

## SHORT COMMUNICATION

# It's cool to be dominant: social status alters short-term risks of heat stress

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## ABSTRACT

Climate change has the potential to trigger social change. As a first step towards understanding mechanisms determining the vulnerability of animal societies to rising temperatures, we investigated interactions between social rank and thermoregulation in three arid-zone bird species: fawn-coloured lark (*Mirafra africanoides*, territorial); African red-eyed bulbul (*Pycnonotus nigricans*, loosely social) and sociable weaver (*Philetairus socius*, complex cooperative societies). We assessed relationships between body temperature ( $T_b$ ), air temperature ( $T_a$ ) and social rank in captive groups in the Kalahari Desert. Socially dominant weavers and bulbuls had lower mean  $T_b$  than subordinate conspecifics, and dominant individuals of all species maintained more stable  $T_b$  as  $T_a$  increased. Dominant bulbuls and larks tended to monopolise available shade, but dominant weavers did not. Nevertheless, dominant weavers thermoregulated more precisely, despite expending no more behavioural effort on thermoregulation than subordinates. Increasingly unequal risks associated with heat stress may have implications for the stability of animal societies in warmer climates.

**KEY WORDS:** Climate change, Cooperative breeding, Dominance, Sociality, Stress-induced hyperthermia, Thermoregulation

## INTRODUCTION

Conflict within animal societies is commonly mediated by dominance hierarchies (Rowell, 1974). Such hierarchies fundamentally influence fitness, with dominant individuals generally having priority access to resources and breeding opportunities (Majolo et al., 2012; Nelson-Flower et al., 2011). Social interactions can also affect organismal physiology; subordinate endotherms often experience elevated body temperature (Bakken et al., 1999; Carere et al., 2001; Meerlo et al., 1996) and corticosterone (Bhatnagar et al., 2006; Keeney et al., 2001) following social defeats.

Social species are disproportionately found in arid, unpredictable environments (Jetz and Rubenstein, 2011), regions that are warming rapidly under climate change (Safriel et al., 2006). The physiological costs of thermoregulation during very hot weather can be substantial, and include elevated water requirements associated with evaporative cooling and performance costs associated with facultative hyperthermia (Boyles et al., 2011).

Social defeats can affect thermoregulation (Keeney et al., 2001), and we predicted that during hot weather, subordinates would maintain less-stable body temperature ( $T_b$ ) compared with dominant individuals. Unequal risks of heat stress could have implications for the stability of animal societies under climate change. We tested this prediction by examining relationships between  $T_b$ , thermoregulatory behaviours and social rank in captive groups of three Kalahari Desert bird species differing in natural levels of sociality: fawn-coloured larks [*Mirafra africanoides*, (Smith 1836); territorial pair breeders], African red-eyed bulbuls [*Pycnonotus nigricans* (Vieillot 1818); loosely social] and sociable weavers [*Philetairus socius* (Latham 1790); colonial, cooperative breeders with stable year-round colonies; Hockey et al., 2005].

## MATERIALS AND METHODS

### Study species and data collection

We captured six fawn-coloured larks, 10 African red-eyed bulbuls and 11 sociable weavers (hereafter, larks, bulbuls and weavers, respectively) within a 9 km radius and housed them as single-species groups in three outdoor aviaries (built from steel mesh panels and shaded at one end, 3 m high×8 m long×3 m wide) near the town of Askham in the Kalahari Desert (26°59'S, 20°51'E). Perches (natural branches) were placed such that birds had similar access to shade in all three aviaries. Birds were weighed and colour-ringed, and a small blood sample (<35 µl) was taken for molecular sexing, as all three species are sexually monomorphic. Table S1 provides further details about each species. Birds were supplied with water and species-appropriate food (mealworms, fruit, seed) *ad libitum*. Temperature-sensitive VHF transmitters (model BD-2TH, Holohil, Carp, ON, Canada; 1.2 g) were implanted intraperitoneally under isoflurane anaesthesia by a registered veterinarian.  $T_b$  data were collected at ~5 min intervals using an automated receiver/data logger (SRX-400, Lotek, Newmarket, ON, Canada) and Yagi antennae. We calibrated the transmitters prior to implantation following Smit and McKechnie (2010). Temperature-sensitive VHF transmitters have been reported to drift (Williams et al., 2009). Most of our transmitters showed a linear drift with deviation of 0.3–1.8°C by the end of the recording period. We corrected for this by fitting linear regressions to the data and using  $y_{\text{corrected}} = y - mx$  (Fig. S1).

