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1 **Extreme and variable environmental temperatures are linked to reduction of social**
2 **network cohesiveness in a highly social passerine.**

3 Margaux Rat ^{*,a}, Hugo Mathe-Hubert ^b, Andrew E. McKechnie ^{c,d}, Cedric Sueur ^{e,f}, Susan J.
4 Cunningham ^a

5 *a: FitzPatrick Institute of African Ornithology, DST-NRF Centre of Excellence, University of*
6 *Cape Town, Rondebosch 7701, South Africa*

7 *b: Eawag, Swiss Federal Institute of Aquatic Science and Technology & Institute of*
8 *Integrative Biology, ETH, Switzerland*

9 *c: FitzPatrick Institute, DST-NRF Centre of Excellence, Department of Zoology and*
10 *Entomology, University of Pretoria, Private Bag X20, Hatfield 0028, South Africa*

11 *d: South African Research Chair in Conservation Physiology, National Zoological Garden,*
12 *South African National Biodiversity Institute, P.O. Box 754, Pretoria 0001, South Africa*

13 *e: Université de Strasbourg, CNRS, IPHC UMR 7178, F-67000 Strasbourg, France*

14 *f: Institut Universitaire de France, 75006 Paris, France*
15

16 ***Corresponding author:**

17 *Email: margaux.rat@uct.ac.za*

18 *Telephone: +27 21 650 3310*
19

20 **Abstract**

21 Organisms living in hot, arid environments face important risks associated with hyperthermia
22 and dehydration which are expected to become more severe with climate change. To mitigate
23 these risks, individuals often modify behaviour, e.g. reducing activity and seeking shade.
24 These behavioural modifications may affect interactions between individuals, with
25 consequences for the social structure of groups. We tested whether the social structure of
26 cooperative groups of sociable weavers (*Philetairus socius*) varied with environmental
27 temperature. We recorded the nature and frequency of interactions at feeders positioned
28 beneath three sociable weaver colonies ($N = 49$ identified birds) in the Kalahari Desert with
29 respect to environmental temperatures over a 30-day period. Using random forest models, we
30 examined whether thermal conditions predicted variation in social network structure. We also
31 conducted focal observations of individual weavers to assess functional links between
32 temperature, intensity of heat dissipation behaviour (panting), and immediate effects on

33 social behaviour. Our results suggest that the social structure of weaver colonies becomes less
34 cohesive and more fragmented at extreme and variable environmental temperatures. These
35 changes in network structure appear to be linked with individuals' heat dissipation behaviour:
36 extreme and variable temperatures were associated with increased panting, which was
37 significantly correlated with an immediate reduction in the frequency of association.
38 Collectively, our results indicate that interactions within groups could be disturbed by
39 environmental temperature variation and extremes. Changing temperature regimes could
40 therefore affect the functioning of animal societies by altering social networks.

41

42 **Keywords:** climate change, temperature variability, thermoregulation costs, social network,
43 environmental disturbance, group cohesiveness

1 **Introduction**

2 Sociality confers a wide range of direct and indirect fitness benefits (Kramer &
3 Meunier, 2016), but social relationships between individuals can be strongly affected by
4 ecological factors. For example, social interactions may be modified when resource
5 availability is reduced, triggering aggression and diminishing affiliative behaviour (Ahola,
6 Laaksonen, Eeva, & Lehikoinen, 2007; Kummerli, van den Berg, Griffin, West, & Gardner,
7 2010). Furthermore, changing biotic and abiotic conditions under global change are expected
8 to affect competition and other interactions between individuals, and the demography of
9 groups (Both, Bouwhuis, Lessells, & Visser, 2006; Destoumieux-Garzón et al., 2018; Sueur,
10 Romano, Sosa, & Puga-Gonzalez, 2017). Hence, climate change may indirectly affect the
11 type and frequency of interactions displayed between conspecifics, with implications for
12 group social organisation and the individual fitness benefits of group-living.

13 Climate change could also affect social interactions directly via the behavioural
14 adjustments animals make when exposed to high temperatures. For example, rising
15 temperatures drive changes in time-activity budgets as individuals retreat to cooler locations
16 within thermal landscapes (Martin, Cunningham, & Hockey, 2015; Mason, Brivio, Stephens,
17 Apollonio, & Grignolio, 2017), spend longer periods inactive (Carroll, Davis, Elmore,
18 Fuhlendorf, & Thacker, 2015) and/or more time dissipating heat via evaporative cooling
19 pathways (e.g. panting; McKechnie & Wolf, 2010). These adjustments for thermoregulation
20 can occur to the detriment of other behaviours, notably foraging (Cunningham, Martin, &
21 Hockey, 2015; du Plessis, Martin, Hockey, Cunningham, & Ridley, 2012; Funghi, McCowan,
22 Schuett, & Griffith, 2019) and social behaviour (Santee & Bakken, 1987); and have been
23 linked to body mass loss and reduced breeding success (Cunningham, Martin, Hojem, &
24 Hockey, 2013; du Plessis et al., 2012; van de Ven, 2017; Wiley & Ridley, 2016).

25 Sociality and cooperation may be particularly important in harsh and unpredictable
26 environments, e.g. arid savannas (Rubenstein & Lovette, 2007). In such environments, many
27 species already live near physiological tolerance limits, experiencing high risks of
28 hyperthermia and dehydration (Wolf, 2000). Social bonds between group members may help
29 to maintain individual and group performance under these conditions via reduction of
30 individual costs (Crick, 1992; Shen, Emlen, Koenig, & Rubenstein, 2017) and promotion of
31 individual benefits such as improved ability to locate food patches and detect predators
32 (Ward and Zahavi 1973, McNamara and Houston 1992, Cornwallis et al., 2017). Yet, climate
33 change models predict a faster increase in the frequency and amplitude of heat waves in arid
34 zones than in most regions of the globe (Akoon et al., 2011; Meehl & Tebaldi, 2004), and
35 there is already evidence of bird community collapse in response to warming in the Mojave
36 Desert (Iknayan & Beissinger, 2018).

37 Although sociality may reduce costs associated with harsh environmental conditions,
38 very little is known about how sensitive these buffering effects are to increments and/or
39 variations in temperature. We test the hypothesis that the social structure of an arid-zone,
40 group-living bird is influenced by high temperatures and/or unpredictable temperature
41 changes via trade-offs between heat dissipation behaviour and social interactions. We carried
42 out a field-based study to examine whether interactions and relationships between colony
43 members altered with changing temperature. Sociable weavers are passerines endemic to
44 southern Africa. They are long-lived (up to 16 year old; Covas, 2012) and colonies roost
45 communally year-round in large cooperatively-built nests so that the same individuals
46 interact frequently and can develop strong social bonds (Maclean, 1973b). We explored
47 whether such alterations were reflected in the social network structure of three wild colonies
48 of sociable weavers ($N = 49$ individuals) in the Kalahari Desert. We predicted that under
49 stressful high and/or variable temperature conditions, the frequency of affiliative and/or

50 agonistic interactions would be altered due to birds engaging more in heat dissipation and
51 avoidance behaviours (Vasse et al., 2017); and colony social structure would become less
52 dense and more disconnected, reflecting a reduction in group cohesiveness.

53 **Materials and methods**

54 Study site and species

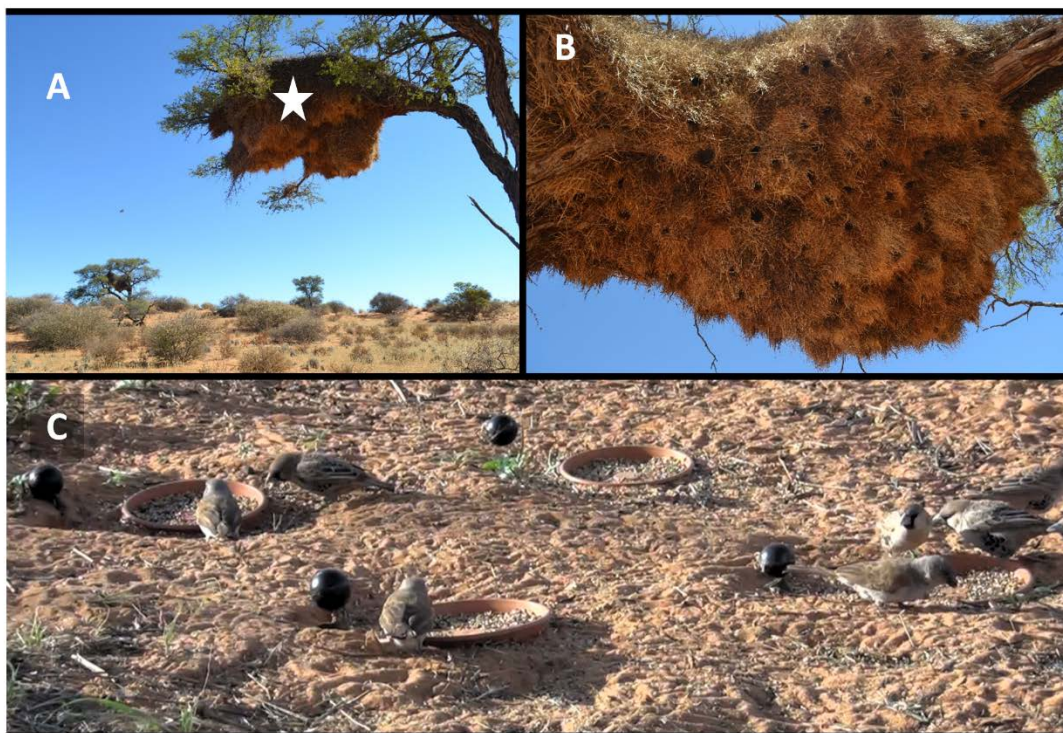
55 We worked at Murray Guest Farm, a privately-owned sheep and cattle farm in the Northern
56 Cape Province of South Africa (26° 59'S, 20° 52'E), during January and February 2016.

