i>	40.8	13.9	44.8	
Common Ostrich	<i>Struthio camelus</i>	68700.0	25.7	44.4	30.1
Common Scimitarbill	<i>Rhinopomastus cyanomelas</i>	32.7	31.0	45.6	39.4
Crimson-breasted Shrike	<i>Laniarius atrococcineus</i>	48.3	25.5	44.0	45.2
Crowned Lapwing	<i>Vanellus coronatus</i>	195.0	24.8	43.7	34.3
Egyptian Goose	<i>Alopochen aegyptiaca</i>	2110.0	28.3		
Familiar Chat	<i>Cercomela familiaris</i>	22.5	17.6	44.7	37.1
Fawn-coloured Lark	<i>Calendulauda africanoides</i>	23.3	31.7	42.1	41.2
Fork-tailed Drongo	<i>Dicrurus adsimilis</i>	43.8	14.6	45.6	34.3
Gabar Goshawk	<i>Melierax gabar</i>	164.0	34.3	44.9	41.2
Golden-tailed Woodpecker	<i>Campethera abingoni</i>	69.5	39.9		
Greater Kestrel	<i>Falco rupicoloides</i>	258.5	35.2	40.9	40.9
Green-winged Pytilia	<i>Pytilia melba</i>	14.8	39.9		

## Appendix 1 continued

Species	Scientific name	Body mass (g)	T <sub>a r mi</sub> (°C)	T <sub>a r ma</sub> (°C)	St <sub>min</sub> (°C)
Grey-backed Sparrowlark	<i>Eremopterix verticalis</i>	17.3	37.1	47.6	42.3
House Sparrow	<i>P. domesticus</i>	25.8	26.5	42.8	42.8
Kalahari Scrub-Robin	<i>Erythropygia paeana</i>	19.7	21.4	46.9	37.9
Kori Bustard	<i>Ardeotis kori</i>	9050.0	36.3	41.8	39
Lanner Falcon	<i>F. biarmicus</i>	590.4	23.6	45.1	40.9
Lappet-faced Vulture	<i>Aegyptius tracheliotos</i>	6700.0	43.1	43.1	
Laughing Dove	<i>S. senegalensis</i>	98.8	25.1	45.6	35.5
Lesser Grey Shrike	<i>L. minor</i>	47.0	24.5	42.8	
Lilac-breasted Roller	<i>Coracias caudatus</i>	107.5	14.6	40.1	43.3
Little Bee-Eater	<i>Merops pusillus</i>	14.6	40.5		
Long-billed Crombec	<i>Sylvietta rufescens</i>	11.05	35.9	40.5	
Marico Flycatcher	<i>B. mariquensis</i>	26.2	18.7	45.2	38.45
Martial Eagle	<i>Polemaetus bellicosus</i>	4005.0	36.2	40.1	
Namaqua Dove	<i>Oena capensis</i>	39.9	27.0	46.9	38.9
Namaqua Sandgrouse	<i>Pterocles namaqua</i>	180.5	37.1	41.3	
Northern Black Korhaan	<i>Eupodotis afroides</i>	739.0	28.6	43.6	34.2
Pink-billed Lark	<i>Spizocorys conirostris</i>	14.3	37.1	43.9	37.1
Pirit Batis	<i>Batis pririt</i>	9.3	27.9	44.5	38.5
Pygmy Falcon	<i>Polinierax semitorquatus</i>	60.5	24.5	42.1	
Red-backed Shrike	<i>L. collurio</i>	28.9	36.5	41.7	
Red-billed Quelea	<i>Quelea quelea</i>	19.2	36.7	39.4	
Red-crested Korhaan	<i>Lophotis ruficrista</i>	674.5	34.2	35.6	35.6
Red-faced Mousebird	<i>Urocolias indicus</i>	56.5	26.5	42.8	42.8
Red-headed Finch	<i>Amadina erythrocephalus</i>	11.5	17.3	44.2	36.5
Red-necked Falcon	<i>F. chiquera</i>	207.5	12.2	44.3	
Rock Kestrel	<i>F. tinnunculus</i>	216.0	40.1	44.5	
Rufous-eared Warbler	<i>Malcorus pectoralis</i>	10.2	34.1	43.5	
Sabota Lark	<i>C. sabota</i>	24.5	28.4	44.1	41.25
Scaly-feathered Finch	<i>Sporopipes squamifrons</i>	11.1	13.1	44.0	41.1
Secretarybird	<i>Sagittarius serpentarius</i>	3610.0	21.7	43.1	31.9
Shaft-tailed Whydah	<i>Vidua regia</i>	14.3	33.9	35.6	
Sociable Weaver	<i>Philetairus socius</i>	27.4	25.0	45.2	40.5
South African Shelduck	<i>Tadorna cana</i>	1240.0	36.0	42.2	36
Southern Grey-headed Sparrow	<i>P. diffusus</i>	24.7	29.5	43.6	37.95
Southern Masked-Weaver	<i>Ploceus velatus</i>	20.6	30.8	43.4	
Southern Pale Chanting Goshawk	<i>M. canorus</i>	822.0	18.6	43.6	37.1
Southern White-faced Scops-Owl	<i>Ptilopsis granti</i>	220.5	39.3	44.1	44.1
Southern Yellow-billed Hornbill	<i>Tockus leucomelas</i>	189.5	42.8		
Speckled pigeon	<i>Columba guinea</i>	334.5	44.7		
Spike-heeled Lark	<i>Chersomanes albofusiata</i>	25.3	20.7	43.0	
Spotted Eagle-Owl	<i>Bubo africanus</i>	645.0	20.1	42.4	40.1
Spotted Flycatcher	<i>Muscicapa striata</i>	16.1	40.1	41.8	
Spotted Thick-knee	<i>Burhinus capensis</i>	472.2	24.3	45.2	39.95
Starks Lark	<i>S. starki</i>	18.6	28.4		
Striped Kingfisher	<i>Halcyon chelicuti</i>	38.7	38.3		