Weavers were captured on one day using mistnets around a single large colony, so birds were likely to be familiar with each other prior to capture. Bulbuls were also all captured in close proximity. All birds were allowed a habituation period of ≥1 week to allow social hierarchies to stabilise prior to data collection.

Birds were observed daily in two sessions: 07:00 h–10:00 h and 14:00 h–17:30 h. We scored all agonistic interactions (including displacements, pecking, threatening to peck, chasing, fighting), noting which individual 'won' or 'lost' each interaction ('losing' individuals retreated), and then calculated David's score (Gammell et al., 2003) to ascertain the dominance hierarchy. Individuals were then assigned a social ranking from 1 (most dominant) to  $n$  (where

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$n$ =total individuals in the group), corresponding to relative David's scores. Hierarchies remained stable during the experimental period.

Instantaneous scan sampling (Altmann, 1974) was carried out twice per bird during each observation session. Scan samples were used to collect binomial data on shade-seeking (score 1 if the bird was in full shade, or 0 if it was wholly or partially exposed to the sun), activity (1 if the bird was hopping, running, flying or otherwise active, 0 if it was immobile) and heat dissipation behaviour (panting; 1 if present, 0 if absent). Panting was easily recognisable as the beak was held open but the bird was not vocalising. Scans were carried out using binoculars by an observer sitting several metres from each aviary to avoid disturbing the birds. Each individual was visually identified via colour-ring combinations and observed in a randomised order to avoid the introduction of order effects.

All data were collected between 24 January and 18 February 2014 (late austral summer), after which birds were released at their capture sites. Air temperature ( $T_a$ ) was measured using a weather station (Vantage Pro2, Davis Instruments, Hayward, CA, USA) placed ~20 m from the aviaries (Fig. S2), and calibrated as described by Smit et al. (2013).

### Statistical analysis

Because birds had consistently higher  $T_b$  during the day (when active) than at night (when resting), data were partitioned into diurnal (06:00 h–19:59 h) and nocturnal (20:00 h–05:59 h) periods using the clear circadian  $T_b$  rhythm as a guide (Fig. S3). Diurnal and nocturnal data were analysed separately for each species using generalised linear mixed models (GLMMs). Response variables were  $T_b$  (modelled using Gaussian error structure) and panting, shade-seeking and activity (diurnal data only, modelled using binomial error structure). Mean  $T_b$  models included the random term 'bird identity' and fixed factor 'social rank'. We included mass and sex (except for larks as all were male) in all models to control for underlying effects of these variables. Models for thermoregulation and behaviour additionally included  $T_a$ . We included all two-way interactions in initial models, subsequently removing non-significant interactions from final models.

We expected *a priori* that heavier individuals would be dominant, potentially introducing multicollinearity into our models. We tested this expectation using Pearson's correlations of body mass against social rank, and found no significant relationship for any species, taking  $P < 0.05$  to indicate significance: larks,  $r = 0.47$ ,  $t = 1.06$ ,  $P = 0.35$ ; bulbuls,  $r = -0.47$ ,  $t = -1.18$ ,  $P = 0.29$ ; weavers,  $r = 0.12$ ,  $t = 0.36$ ,  $P = 0.72$ . In all other analyses, statistical significance

was inferred if 95% confidence intervals (CIs) excluded zero. Data were analysed using the R (R Core Development Team, 2009) packages lme4 v.1.0-5 (<https://CRAN.R-project.org/package=lme4>), multcomp v.1.3-3 (<https://CRAN.R-project.org/package=multcomp>) and ggplot2 v.1.10 (<https://CRAN.R-project.org/package=ggplot2>).

Sample size for weavers and bulbuls was higher for behaviour ( $n = 11$  and  $10$ , respectively) than  $T_b$  data ( $n = 9$  and  $7$ , respectively), because of transmitter failures. Additionally, two weavers with leg strain injuries were introduced into the weaver aviary for rehabilitation ~2 weeks prior to the beginning of data collection. These birds were excluded from  $T_b$  and behaviour analyses, but were included in construction of David's scores as they were part of the social hierarchy.