57 Vegetation at the farm is typical of Kalahari arid savanna; characterised by red sand dunes,
58 sparse grass, scattered trees and shrubs dominated by *Vachellia erioloba* and *Senegalia*
59 *mellifera* (Fig. 1). The study was conducted during the austral summer when climate is hot
60 and rainfall occurs as unpredictable, localised thunderstorms (Tyson & Crimp, 1998; daily
61 average minimum-maximum air temperature: 18.4-36.8°C; and rainfall: 0-65.9 mm; data
62 from Twee Rivieren Nov-Feb 1999-2015; provided by the South African Weather Service).

63 Sociable weavers live year-round in colonial nests which can host hundreds of
64 individuals and are built and maintained cooperatively through generations (Maclean, 1973a).
65 Colonies consist of multiple social sub-units of individuals roosting in separate nest chambers
66 with downwards-facing entrances on the underside of the nest (Fig. 1). These units typically
67 constitute of a breeding pair with helpers-at-the-nest, so 2-7 individuals can roost in the same
68 nest chamber (Covas, du Plessis, & Doutrelant, 2008). Helpers are mostly male offspring
69 from previous breeding attempts, but more distantly related individuals also help (Covas,
70 Dalecky, Caizergues, & Doutrelant, 2006; Doutrelant & Covas, 2007; Doutrelant, Covas,
71 Caizergues, & du Plessis, 2004). Individuals of the same colony interact with high frequency
72 over both short and long time-scales, as all colony members roost in the same nest and forage
73 together in gregarious flocks year-round (Ferreira et al., 2019; Flower & Gribble, 2012).

74 During the study period, our study site hosted approximately 70 active sociable weaver
75 colonies, comprising on average 46 occupied chambers per colonial nest (range: 1-180). Our
76 study focused on three of these colonies. The genetic variation between colonies is typically
77 lower than 0.02 and negatively associated with geographic distance (van Dijk, Covas,
78 Doutrelant, Spottiswoode, & Hatchwell, 2015).

79 Between 23 and 28 January 2016, we caught 21, 18 and 11 sociable weavers
80 respectively from three small colonies, hereafter colonies A, B and C (see Covas, Brown,
81 Anderson, & Brown, 2002; van Dijk, Covas, Doutrelant, Spottiswoode, & Hatchwell, 2015
82 for more details on the captures). Each bird was colour-ringed for individual identification.
83 We attempted to catch entire colonies, but five individuals escaped and remained un-ringed
84 (respectively 2, 1 and 2 individuals).



85

86 Figure 1: Photographs A, B and C of the study system: Photo A illustrates the study site in
87 the Kalahari desert. A colonial nest of the study species, the sociable weaver, is indicated by
88 a star. Photo B offers a closer view of underneath the colonial nest. The nest is built

89 cooperatively over many generations and it is used year-round for roosting. Photo C shows
90 the type of experimental design set up under three colonies of sociable weavers. We recorded
91 the co-occurrence of individuals foraging at the same feeder to establish associations between
92 individuals. The feeders were filled with a seed mixture and a blackbulb thermometer
93 positioned next to each feeder recorded the environmental temperature every 5 minutes.

94 Field experiment

95 We positioned artificial feeders (8 cm diameter plastic dishes) with an *ad libitum* seed
96 mixture at each colony between 26 January and 26 February 2016. Each colony had one feeder
97 per ~5 birds to ensure equal possibility of spatial clustering (i.e. N/5 feeders per colony, where N =
98 number of birds in the colony). Feeders were located on the ground underneath the nest
99 equidistant from each other (ca. 50 cm apart; Fig. 1). To habituate the weavers to the
100 experimental set-up, a video camera (Sony HDRCX130), tripod and feeders were positioned
101 all day beneath each colony until the first individual was observed to feed (range: 1-5 days).
102 Feeders were then removed and replaced for 2 hrs per day per colony, during which time
103 birds were observed visually and with a video-camera (details below). These 2-hr observation
104 blocks were rotated between three different time-of-day periods: morning (AM) observations
105 began between 6:30 and 7:15 am, corresponding to 30 min after sunrise; mid-day (MID)
106 observations began between 1:15-2:00 pm, matching the hottest time of the day; and
107 afternoon (PM) observations began between 4:15-5:00 pm and ended 30 min prior to sunset.
108 We conducted our observations over short time scales as this appeared to be the most
109 appropriate method to identify meaningful associations between individuals within flocks of
110 this highly gregarious species (Ferreira et al., 2019). Observations were distributed equally
111 between the three colonies and time periods.

112 - Behavioural data; extraction of association networks and social metrics:

113 Two types of observational data were collected: scan samples extracted from video-camera
114 footage; and focal observations ('focals') of individuals.

115 Scan samples: For all 2-hr observation blocks, the video camera was set up to record
116 activity at all feeders as well as 30-cm around them. We extracted still frames from the
117 footage at 1-minute intervals for each 2-hr observation block (hereafter ‘scan samples’). We
118 regarded the co-occurrence of individuals at the same feeder during the same scan sample as
119 a proxy for social association (Table 1). This measure was used to establish two types of
120 association networks: HWi and instant; for each 2-hr observation block.

121 ‘HWi networks’ were established using identity of colour-ringed colony members
122 feeding, and the identity of the feeder used (‘feeder position’; Table 1). HWi networks are
123 based on the calculation of the Half-Weight index (HWi), a measure of affinity between two
124 individuals of a group based on the proportion of time spent together (Whitehead & Dufault,
125 1999). Some other association indexes could have been used, but as pointed by Hoppitt &
126 Farine (2018; and references herein), for our type of dataset (only some individuals are
127 missing, not groups), most association indexes are valid for relative associations, scale-free
128 networks and node statistics. HWi indices were computed for every possible dyad of colour-
129 ringed weavers that were observed at a feeder at least once per 2hr observation block. The
130 structure of each HWi network was characterised by a set of social metrics, estimated once
131 per 2-hr observation block (Table 2). We excluded unringed sociable weavers to avoid biases
132 due to the impossibility of determining whether the same unringed individuals were sighted
133 during different scan samples within a single observation block (Cairns & Schwager, 1987;
134 Whitehead & Dufault, 1999). The median number of observations per ringed individual was
135 194 times, but the number of observations was highly variable, with a standard deviation of
136 71.7, in particular three individuals were observed only 1, 4 and 13 times.

137 ‘Instant networks’ were established to include unringed individuals; as these
138 represented 16% of birds for all scan samples. For these, we additionally recorded the feeder
139 position of unringed weavers in each scan sample. Instant network structure was

140 characterised by a set of social metrics calculated per scan sample (Table 2) and then
141 averaged to obtain one value per social metric per 2-hr observation block.

142 We included colony identity as a covariate in all analyses to account for effect(s)
143 induced by variation in the number of feeders. Additionally, we estimated network size using
144 the average number of individuals present per scan sample and corrected all social metrics for
145 this variable (*Supp. Mat. S1*; Smith, Moody, & Morgan, 2017). We also recorded the number
146 of southern grey-headed sparrows (*Passer griseus*; hereafter ‘sparrows’; the only other
147 species frequently visiting the feeders and interacting with sociable weavers) per scan
148 sample, to test whether their presence affected the sociable weaver network size and
149 structure.

150 We use both HWi and instant networks in our analyses because although the instant
151 networks included unidentified and unringed individuals, they also considered each scan
152 sample separately, which oversimplifies the real network (Hoppitt & Farine, 2018; Silk,
153 2018; Smith et al., 2017). By contrast, HWi networks capture this complexity by integrating
154 all scan samples from a given 2-hr observation block. Using both types of networks allowed
155 us to examine network structure including interactions between known individuals (HWi
156 networks) while also correctly estimating network size by including unringed/unidentified
157 individuals (instant networks).