## Appendix 1 continued

Species	Scientific name	Body mass (g)	T <sub>a r mi</sub> (°C)	T <sub>a r ma</sub> (°C)	St <sub>min</sub> (°C)
Swallow-tailed Bee-eater	<i>M. hirundineus</i>	20.0	22.5	44.2	38.4
Tawny Eagle	<i>A. rapax</i>	2050.0	22.6	45.1	39.75
Three-banded Plover	<i>Charadrius tricollaris</i>	33.1	28.3		
Verreaux's Eagle-Owl	<i>B. lacteus</i>	2045.0	24.5	37.8	34.5
Violet-eared Waxbill	<i>Uraeginthus granatinus</i>	11.8	35.6	40.7	
Wattled Starling	<i>Creatophora cinerea</i>	73.0	24.5	33.4	
White-backed Vulture	<i>Gyps africanus</i>	5540.0	36.5	43.1	40.4
White-browed Sparrow-Weaver	<i>Plocepasser mahali</i>	47.5	24.5	45.6	37.1
Yellow Canary	<i>C. flaviventris</i>	17.5	16.6	44.5	39.2
Yellow-bellied Eremomela	<i>Eremomela icteropygialis</i>	7.9	16.4	44.9	43.3

**Appendix 2** Percentage (%) of observations within which the most common species (n=22) were seen displaying different types of behaviour (n=5) over a range of temperatures. T<sub>1</sub> = 30-35°C, T<sub>2</sub> = 36-40°C, and T<sub>3</sub> = over 40 °C +.

Species	Body mass (g)	0 T <sub>1</sub>	0 T <sub>2</sub>	4 T <sub>3</sub>	0 T <sub>1</sub>	13 T <sub>2</sub>	17 T <sub>3</sub>	0 T <sub>1</sub>	0 T <sub>2</sub>	0 T <sub>3</sub>	7 T <sub>1</sub>	74 T <sub>2</sub>	0 T <sub>3</sub>	2 T <sub>1</sub>	9 T <sub>2</sub>	13 T <sub>3</sub>
		Stressed			Full sun - active			Full sun - sedentary			Shade - active			Shade - sedentary		
Black-chested Prinia	8.9	0	0	0	17	0	5	1	1	2	67	71	60	0	26	25
Cape Crow	537.0	38	61	100	0	0	0	23	8	0	23	8	0	8	3	0
Cape Glossy Starling	82.5	0	7	0	4	3	0	0	7	0	31	28	0	51	52	100
Cape Sparrow	29.5	0	12	43	12	0	0	14	3	0	33	44	7	28	38	50
Cape Turtle-Dove	130.3	2	5	28	1	2	0	8	2	0	17	14	8	57	75	59
Chestnut-vented Tit-Babbler	15.7	0	8	6	0	0	6	0	0	0	100	59	78	0	33	11
Common Ostrich	68700.0	63	72	68	5	5	3	4	11	0	21	5	4	5	4	10
Crowned Lapwing	195.0	2	3	15	5	0	0	7	14	0	17	0	0	51	84	85
Familiar Chat	22.4	0	12	5	0	6	5	7	6	0	43	12	21	50	65	68
Fork-tailed Drongo	43.8	1	5	18	11	6	5	9	6	3	30	22	25	35	58	49
Grey-backed Sparrowlark	17.3	0	0	23	0	0	0	0	8	5	0	0	3	0	77	70
Kalahari Scrub-Robin	20.0	0	3	7	11	3	7	0	0	0	44	34	27	44	55	60
Laughing Dove	98.8	0	11	15	0	0	0	0	0	0	35	30	8	50	59	77
Marico Flycatcher	26.2	0	2	4	13	4	1	10	5	1	38	42	33	20	46	57
Namaqua Dove	39.9	0	1	3	2	13	10	1	15	6	10	9	12	76	56	62
Red-headed Finch	11.5	0	1	0	0	10	16	9	1	2	11	48	13	62	4	59
Scaly-feathered Finch	11.1	0	0	0	12	5	4	13	2	4	40	37	44	35	49	47
Sociable Weaver	27.4	0	1	2	4	6	2	1	1	0	73	60	36	22	32	60
Swallow-tailed Bee-eater	20.0	0	1	0	13	20	13	4	4	0	4	9	8	3	18	26
White-browed Sparrow-Weaver	47.5	0	4	13	0	3	0	2	0	0	64	59	29	29	34	58
Yellow Canary	17.5	0	12	0	25	0	0	6	0	0	56	44	9	13	44	91

## DECLARATION

1. I know that plagiarism is wrong. Plagiarism is to use another's work and to pretend that it is one's own. This includes copying phrases and sentences from another's writing, and inserting these into one's own work.
  
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