### Ethics

Experiments were approved by the University of Pretoria Animal Ethics Committee (protocol EC010-15) and the Department of the Environment, Northern Cape, South Africa (permit FAUNA 1088/2013).

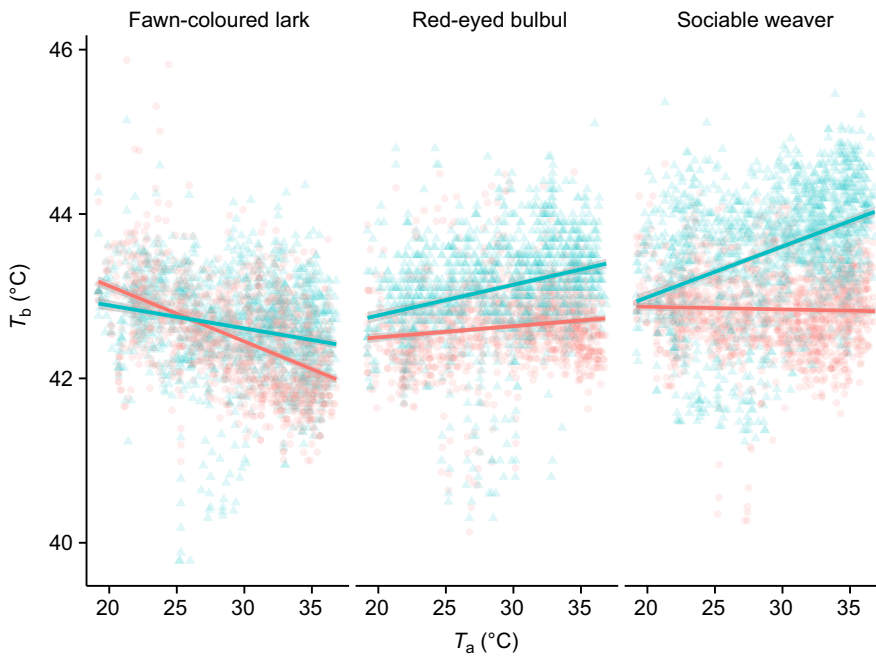
### RESULTS AND DISCUSSION

Our data reveal the  $T_b$  of socially dominant individuals of three arid-zone bird species was less affected by high  $T_a$  than that of subordinates. Subordinate weavers and bulbuls, but not larks, had higher mean diurnal  $T_b$  than dominant conspecifics. On average,  $T_b$  increased by  $0.15^\circ\text{C}$  (95% CI:  $0.08$ – $0.21^\circ\text{C}$ ;  $t = 5.91$ ) in weavers and  $0.10^\circ\text{C}$  (95% CI:  $0.03$ – $0.16^\circ\text{C}$ ;  $t = 3.79$ ) in bulbuls with each rank increment away from the most dominant position (see Table S1 for  $T_b$  means and ranges). Interactions between social rank and  $T_a$  were significant predictors of diurnal  $T_b$  in all three species, with dominant individuals maintaining more stable  $T_b$  with increasing  $T_a$  compared with subordinates (Table 1, Fig. 1). Our sample size was limited to one group of 6–11 individuals per species for ethical and logistical reasons, and our study could be criticised on grounds of pseudoreplication. However, our aim was to establish whether correlations between social status and thermoregulation under hot conditions exist, not to test predictions concerning interspecific variation. That such correlations occurred in three species differing greatly in natural levels of sociability suggests our sample size was adequate for demonstrating the existence of this phenomenon, and raises the possibility that the underlying mechanisms driving these relationships might be widespread among birds. These findings are also broadly consistent with relationships between social status and  $T_b$  under less thermally stressful conditions documented for captive-bred

**Table 1. Diurnal body temperature ( $T_b$ ) as a function of mass, sex, social rank (1=highest), air temperature ( $T_a$ ) and significant interactions**