158 Focals: During a subset of 27 (from 84) 2-hr observation blocks, one observer (MR)
159 conducted focal observations on individual birds from a hide ~10 meters from the colony, to
160 explore links between heat dissipation behaviour (panting) and social behaviours not directly
161 related to a feeding context. During focals, the observer followed a randomly-chosen
162 individual weaver until it approached a feeder or went out of sight. At this point, another
163 individual would be chosen and ‘focalled’; avoiding any individuals which had been

164 previously targeted during the observation period. The average focal duration per individual
 165 was 263 ± 172 s (mean \pm SE). During each focal, the observer recorded: i) the time spent
 166 panting (defined as: panting is an heat dissipation behaviour associated with evaporative
 167 cooling; Smit, Harding, Hockey, & McKechnie, 2013); ii) the number of ‘affiliations’
 168 (defined as the focal individual being $<$ half a sociable weaver body-length away from
 169 another sociable weaver: approximately 7 cm or less); and iii) the number of four kinds of
 170 agonistic interactions the focal individual perpetrated or was subject to (Table 1).

171 Table 1: Behavioural data recorded during scan samples from video-recordings and focal
 172 observations: their specific nature; the proxy used for collection; and definition. Note that
 173 social behaviour collected from focals is directional (initiated or received by the focal
 174 individual) while data collected from video-recordings are symmetrical.

Method	Behav. Data	Nature	Proxy	Definition
Scan samples	Network of associations	Co-occurrence	Spatial proximity	Co-occurrence at the same feeder at the same time
Focal observations	Frequency of associations	Co-occurrence	Spatial proximity	The focal individual is $< \frac{1}{2}$ a sociable weaver body-length away from another individual
	Heat dissipation	Panting	Time spent panting	Duration of panting by the focal individual
	Agonistic interactions	High intensity	Aggression	Focal individual physically attacks another individual.
			Displacement	Focal individual moves in the direction of a second individual until this individual moves away.
	Low intensity	Avoidance	Focal individual is avoided by second individual.	
			Threat	Focal individual makes a movement of the head toward a second individual until this individual moves away.

175 - Environmental temperature measurements

176 To monitor the temperatures experienced by individuals at the feeders, we used black-bulb
 177 thermometers logging at 5-min intervals (Cunningham et al., 2015). These comprised an
 178 iButtonTM temperature logger (Model DS1922L; Maxim Semiconductors, Dallas, Texas,
 179 USA) within a 30-mm diameter black-painted hollow copper sphere (approximating the
 180 dorso-ventral length of a small passerine). Black-bulb thermometers provide a single-number
 181 estimate of operative environmental temperature (T_{env}), integrating the effects of wind, air

182 temperature, radiation, conduction and convection. While not able to exactly replicate the
183 heat-load experienced by a living bird (see Bakken et al. 1985), they provide an estimate of
184 thermal conditions and quantify variation in T_{env} during the 2-hr observation block. We
185 calibrated the iButtons in a water bath against a mercury-in-glass thermometer with NIST-
186 traceable accuracy prior to deployment, following (Cunningham et al., 2015).

187 For each colony, we positioned a black-bulb thermometer on the ground adjacent to
188 each feeder (Fig. 1) and another in the shade 2 m above the ground in the colony tree to
189 approximate potential ‘thermal refuge’ temperatures ($T_{env}^{\circ C Tree}$). Environmental
190 temperature at the feeders ($T_{env}^{\circ C Ground}$) for each colony and time-point was calculated as
191 the average temperature recorded by all feeder-adjacent black-bulbs for that colony.

192 Statistical analyses

193 Statistical analyses were performed using R version 3.0 (or higher; (R-Core-Team, 2016).

194 - Temperature variables

195 For each 2-hr observation block, we examined the distribution of $T_{env}^{\circ C Ground}$ and $T_{env}^{\circ C$
196 *Tree*. We estimated the lowest, highest and average T_{env} , using the quantile 0.05 ($Q_{0.05}$), the
197 quantile 0.95 ($Q_{0.95}$), and the mean ($Mean T_{env}^{\circ C}$), respectively. We additionally estimated
198 immediate temperature stability by calculating the mean change between measurements at
199 consecutive 5-min time points ($E[|\Delta T_{env}^{\circ C}|]$), temperature range over the 2-hr observation
200 block ($Range T_{env}$) and the moments of order 2 ($Var T_{env}^{\circ C}$), order 3 ($Var_3 T_{env}^{\circ C}$) and order
201 4 ($Var_4 T_{env}^{\circ C}$) which respectively measure the variance, the asymmetric variance (i.e.
202 skewness), and the variance due to extreme values of T_{env} (Supp. Mat. S2; Grubbström &
203 Tang, 2006). To evaluate whether past temperatures influenced social behaviour during the 2-
204 hr observation block, we used the mean of $T_{env}^{\circ C Ground}$ and $T_{env}^{\circ C Tree}$ over either 2 hr (-

205 *2hr Mean T_{env}°C*) or 24 hr (*-24hr Mean T_{env}°C*) immediately prior to the 2-hr observation
206 block.

207 - Association network and social metrics

208 We used a principal component analysis (PCA) to explore the relationships between social
209 metrics for both HWi and instant networks (respectively 14 and 4 social metrics corrected for
210 network size; Table 2) and to summarize the variation in social network structure (Bollen,
211 Van de Sompel, Hagberg, & Chute, 2009; Viblanc, Pasquaretta, Sueur, Boonstra, & Dobson,
212 2016). We retained principal components (PCs) that explained > 15% of variation using the
213 function *testdim* of the package *ade4* (Dray, 2008; Dray, Dufour, & Thioulouse, 2007). A
214 sequential Bonferroni correction was applied to the *p*-values of this test to retain only
215 statistically meaningful variables.

216 We used random forest models (RFs) with conditional inference trees (Jones and Linder,
217 (2015) in the package *party* (Hothorn, Hornik, Strobl, & Zeileis, 2010), to identify predictors
218 best explaining variation in social network size and structure. We used the RF approach
219 because it is an appropriate statistical analysis method to account for multicollinearity and
220 high numbers of predictors (Hothorn, Hornik, Strobl, & Zeileis, 2010; Strobl, Boulesteix,
221 Kneib, Augustin, & Zeileis, 2008). We fitted one RF for the network size and one RF for
222 each of the three PCs retained, which together summarise 76% of the variation in the network
223 structure. In these four RFs, predictor variables included all temperature variables described
224 above, colony identity (*Colony*), time-period (AM, MID or PM; '*Day Period*') and the
225 average number of sparrows (*N Sparrow*) present during the 2-hr observation block.

226 Following Hapfelmeier & Ulm, 2013, we used a permutation approach to estimate *p*-values
227 for each predictor variable within each RF and adjusted these to keep the false discovery rate
228 (FDR) at 5% (Benjamini and Hochberg 1995(hereafter FDR; Hapfelmeier & Ulm, 2013). We
229 estimated the standardized effect size of each predictor for which FDR-adjusted *p*-values

230 (hereafter P_{ADJ}) was significant following Cafri and Bailey (2016), and present these P_{ADJ} -
231 values together with the standardized effect sizes throughout. Standardised effect sizes range
232 from -1 to 1 , where 0 = no effect. Further details are provided in the Supplementary
233 Materials.

234 Table 2: Social metrics computed to describe network structures. Social networks consist of
 235 nodes representing individuals and edges between nodes symbolizing direct association
 236 between individuals. Indirect associations (e.g. “friends-of-friends”) are represented by paths
 237 formed by a chain of nodes. “Level” defines whether social metrics were computed at the
 238 level of the whole colony network: “network-based”; or for each individual within a colony
 239 network, then averaged across all individuals in the network: “individual-based”. With
 240 respect to network type, “HWi” indicates metrics computed for HWi networks established
 241 per 2-hr observation block. “Instant” indicates metrics computed for instant networks
 242 established per scan sample and then averaged to produce one value per 2-hr observation
 243 block. Social metrics were corrected for network size.

Level	Social metric	Network type	Definition
NETWORK-BASED	Network size	Instant	The number of individuals at the feeders per scan sample.
	Diameter	HWi	The shortest number of edges (i.e. distance) between the two most distant individuals in the network.
	Density	HWi and Instant	Number of existing associations divided by number of possible associations.
	Isolate	HWi and Instant	Proportion of individuals that did not associate with any other individual.
	Cluster size	HWi and Instant	Mean size of groups of interconnected individuals.
	Cluster N	HWi	Number of groups of interconnected individuals.
	Global clustering coefficient	HWi	A measure of an "all-my-friends-know-each-other" property. This metric is also called “transitivity”. More precisely, the clustering coefficient of a node is the ratio of existing links connecting a node's neighbours to each other to the maximum possible number of such links.
	Average Path Length	HWi	A measure of indirect associations based on the average number of intermediate individuals (i.e. steps) needed to connect two members of the network.
	Closeness	HWi	A measure of indirect association based on the number of intermediate individuals required for an individual to be connected to every other individual in its network.
	Betweenness	HWi	A measure of individual centrality in the network, based on the number of shortest paths connecting a pair of individuals that pass through the focal individual. A high betweenness indicates that the shortest paths are long since they involve a lot of individuals.
INDIVIDUAL-BASED	Degree	HWi and Instant	The number of individuals directly connecting/associating with the focal individual.
	Strength	HWi	The number of individuals directly connecting/associating with the focal individual weighted by the frequency of this association over the 2-hr observation block (weighted Degree).
	Fidelity	HWi	The difference between Strength and Degree metrics for each individual. A high score indicates that an individual tends to associate many times with only a few other individuals, hence exhibiting high “fidelity” to those individuals.
	Eigenvalue centrality	HWi	A measure of approximate importance of each focal individual in their network based on the number of individuals they directly associate with and the number of individuals those individuals directly associate with and so on. A high average value indicates a dense network.

244 - Heat dissipation behaviour

245 For focals > 100 seconds long (minimum threshold set to ensure accuracy when estimating
246 the frequency of an observed behaviour), we used the same RF model approach to test for
247 relationships between different measures of T_{env} and the proportion of time individuals spent
248 panting during focals. We then examined whether panting correlated with immediate social
249 behaviour of individuals, by modelling the number of affiliations and agonistic interactions
250 (combined and by types) using a zero-inflated Poisson GLMM (package *glmmADMB*)
251 including the following predictors: proportion of time spent panting (arcsine transformed);
252 period of the day; and focal duration. Individual identity nested in colony identity was
253 included as a random effect. We checked models for overdispersion following (McCullagh &
254 Nelder, 1989).

255 **Results**

256 Environmental temperature

257 During the 2-hr observation blocks, the variable $T_{env}^{\circ C}$ *Ground* ranged from 17.2 -
258 54.7°C (mean \pm SD = $38 \pm 7.9^{\circ C}$), and the variable $T_{env}^{\circ C}$ *Tree* from 18.5 - 50.2°C (mean \pm
259 SD = $35 \pm 7.2^{\circ C}$). These values were averaged across the three colonies.

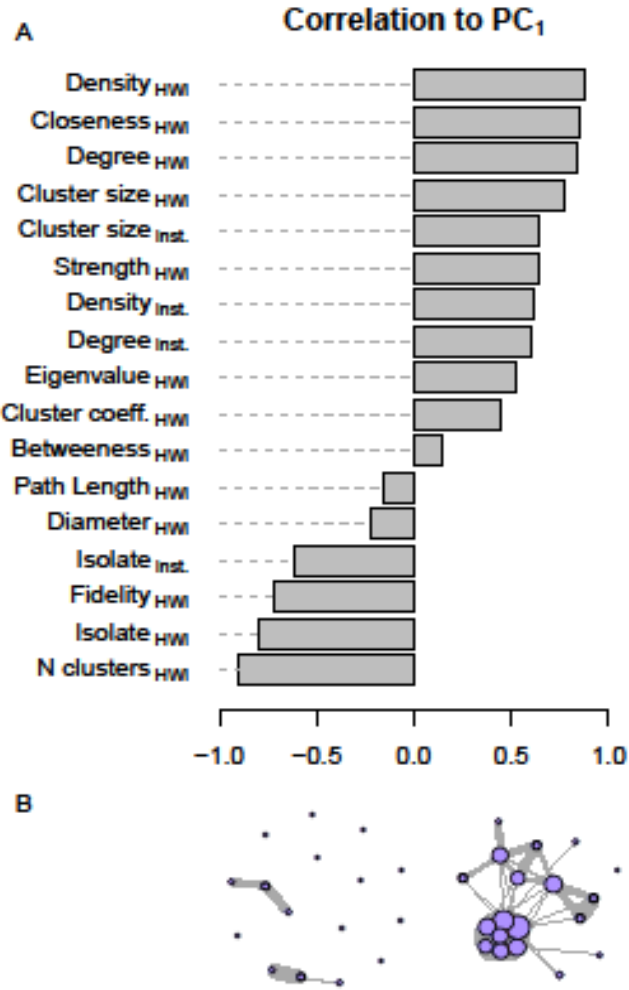
260 - Network size

261 Instant network size (i.e. average number of sociable weavers feeding within each scan
262 sample for each 2-hr observation block) was positively correlated with the range of $T_{env}^{\circ C}$
263 *Ground* during the 2-hr observation block ($P_{ADJ} = 0.01$, standardised effect size = 0.2; Fig. 2;
264 *Supp. Mat. S3*) and the average number of sparrows also feeding ($P_{ADJ} = 0.01$, standardised
265 effect size = 0.1; Fig. 4; Table S4). Network size was also affected by colony identity ($P_{ADJ} =$
266 0.01, standardised effect sizes from -0.1 to 0.1 depending on colony; Fig. 3; *Supp. Mat. S3*);
267 independently of colony size.

268 - Association networks

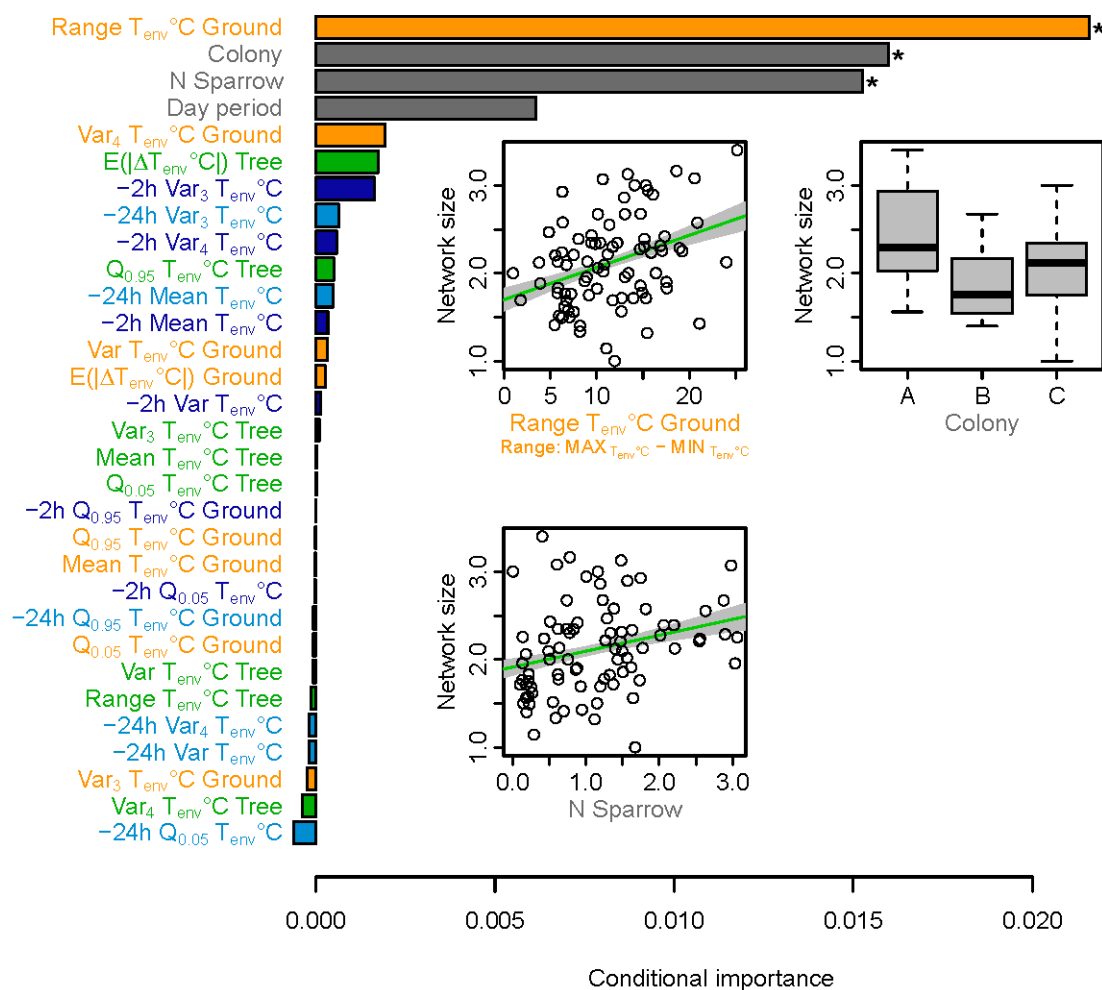
269 We constructed 84 HWi networks: 30 for AM, 28 for MID and 26 for PM time periods; and
270 120 instant networks per HWi network. A total of 49 ringed individuals were involved in all
271 HWi networks combined. Feeder visits and social associations were recorded on average
272 182.1 times per ringed individual (8921 feeder visits recorded in total). In addition, 1742
273 feeder visits by unringed or unidentified individuals were recorded.