Species	Mass (g)	Sex	Social rank	$T_a$ ( $^\circ\text{C}$ )	Mass: $T_a$	Sex: $T_a$	Social rank: $T_a$	<i>N</i>
Fawn-coloured lark	0.08 (-0.08–0.23) $t = 1.16$		-0.17 (-0.25 to -0.09) $t = -5.19$	-0.05 (-0.06 to -0.05) $t = -19.49$			0.007 (0.005–0.008) $t = 9.34$	6
Red-eyed bulbul	0.18 (0.08–0.29) $t = 4.47$	-1.40 (-2.01 to -0.80) $t = -6.11$	-0.14 (-0.25 to -0.04) $t = -3.56$	0.02 (-0.08–0.12) $t = 0.63$	-0.003 (-0.006–0.0004) $t = -2.30$	0.04 (0.03–0.06) $t = 7.10$	0.008 (0.005–0.01) $t = 7.48$	7
Sociable weaver	-0.13 (-0.35–0.10) $t = -1.52$	0.92 (0.37–1.47) $t = 4.56$	0.01 (-0.06–0.09) $t = 0.55$	0.18 (0.11–0.25) $t = 6.80$	-0.01 (-0.01 to -0.005) $t = -6.84$	-0.02 (-0.02 to -0.01) $t = -5.66$	0.004 (0.003–0.005) $t = 12.36$	9

Data are presented as model estimates (with 95% confidence intervals in parentheses) and *t*-values. Sex is not included for fawn-coloured larks as all individuals were male. Effect size for sex is the difference between mean  $T_b$  for males compared with females; for other variables, it is change in  $T_b$  per 1 unit increase in the predictor variable. Models are GLMMs with Gaussian error distribution and identity link function with individual bird identity as a random factor. Bold indicates 95% confidence intervals excluding zero. *N*, number of individual birds from which data were collected.



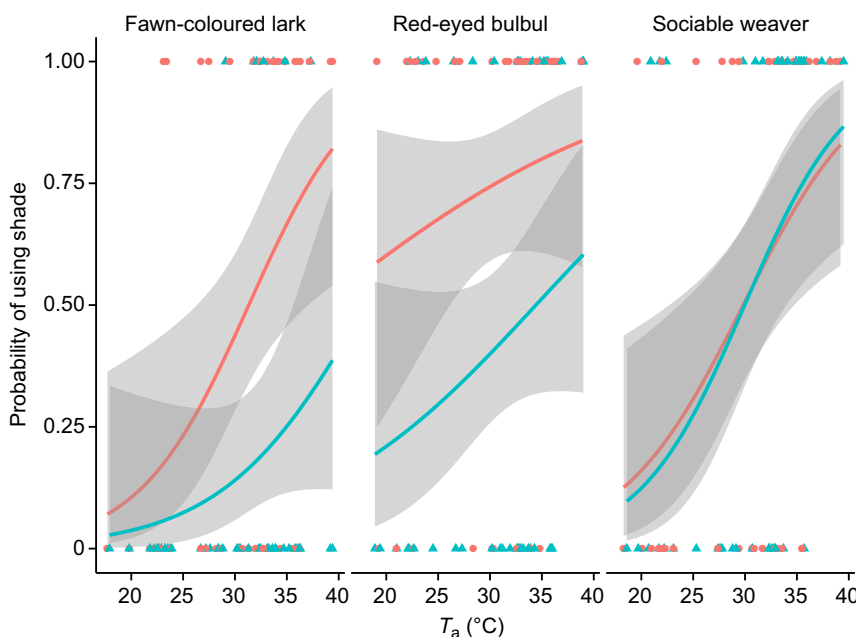
**Fig. 1. Change in body temperature ( $T_b$ ) as a function of air temperature ( $T_a$ ) in dominant and subordinate larks, bulbuls and weavers.**  $T_b$  data are shown for a dominant (social rank 1 for larks and weavers, social rank 2 for bulbuls as the rank 1 bird had a weak transmitter; red model-fit lines and data points) versus the most subordinate individual (blue model-fit lines and data points) of each species. Models are GLMMs with Gaussian error structure; the interaction term  $T_a \times \text{social rank}$  was significant in all cases [95% confidence intervals (CIs) excluded zero]. Two individuals per species only are presented for clarity; models were fitted to the entire dataset. Grey shading represents 95% CI around model fits.

and laboratory animals (e.g. Meerlo et al., 1996; Bakken et al., 1999; Carere et al., 2001).