274 Three principal components (PCs) explained 76% of the variance in the set of social
275 metrics; controlling for network size. PC₁ explained 42% of the variance and characterized
276 network “cohesiveness”. High loadings on PC₁ indicate: a dense HWi network; low
277 proportion of isolated individuals in both HWi and instant networks; and few, large, clusters
278 of individuals with high degree and strength but low fidelity (Fig. 2). PC₂ explained 18% of
279 the variance and characterized network cohesiveness of dense instant networks rather than
280 HWi networks (*Supp. Mat. S4-A*). PC₃ explained 16% of the variance and characterized
281 “cluster fragility”: high loadings indicate HWi networks with high path length; high
282 betweenness; high diameter; and low eigenvalue: i.e. fragile cluster(s) reliant mostly on
283 indirect and weak connections between individuals (*Supp. Mat. S5-A*).



284

285 Figure 2: Social networks characterised by PC₁: ‘network cohesiveness’. (A) Correlation of
 286 social metrics defined in Table 2 to PC₁. (B) Visualisation of social network structures with
 287 low (left) versus high (right) loadings on PC₁. Nodes (individuals) are represented by circles,
 288 edges (social associations) by straight lines. Circle size indicates the number of associations
 289 involving the individual. Edge thickness indicates the number of associations between the
 290 two connected individuals. Metrics were controlled for network size; N = 84 sociable weaver
 291 networks.



292

293 Figure 3: Factors associated with variation in average instant network size. Coloured
 294 horizontal bars (left) indicate predictor conditional importance, including both simple and
 295 interactive effects, estimated from a Random Forest model. Orange bars: temperatures
 296 recorded on the ground next to feeders ($T_{env}^{\circ}C$ Ground); green bars: temperatures in the tree
 297 hosting the colonial nest ($T_{env}^{\circ}C$ Tree); blue bars: mean of ground and tree temperatures
 298 recorded over the preceding 2 hours ($-2h$ $T_{env}^{\circ}C$, dark blue) or 24 hours ($-24h$ $T_{env}^{\circ}C$, light
 299 blue). Stars at the end of a bar indicate FDR-adjusted statistical significance (e.g. $* = P_{ADJ} <$
 300 0.05). Inset plots show relationships between significant predictors and network size, with
 301 fitted linear regressions (green line) \pm S.E. (grey shading). Predictor abbreviations: *N*
 302 *sparrow* = average number of sparrows present in each scan sample; *Day Period* = AM, MID
 303 or PM observation period (see methods); *Range $T_{env}^{\circ}C$* = the difference between the
 304 maximum and minimum environmental temperature recorded during the 2-hr observation
 305 period; *Var*, *Var₃*, and *Var₄* = respectively the variance of moment of order 2, 3 and 4. *Q_{0.05}*
 306 *T_{env}^{°C}* and *Q_{0.95} T_{env}^{°C}* = 5 and 95% quantiles of environmental temperature; $E(|\Delta T_{env}^{\circ}C|)$ =
 307 average absolute value of the difference between two consecutive $T_{env}^{\circ}C$ measurements (i.e. a
 308 measure of the magnitude of fine scale temperature oscillations).

309 - Social network cohesiveness (PC₁)

310 High variation in $T_{env}^{\circ}C$ *Ground* correlated with reduced HWi network cohesiveness (PC₁).

311 This effect was statistically significant for three measures of temperature variability: range;

312 variance (moment 2); and variance due to incidences of extreme $T_{env}^{\circ}C$ *Ground* relative to the

313 mean (moment 4) (P_{ADJ} -values = 0.03, 0.02 and 0.02; standardised effect sizes = -0.4, -0.7

314 and -0.6, respectively; Fig. 4 and *Supp. Mat. S3*). This reduction in HWi network

315 cohesiveness was 2 - 3.5 times larger than the concomitant increase in network size with

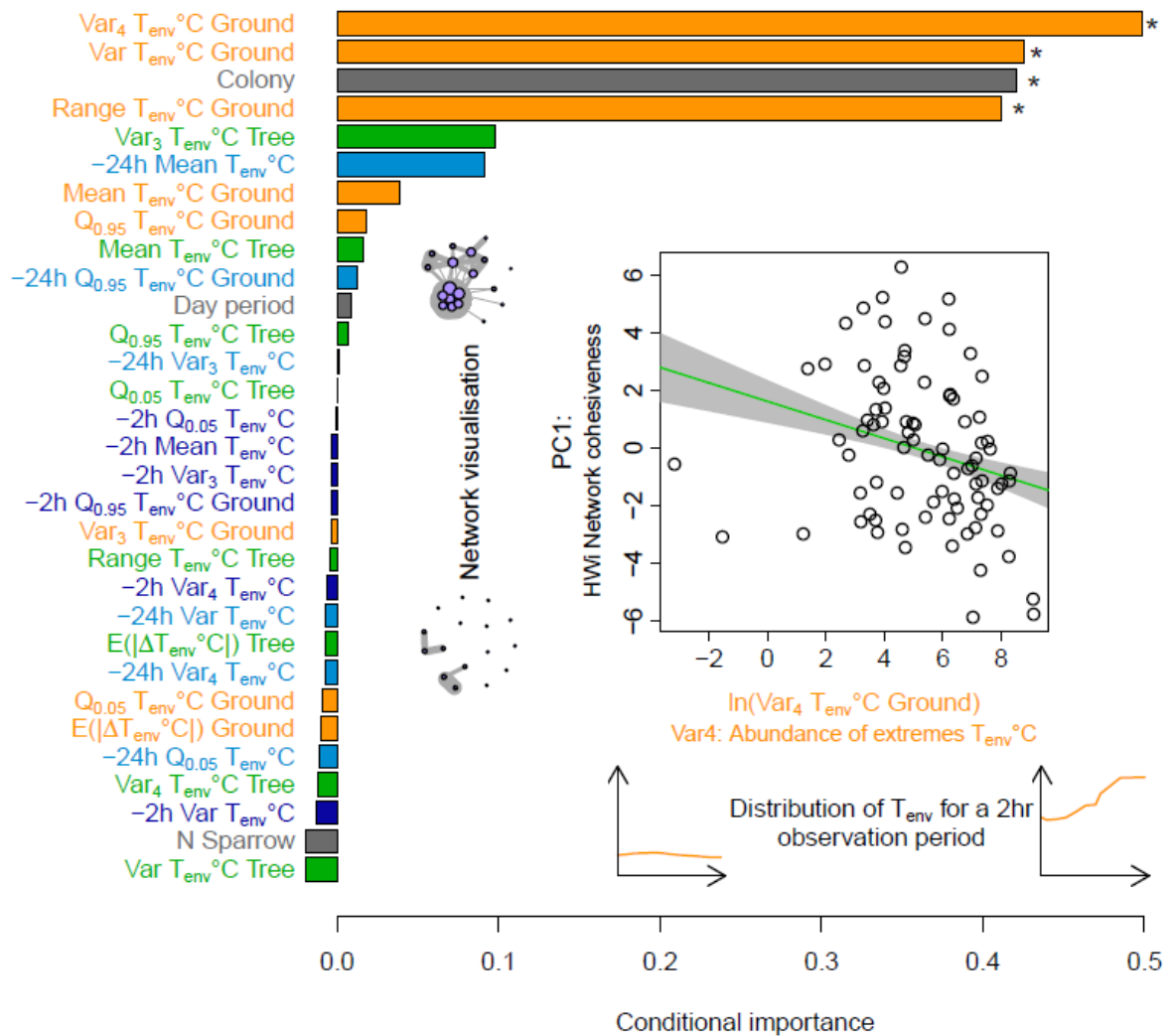
316 increased $T_{env}^{\circ}C$ *Ground* range (*Supp. Mat. S3*). Network cohesiveness also differed more

317 between colonies than did network size (standardised effect sizes = -0.2, 0.6 and -0.3; P_{ADJ}

318 = 0.02; Fig 3 and *Supp. Mat. S3*). No other variable tested significantly predicted variation in

319 PC₁, PC₂ and the PC₃ were mostly explained by respectively a positive effect of the number

320 of sparrows and the identity of the colony (*Supp. Mat. S3*).



321

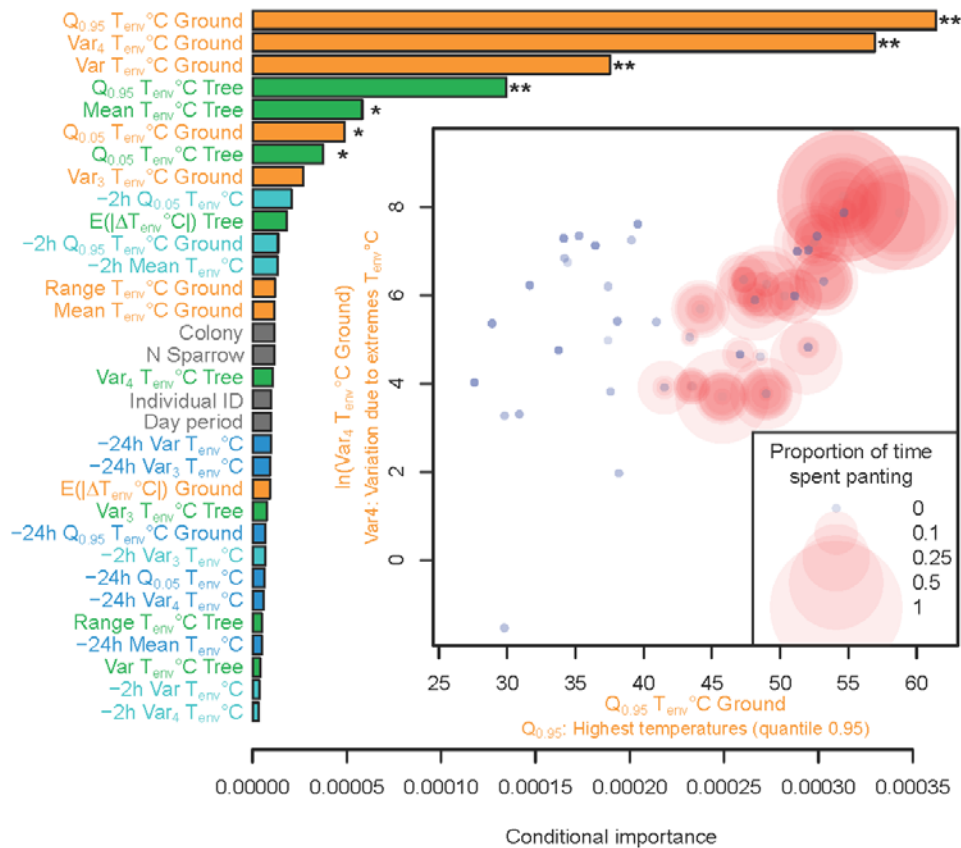
322 Figure 4: Factors associated with the variation in PC1: HWi network cohesiveness. Coloured
 323 horizontal bars (left) indicate conditional importance of predictors, including both simple and
 324 interactive effects, as estimated by a Random Forest model. Stars at the end of a bar indicate
 325 FDR-adjusted statistical significance (e.g. $* = P_{ADJ} < 0.05$). Inset scatterplot: the effect of
 326 $\text{Var}_4 T_{env} \text{ } ^\circ\text{C Ground}$ on PC1 (HWi network cohesiveness), with fitted linear regression (green
 327 line) \pm S.E. (grey shading). Left of the scatterplot: visualisations of social networks with high
 328 (upper network) and low (lower network) values of PC1. Below the scatterplot: example
 329 distributions of $T_{env} \text{ } ^\circ\text{C Ground}$ over a 2-hr observation block with low (left) and high (right)
 330 Var_4 . Bar colours and predictor abbreviations as for Figure 2.

331

332 Heat dissipation behaviour

333 Seven variables related to T_{env} were important in explaining the time spent panting by
 334 individuals during focals (Fig. 5 and *Supp. Mat. S3*). Hot ($Q_{0.95} T_{env} \text{ } ^\circ\text{C Ground}$) and variable
 335 and extreme temperatures ($\text{Var}_4 T_{env} \text{ } ^\circ\text{C Ground}$) had the strongest effects, mostly because of

336 their interaction (standardised effect sizes = 0.06, 0.04 and 0.2 for effects in interaction; P_{ADJ}
337 = 0.008 and 0.008; Fig. 5 and *Supp. Mat. S3*). Panting was initiated when the hottest
338 temperatures experienced (i.e. $Q_{0.95} T_{env} Ground$) were $\geq 41.5^{\circ}\text{C}$ (value determined by
339 analysing the partial dependency plot; not shown). Once initiated, panting duration (as a
340 proportion of the duration of the focal) increased when temperatures were variable, correlated
341 with the presence of frequent instances of extreme temperature (high Var_4) (Fig. 5).



342

343 Figure 5: Factors associated with variation in heat dissipation behaviour displayed by focal
 344 individuals (i.e. proportion of time spent panting). Coloured horizontal bars (left) indicate
 345 conditional importance of predictors, including both simple and interactive effects, as
 346 estimated by a Random Forest model. Stars at the end of a bar indicate level of statistical
 347 significance (e.g. $* = P_{ADJ} < 0.05$). The scatterplot inset shows the interactive effect of $Q_{0.95}$
 348 $T_{env} \text{ } ^\circ\text{C Ground}$ and $Var_4 T_{env} \text{ } ^\circ\text{C Ground}$, the two variables with the highest conditional
 349 importance, on proportion of time spent panting. Each symbol corresponds to one individual
 350 weavers in a focal observation). Bar colours and predictor abbreviations as for Figure 2.

351 The proportion of time individuals spent panting was significantly negatively correlated with
 352 their propensity to associate with conspecifics, estimate \pm SE = -0.27 ± 0.08 ; $p < 0.001$;
 353 controlling for focal duration and the period of the day. There was more chance of observing
 354 the focal individual associating with a conspecific when the focal was longer: estimate \pm SE
 355 = 0.09 ± 0.31 ; $p = 0.003$; and when observations were conducted later in the day: estimate \pm
 356 SE = 0.35 ± 0.11 ; $p = 0.001$ (Table 3).

357 However, there was no effect of the proportion of time spent panting on the number of active
 358 (estimate \pm SE = -0.10 ± 0.11 ; $P = 0.39$) or passive (estimate \pm SE = -0.18 ± 0.11 ; $P = 0.09$)
 359 agonistic interactions displayed by individuals. The number of passive agonistic interactions
 360 varied only with day period; with 0.28 agonistic interactions displayed on average per
 361 individual during mid-day (MID) versus 0.51 in the evening (PM). All other covariates were
 362 not significant ($P > 0.08$).

363 Table 3: Parameter estimates from a zero-inflated Poisson GLMM investigating the number
 364 of associations exhibited by an individual in relation to the proportion of focal time spent
 365 panting (N = 498 focals for 54 individuals). Zero-inflation was estimated at 0.123.

366

Variable	Estimate \pm SE	Z value	<i>P</i>
Intercept	-0.39 ± 0.14	-2.77	0.006
Proportion of panting	-0.27 ± 0.08	-3.49	<0.001
Duration of focal	0.09 ± 0.31	2.93	0.003
Day period (AM, MID, PM)	0.35 ± 0.11	3.21	0.001

367

368 Discussion

369 Environmental changes have the potential to affect relationships between individuals,
 370 in turn altering the social structure of cooperative groups and potentially affecting their

371 functioning (Leu, Farine, Wey, Sih, & Bull, 2016; Rubenstein, 1992). We tested whether
372 natural variation in environmental temperature was correlated with the social network
373 topology of free-living colonies of sociable weavers observed in a foraging context. Over
374 short time-scales, network cohesiveness was reduced when temperatures were extreme and
375 variable; despite an increase in the size of the network when sociable weavers were
376 experiencing a large range of temperatures. In addition, high and variable temperatures were
377 associated with individual birds spending a greater proportion of time panting: an indication
378 they were expending water (employing evaporative heat loss) to maintain body temperatures
379 within a safe range. Individual sociable weavers showed significantly reduced levels of
380 association with conspecifics while panting; but stable levels of agonistic behaviour. This
381 suggests the reduction in social cohesiveness we observed may have been mediated via
382 reduction in overall affiliative behaviour.

383 The importance of social cohesiveness

384 Social cohesiveness is an extremely important mediator of the fitness benefits of
385 sociality. For example, theoretical models show that social cohesiveness regulates the extent
386 of cooperative behaviour displayed in social groups and the amount of information
387 exchanged between individuals (Puga-Gonzalez et al., 2018; Romano, Shen, Pansanel,
388 MacIntosh, & Sueur, 2018). Empirical studies show that social cohesiveness also favours
389 protection against predators (e.g. in fish, Handegard et al., 2012; and other taxa, Krause &
390 Ruxton, 2002) and increased foraging success (e.g. in crabs, Tanner & Jackson, 2012). In
391 primates, well-connected individuals with strong social bonds to others within their social
392 groups may have higher survival (Alberts 2019), and higher reproductive success than more
393 poorly connected individuals (Silk et al. 2003, Silk 2007). The advantages conferred by
394 sociality may buffer individuals against environmental harshness and unpredictability,

395 perhaps explaining the overrepresentation of social species in arid environments (Cornwallis
396 et al., 2017).