Panting increased significantly with  $T_a$  in all species (larks:  $\beta$  estimate 0.22, 95% CI: 0.09–0.36,  $z=4.07$ ; bulbuls:  $\beta$  estimate 0.28, 95% CI: 0.19–0.37,  $z=7.97$ ; weavers:  $\beta$  estimate 0.35, 95% CI: 0.19–0.52,  $z=5.53$ ), whereas activity levels were suppressed at high  $T_a$  only in weavers ( $\beta$  estimate  $-0.07$ , 95% CI:  $-0.12$  to  $-0.03$ ,  $z=-4.13$ ). In larks and bulbuls, the interaction between  $T_a$  and social status on  $T_b$  may have been amplified by captivity, as dominant birds tended to monopolise shaded sites. Dominant larks used shade significantly more than subordinates, and dominant bulbuls showed a similar tendency (larks:  $\beta$  estimate  $-0.36$ , 95% CI:  $-0.64$  to  $-0.08$ ,  $z=-3.06$ ; bulbuls:  $\beta$  estimate  $-0.20$ , 95% CI:  $-0.42$ – $0.03$ ,  $z=-2.21$ ; Fig. 2). This was probably particularly important in the larks, which are territorial in the wild. In contrast, dominant weavers

did not control access to shade, reduce activity or increase panting compared with subordinate birds as  $T_a$  increased (Table S2), suggesting dominant individuals of this highly social species thermoregulate more precisely (Table 1, Fig. 1) despite expending no additional behavioural effort on thermoregulation (Fig. 2). Weavers live year-round in stable groups with individuals foraging and roosting together (Maclean, 1973), suggesting the social conditions we created in captivity are not dissimilar to those experienced in the wild. Differences in thermoregulatory strategies observed in individuals of different social status might also occur in the wild, a possibility that deserves further investigation.

The consistently higher mean diurnal  $T_b$  of subordinate weavers and bulbuls was probably driven by stress-induced hyperthermia (SIH), a well-documented response to social defeats in endotherms (Bhatnagar et al., 2006; Carere et al., 2001; Keeney et al., 2001;



**Fig. 2. Shade-seeking behaviour as a function of  $T_a$  in dominant and subordinate larks, bulbuls and weavers.** Data and model fits are for the same individuals as in Fig. 1 (dominant: red model-fit line and red circular data points; subordinate: blue model-fit line and blue triangular data points). Models are GLMMs with binomial error structure. The interaction term  $T_a \times \text{social rank}$  was significant for fawn-coloured larks ( $\beta$  estimate  $-0.36$ , 95% CI:  $-0.64$  to  $-0.08$ ,  $z=-3.06$ ), near significant for red-eyed bulbuls ( $\beta$  estimate  $-0.20$ , 95% CI:  $-0.42$ – $0.03$ ,  $z=-2.21$ ) and non-significant for sociable weavers. Two individuals per species only are presented for clarity; models were fitted to the entire dataset. Grey shading represents 95% CI around model fits.



Meerlo et al., 1996; Schmelting et al., 2014). Our postulated role of SIH as a determinant of these patterns during the active phase is supported by the fact that correlations between  $T_b$  and social rank vanished (weavers and bulbuls) or were reversed at night (subordinate larks had lower nocturnal  $T_b$  than dominant individuals:  $-0.13^\circ\text{C}$  change in  $T_b$  with each rank increment, 95% CI:  $-0.22$  to  $-0.04^\circ\text{C}$ ;  $t=-3.51$ ; Table S3). The interaction between social rank and  $T_a$  on  $T_b$  (Fig. 1, Table 1), particularly in weavers where there was no observable behavioural correlate (Fig. 2, Table S2), is more difficult to explain. We suggest two non-mutually exclusive hypotheses. First, dominant birds might inherently thermoregulate better, if dominance is linked to physiological performance and capacity to maintain thermal homeostasis (for example, via increased capacity to allocate energy and water resources to thermoregulation – although dominant weavers were not observed to pant more than subordinates). Second, socially stressed subordinates might be more prone to elevated SIH caused by additional stressors (Bakken et al., 1999), in this instance thermal stress. This phenomenon might have been especially acute in larks, as this species (unlike the bulbuls and weavers) is not naturally social and the formation of a ‘dominance hierarchy’ in captivity may not have significantly reduced conflicts. Nevertheless, we think it is pertinent that the observed patterns were consistent across both naturally social species, which we assume formed true dominance hierarchies in this study, and pair-living species. SIH in this context is distinct from facultative hyperthermia, where controlled increases in set-point  $T_b$  enhance thermal gradients for heat dissipation and potentially serve as a water conservation mechanism (Tieleman and Williams, 1999).