397 Sociable weavers are one such arid-zone social species. Their distribution is centred
398 on southern Africa's Kalahari Desert (Spottiswoode, 2005), an area warming rapidly under
399 climate change (van Wilgen, Goodall, Holness, Chown, & McGeoch, 2015). Sublethal fitness
400 losses linked to behavioural responses to high temperatures have already been documented in
401 several arid-zone species (du Plessis et al 2012; van de Ven 2017; Cunningham et al 2013,
402 2015; Catry et al 2015). It is increasingly clear that cumulative, sublethal fitness costs may
403 threaten population persistence under ongoing climate change, even if temperatures
404 exceeding physiological tolerance limits are not reached (Conradie et al. 2019). Fitness losses
405 associated with the reduction of social cohesiveness are therefore of serious conservation
406 concern for species like sociable weavers; especially if these effects become chronic in the
407 context of climate change.

408 The role of panting behaviour

409 In this study, social cohesiveness co-varied with variable temperatures, while panting
410 behaviour co-varied with both hot and variable temperatures. Environmental temperatures on
411 the ground during this study were generally high (mean 38°C) and close to sociable weaver
412 body temperature (41°C; Whitfield, Smit, McKechnie, & Wolf, 2015). In addition, 2-hr
413 observation blocks during which temperatures were extremely hot (frequently well above
414 weaver body temperature) were associated high variance in temperature because of extreme
415 values ($Var_4 T_{env} C^\circ Ground$; Figure 4). Under these conditions, maintaining body
416 temperature below lethal limits is possible only via evaporative cooling, the major avenue of
417 which in sociable weavers is panting. Because panting is associated with an immediate
418 reduction in affiliative behaviour, it may be involved in the mediation between temperature
419 and reduction in network cohesiveness. Panting has been shown to trade-off against other

420 important behaviours, notably foraging, with implications for fitness in other arid-zone birds
421 (du Plessis et al 2012, van de Ven 2017). Under extremely hot conditions where the
422 immediate risk of lethal hyperthermia is high, heat dissipation via panting is critical and
423 might be favoured over the maintenance of social relationships.

424 Panting is widespread among birds and is the primary avenue of evaporative cooling
425 in passerines and several other taxa (Dawson, 1982). In these taxa, panting is routine during
426 hot conditions and often occurs while body temperatures are still well within the
427 normothermic range (e.g. McKechnie et al., 2017; Thompson, Cunningham, & McKechnie,
428 2018). However, in some taxa evaporative heat loss is less dependent on panting; among
429 columbids most evaporative heat loss occurs via cutaneous evaporation, and taxa including
430 caprimulgids, quails, cuckoos and sandgrouse make use of gular flutter, a rapid pulsation of
431 the hyoid bone that ventilates the buccal cavity (Lasiewski & Seymour, 1972; Marder,
432 Gavrieli-Levin, & Raber, 1986; Smit et al., 2018). Assuming the temperature-dependence of
433 social cohesiveness we documented here in sociable weavers is indeed functionally linked to
434 panting behaviour, we predict that social cohesiveness is likely to be affected at high
435 temperatures in other taxa which rely on this mechanism for thermoregulation (e.g. other
436 passerine birds); but perhaps less so in taxa in which panting is not the primary mechanism of
437 thermoregulation in the heat (e.g. columbids).

438 Interindividual variation and the emergence of 'isolates'

439 Avian responses to heat may vary among species, between (Noakes, Wolf, &
440 McKechnie, 2016) and within populations (Cunningham, Thompson, & McKechnie, 2017).
441 In sociable weavers, dominant birds seem better able to maintain stable body temperatures
442 than subordinates when exposed to high air temperatures (Cunningham et al., 2017). In the
443 present study, reduction of social network cohesiveness included the emergence of isolated
444 individuals without any social connections. If the management of thermal challenges results

445 in reduction of social behaviour (this study), and subordinate sociable weavers struggle most
446 with thermal loads (Cunningham et al., 2017), it seems possible these isolates are subordinate
447 birds. We therefore speculate that already-vulnerable individuals may become more
448 vulnerable to the loss of benefits of sociality under thermally challenging conditions.
449 However, subordinates play important roles in the functioning of societies (Crick, 1992) and
450 their increased vulnerability may compound the vulnerability of the group.

451 Conclusions

452 To the best of our knowledge, our data provide the first evidence that short-term
453 temperature variation could impact social network structure of a co-operative species,
454 reducing the cohesiveness of social groups and thus potentially increasing the vulnerability of
455 societal systems. Furthermore, social cohesiveness responded to the frequency of
456 temperatures that were extreme with respect to the current mean temperature. This adds
457 evidence of the importance of increases in temperature variation in terms of impacts on
458 species (Ruel and Ayres 1999, Vasseur, DeLong et al. 2014).

459 The conclusions drawn here are based on a study of three colonies of sociable
460 weavers in the Kalahari Desert and therefore need to be treated with caution. Nonetheless,
461 social network cohesiveness was reduced consistently across all three groups of birds under
462 highly variable temperatures including hot temperature extremes; and N = 49 colour-ringed
463 and identifiable individuals showed reduction in affiliative behaviour under thermally
464 stressful conditions; suggesting that social behaviour may indeed be vulnerable to changing
465 environmental conditions over short time-scales. These reductions in the amount of social
466 interactions over short timescales may have longer term consequences for social benefits such
467 as the transfer of information and cooperation; but this remains unknown.

468 Given the overrepresentation of social species in hot and arid zones (Cornwallis et al
469 2017) and the vulnerability of these regions to climate warming (Allen et al., 2014; Easterling
470 et al., 2000), our results warrant further investigation. Further research is needed to identify
471 whether other social species show similar reductions in social network cohesiveness under
472 short-term thermal stress and identify the longer-term impacts for individual fitness and
473 group survival. Despite the unknowns, our results overall raise concern about the potential
474 vulnerability of social species in arid zones under ongoing and severe increases in the
475 frequency of extreme climatic events.

476 **Speculations**

477 According to socioecological factors, animals adapt with whom they interact and how they
478 collectively decide to increase their fitness. This may result in group phenotypic composition
479 dependent on ecological factors. This has been referred to as a ‘collective social niche
480 construction’ (Sueur et al., 2019). Usually, ecological factors as information acquisition,
481 pathogens loads or predation are studied to see how individuals change their behavioural
482 strategies and are more or less cohesive, cooperative or aggressive. These behavioural
483 changes affect their fitness as well as the network topology. In this paper, we showed that
484 temperature is also a factor affecting the network topology. This means that the global
485 changes coming may greatly affect other patterns depending on the network topology as
486 information transmission, disease transmission or cooperation. So these global changes may
487 have a cascade effect conducting to deaths of individuals and population extinction. This link
488 between the network topology and dependence between the different ecological factors is of
489 major concern and a research effort topic in the future.

490 **Declarations**

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502 AEM & CS contributed to the manuscript write-up. SJC, AEM & CS funded the research.
503 Conflicts of interest: the authors declare no conflicts of interest.

504 Permits: The Rossouw family of Murray Guest Farm kindly authorized research on their
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508 under SAFRING permit number 12886 and the collection of blood samples under South
509 African Veterinary Council certification number AL16/15771.

510 **Data accessibility**

511 The data used in our analyses will be available on the dryad digital repository (datadryad.org)
512 after acceptance.

513 **References**

- 514 Ahola, M. P., Laaksonen, T., Eeva, T., & Lehikoinen, E. S. A. (2007). Climate change can
515 alter competitive relationships between resident and migratory birds. *Journal of*
516 *Animal Ecology*, 76(6), 1045-1052. doi:10.1111/j.1365-2656.2007.01294.x
- 517 Akoon, I., Archer, E., Colvin, C., Davis, C., Diedericks, G., & Maherry, A. (2011). South
518 African risk and vulnerability atlas. *Pretoria: Department of Science and Technology*.
- 519 **Alberts, S. (2019)**
- 520 Allen, M. R., Barros, V. R., Broome, J., Cramer, W., Christ, R., Church, J. A., et al. (2014).
521 *IPCC fifth assessment synthesis report-climate change 2014 synthesis report*.
522 Retrieved from <https://www.ipcc.ch/report/ar5/syr/>:
- 523 Bollen, J., Van de Sompel, H., Hagberg, A., & Chute, R. (2009). A principal component
524 analysis of 39 scientific impact measures. *Plos One*, 4(6), e6022.
- 525 Both, C., Bouwhuis, S., Lessells, C., & Visser, M. E. (2006). Climate change and population
526 declines in a long-distance migratory bird. *Nature*, 441(7089), 81-83.
- 527 Cafri, G., & Bailey, B. A. (2016). Understanding variable effects from black box prediction:
528 Quantifying effects in tree ensembles using partial dependence. *Journal of Data*
529 *Science*, 14(1), 67-95.
- 530 Cairns, S. J., & Schwager, S. J. (1987). A comparison of association indices. *Animal*
531 *Behaviour*, 35(5), 1454-1469.
- 532 Carroll, J. M., Davis, C. A., Elmore, R. D., Fuhlendorf, S. D., & Thacker, E. T. (2015).
533 Thermal patterns constrain diurnal behavior of a ground-dwelling bird. *Ecosphere*,
534 6(11), 1-15.
- 535 Conradie, S. R., Woodborne, S. M., Cunningham, S. J., & McKechnie, A. E. (2019). Chronic,
536 sublethal effects of high temperatures will cause severe declines in southern African

537 arid-zone birds during the 21st Century. *Proceedings of the National Academy of*
538 *Sciences* 116 (28), 14065-14070

539 Cornwallis, C. K., Botero, C. A., Rubenstein, D. R., Downing, P. A., West, S. A., & Griffin,
540 A. S. (2017). Cooperation facilitates the colonization of harsh environments. *Nature*
541 *Ecology & Evolution*, 1, 0057.