Regardless of the underlying mechanisms, the within-group variation in thermoregulation suggests subordinate individuals in social groups might be less able to cope with natural climate variability, consequently facing greater risks under climate change. Global warming is therefore likely to compound negative effects of low social status. Physiological performance under hot conditions is tightly coupled to  $T_b$  and the consequences of uncontrolled hyperthermia include rapid loss of performance and death (Boyles et al., 2011). Weavers inhabit the rapidly warming Kalahari Desert (Kruger and Sekele, 2013; van Wilgen et al., 2016). Their diurnal  $T_b$  under laboratory conditions is  $\sim 41$ – $42^\circ\text{C}$ , with heat tolerance limits at  $T_b \approx 44^\circ\text{C}$  and  $T_a \approx 52^\circ\text{C}$  (Whitfield et al., 2015). In the present study, the  $T_b$  of subordinate weavers in a semi-natural thermal environment approached  $44^\circ\text{C}$  at a substantially lower  $T_a \approx 40^\circ\text{C}$ .

In conclusion, our data suggest that subordinate birds thermoregulate closer to upper  $T_b$  limits than dominant individuals, hence maintaining smaller thermal safety margins. Subordinates often play important roles within social groups, contributing to common good activities and aiding breeding attempts (Crick, 1992). These roles reduce costs incurred by group members as a whole (Crick, 1992). Higher vulnerability of subordinate individuals to heat stress could therefore have far-reaching implications for dynamics and cohesion of social groups under ongoing climate change.

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#### Competing interests

The authors declare no competing or financial interests.

#### Author contributions

S.J.C. and M.L.T. conceived the study and carried out field work and analyses. A.E.M. contributed to study design and provided logistical and intellectual support. S.J.C. drafted the manuscript with input from all authors. All authors gave final approval for publication.

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#### Data availability

Data are available from the Dryad Digital Repository (Cunningham et al., 2017): <http://dx.doi.org/10.5061/dryad.01th0>

#### Supplementary information

Supplementary information available online at <http://jeb.biologists.org/lookup/doi/10.1242/jeb.152793.supplemental>

#### References

- Altmann, J. (1974). Observational study of behavior: sampling methods. *Behaviour* **49**, 227–266.
- Bakken, M., Oppermann Moe, R., Smith, A. J. and Selle, G.-M. E. (1999). Effects of environmental stressors on deep body temperature and activity levels in silver fox vixens (*Vulpes vulpes*). *Appl. Anim. Behav. Sci.* **64**, 141–151.
- Bhatnagar, S., Vining, C., Iyer, V. and Kinni, V. (2006). Changes in hypothalamic-pituitary-adrenal Function, body temperature, body weight and food intake with repeated social stress exposure in rats. *J. Neuroendocrinol.* **18**, 13–24.
- Boyles, J. G., Seebacher, F., Smit, B. and McKechnie, A. E. (2011). Adaptive thermoregulation in endotherms may alter responses to climate change. *Integr. Comp. Biol.* **51**, 676–690.
- Carere, C., Welink, D., Drent, P. J., Koolhaas, J. M. and Groothuis, T. G. G. (2001). Effect of social defeat in a territorial bird (*Parus major*) selected for different coping styles. *Physiol. Behav.* **73**, 427–433.
- Crick, H. Q. P. (1992). Load-lightening in cooperatively breeding birds and the cost of reproduction. *Ibis* **134**, 56–61.
- Cunningham, S. J., Thompson, M. L. and McKechnie, A. E. (2017). Data from: It's cool to be dominant: social status alters short-term risks of heat stress. *Dryad Digital Repository* <http://dx.doi.org/10.5061/dryad.01th0>.
- Gammell, M. P., de Vries, H., Jennings, D. J., Carlin, C. M. and Hayden, T. J. (2003). David's score: a more appropriate dominance ranking method than Clutton-Brock et al.'s index. *Anim. Behav.* **66**, 601–605.
- Hockey, P. A. R., Dean, W. R. J. and Ryan, P. G. (ed.). (2005). *Roberts Birds of Southern Africa*. 7th edn. Cape Town: The Trustees of the John Voelcker Bird Book Fund.
- Jetz, W. and Rubenstein, D. R. (2011). Environmental uncertainty and the global biogeography of cooperative breeding in birds. *Curr. Biol.* **21**, 72–78.
- Keeney, A. J., Hogg, S. and Marsden, C. A. (2001). Alterations in core body temperature, locomotor activity, and corticosterone following acute and repeated social defeat of male NMRI mice. *Physiol. Behav.* **74**, 177–184.
- Kruger, A. C. and Sekele, S. S. (2013). Trends in extreme temperature indices in South Africa: 1962–2009. *Int. J. Climatol.* **33**, 661–676.
- Maclean, G. L. (1973). The sociable weaver, part 2: nest architecture and social organization. *Ostrich* **44**, 191–218.
- Majolo, B., Lehmann, J., de Bortoli Vizioli, A. and Schino, G. (2012). Fitness-related benefits of dominance in primates. *Am. J. Phys. Anthropol.* **147**, 652–660.
- Meerlo, P., de Boer, S. F., Koolhaas, J. M., Daan, S. and van den Hoofdakker, R. H. (1996). Changes in daily rhythms of body temperature and activity after a single social defeat in rats. *Physiol. Behav.* **59**, 735–739.
- Nelson-Flower, M. J., Hockey, P. A. R., O'Ryan, C., Raihani, N. J., du Plessis, M. A. and Ridley, A. R. (2011). Monogamous dominant pairs monopolize reproduction in the cooperatively breeding pied babbler. *Behav. Ecol.* **22**, 559–565.
- R Core Development Team. (2009). R: A language and environment for statistical computing. Vienna, Austria: the R Foundation for Statistical Computing. ISBN: 3-900051-07-0. Available online at <http://www.R-project.org/>
- Rowell, T. E. (1974). The concept of social dominance. *Behav. Biol.* **11**, 131–154.
- Safriel, U., Ezcurra, E., Tegen, I., Schlesinger, W. H., Nelleman, C., Batjes, N. H., Dent, D., Groner, E., Morrison, S., Rosenfeld, D. et al. (2006). Deserts and the planet – linkages between deserts and non-deserts. In *Global Deserts Outlook* (ed. E. Ezcurra), pp. 49–72. Nairobi: Scanprint, Denmark.
- Schmelting, B., Corbach-Söhle, S., Kohlhaas, S., Schlumbohm, C., Flügge, G. and Fuchs, E. (2014). Agomelatine in the tree shrew model of depression: effects

- on stress-induced nocturnal hyperthermia and hormonal status. *Eur. Neuropsychopharmacol.* **24**, 437–447.
- Smit, B. and McKechnie, A. E.** (2010). Do owls use torpor? Winter thermoregulation in free-ranging pearl-spotted owlets and African scops-owls. *Physiol. Biochem. Zool.* **83**, 149–156.
- Smit, B., Harding, C. T., Hockey, P. A. R. and McKechnie, A. E.** (2013). Adaptive thermoregulation during summer in two populations of an arid-zone passerine. *Ecology* **94**, 1142–1154.
- Tieleman, B. I. and Williams, J. B.** (1999). The role of hyperthermia in the water economy of desert birds. *Physiol. Biochem. Zool.* **72**, 87–100.
- Van Wilgen, N. J., Goodall, V., Holness, S., Chown, S. L. and McGeoch, M. A.** (2016). Rising temperatures and changing rainfall patterns in South Africa's national parks. *Int. J. Climatol.* **36**, 706–721.
- Whitfield, M. C., Smit, B., McKechnie, A. E. and Wolf, B. O.** (2015). Avian thermoregulation in the heat: scaling of heat tolerance and evaporative cooling capacity in three southern African arid-zone passerines. *J. Exp. Biol.* **218**, 1705–1714.
- Williams, J. B., Tieleman, B. I. and Shobrak, M.** (2009). Validation of temperature-sensitive radio transmitters for measurement of body temperature in small animals. *Ardea* **97**, 120–124.