542 Covas, R. (2012). The benefits of long-term studies: 16-year old sociable weaver caught at
543 Benfontein Game Reserve. *Safring News*, 41, 11-12.

544 Covas, R., Brown, C. R., Anderson, M. D., & Brown, M. B. (2002). Stabilizing selection on
545 body mass in the sociable weaver (*Philetairus socius*). *Proceedings of the Royal*
546 *Society of London, Series B: Biological Sciences*, 269(1503), 1905-1909.
547 doi:10.1098/rspb.2002.2106

548 Covas, R., Dalecky, A., Caizergues, A., & Doutrelant, C. (2006). Kin associations and direct
549 vs indirect fitness benefits in colonial cooperatively breeding sociable weavers
550 *Philetairus socius*. *Behavioral Ecology and Sociobiology*, 60(3), 323-331.
551 doi:10.1007/s00265-006-0168-2

552 Covas, R., du Plessis, M. A., & Doutrelant, C. (2008). Helpers in colonial cooperatively
553 breeding sociable weavers (*Philetairus socius*) contribute to buffer the effects of
554 adverse breeding conditions. *Behavioral Ecology and Sociobiology*, 63(1), 103-112.

555 Crick, H. (1992). Load-lightening in cooperatively breeding birds and the cost of
556 reproduction. *Ibis*, 134(1), 56-61.

557 Cunningham, S. J., Martin, R. O., & Hockey, P. A. R. (2015). Can behaviour buffer the
558 impacts of climate change on an arid-zone bird? *Ostrich*, 86(1-2), 119-126.
559 doi:10.2989/00306525.2015.1016469

560 Cunningham, S. J., Martin, R. O., Hojem, C. L., & Hockey, P. A. (2013). Temperatures in
561 excess of critical thresholds threaten nestling growth and survival in a rapidly-
562 warming arid savanna: a study of common fiscals. *Plos One*, 8(9), e74613.

563 Cunningham, S. J., Thompson, M. L., & McKechnie, A. E. (2017). It's cool to be dominant:
564 social status alters short-term risks of heat stress. *Journal of Experimental Biology*,
565 220(9), 1558-1562.

566 Dawson, W. R. (1982). Evaporative losses of water by birds. *Comparative Biochemistry and*
567 *Physiology Part A: Physiology*, 71(4), 495-509.

568 Destoumieux-Garzón, D., Mavingui, P., Boetsch, G., Boissier, J., Darriet, F., Duboz, P., et al.
569 (2018). The one health concept: 10 years old and a long road ahead. *Frontiers in*
570 *veterinary science*, 5, 14.

571 Dijk, René E. Van, Rita Covas, Claire Doutrelant, Claire N. Spottiswoode, and Ben J .
572 Hatchwell. (2015). Fine-Scale Genetic Structure Reflects Sex-Specific Dispersal
573 Strategies in a Population of Sociable Weavers (*Philetairus Socius*). *Molecular*
574 *Ecology*. 24(16), 4296-4311.

575 Doutrelant, C., & Covas, R. (2007). Helping has signalling characteristics in a cooperatively
576 breeding bird. *Animal Behaviour*, 74, 739-747. doi:10.1016/j.anbehav.2006.11.033

577 Doutrelant, C., Covas, R., Caizergues, A., & du Plessis, M. (2004). Unexpected sex ratio
578 adjustment in a colonial cooperative bird: pairs with helpers produce more of the
579 helping sex whereas pairs without helpers do not. *Behavioral Ecology and*
580 *Sociobiology*, 56(2), 149-154. doi:10.1007/s00265-004-0756-y

581 Dray, S. (2008). On the number of principal components: A test of dimensionality based on
582 measurements of similarity between matrices. *Computational Statistics & Data*
583 *Analysis*, 52(4), 2228-2237.

584 Dray, S., Dufour, A. B., & Thioulouse, J. (2007). The ade4 package: implementing the
585 duality diagram for ecologists. *Journal of Statistical Software*, 22(4), 1-20.

586 du Plessis, K. L., Martin, R. O., Hockey, P. A., Cunningham, S. J., & Ridley, A. R. (2012).
587 The costs of keeping cool in a warming world: implications of high temperatures for
588 foraging, thermoregulation and body condition of an arid-zone bird. *Global Change
589 Biology*, 18(10), 3063-3070.

590 Easterling, D. R., Meehl, G. A., Parmesan, C., Changnon, S. A., Karl, T. R., & Mearns, L. O.
591 (2000). Climate Extremes: Observations, Modeling, and Impacts. *Science*, 289(5487),
592 2068-2074. doi:10.1126/science.289.5487.2068

593 Ferreira, A. C., Covas, R., Silva, L. R., Esteves, S. C., Duarte, I. F., Fortuna, R., et al. (2019).
594 How to make methodological decisions when inferring social networks. *bioRxiv*,
595 739789. doi:10.1101/739789

596 Flower, T. P., & Gribble, M. (2012). Kleptoparasitism by attacks versus false alarm calls in
597 fork-tailed drongos. *Animal Behaviour*, 83(2), 403-410.
598 doi:<http://dx.doi.org/10.1016/j.anbehav.2011.11.009>

599 Funghi, C., McCowan, L. S. C., Schuett, W., & Griffith, S. C. (2019). High air temperatures
600 induce temporal, spatial and social changes in the foraging behaviour of wild zebra
601 finches. *Animal Behaviour*, 149, 33-43.
602 doi:<https://doi.org/10.1016/j.anbehav.2019.01.004>

603 Grubbström, R. W., & Tang, O. (2006). The moments and central moments of a compound
604 distribution. *European Journal of Operational Research*, 170(1), 106-119.

605 Handegard, N. O., Boswell, K. M., Ioannou, C. C., Leblanc, S. P., Tjøstheim, D. B., &
606 Couzin, I. D. (2012). The dynamics of coordinated group hunting and collective
607 information transfer among schooling prey. *Current Biology*, 22(13), 1213-1217.

608 Hapfelmeier, A., & Ulm, K. (2013). A new variable selection approach using random forests.
609 *Computational Statistics & Data Analysis*, 60, 50-69.

610 Hoppitt, W. J., & Farine, D. R. (2018). Association indices for quantifying social
611 relationships: how to deal with missing observations of individuals or groups. *Animal*
612 *Behaviour*.

613 Hothorn, T., Hornik, K., Strobl, C., & Zeileis, A. (2010). Party: A laboratory for recursive
614 partytioning.

615 Iknayan, K. J., & Beissinger, S. R. (2018). Collapse of a desert bird community over the past
616 century driven by climate change. *Proceedings of the National Academy of Sciences*,
617 115(34), 8597-8602.

618 Jones, Z., & Linder, F. (2015). *Exploratory data analysis using random forests*. Paper
619 presented at the 73rd annual MPSA conference.

620 Kramer, J., & Meunier, J. (2016). Kin and multilevel selection in social evolution: a never-
621 ending controversy? *F1000Research*, 5.

622 Krause, J., & Ruxton, G. D. (2002). *Living in groups*. Oxford: Oxford University Press.

623 Kummerli, R., van den Berg, P., Griffin, A. S., West, S. A., & Gardner, A. (2010).
624 Repression of competition favours cooperation: experimental evidence from bacteria.
625 *Journal of Evolutionary Biology*, 23(4), 699-706. doi:10.1111/j.1420-
626 9101.2010.01936.x

627 Lasiewski, R. C., & Seymour, R. S. (1972). Thermoregulatory responses to heat stress in four
628 species of birds weighing approximately 40 grams. *Physiological Zoology*, 45(2),
629 106-118.

630 Leu, S. T., Farine, D. R., Wey, T. W., Sih, A., & Bull, C. M. (2016). Environment modulates
631 population social structure: experimental evidence from replicated social networks of

632 wild lizards. *Animal Behaviour*, 111, 23-31.

633 doi:<https://doi.org/10.1016/j.anbehav.2015.10.001>

634 Maclean, G. L. (1973a). The sociable weaver, Part 2: Nest architecture and social
635 organization. *Ostrich*, 44, 191-218.

636 Maclean, G. L. (1973b). The sociable weaver, Part 5: Food, feeding and general behaviour.
637 *Ostrich*, 44, 254-261.

638 Marder, J., Gavrieli-Levin, I., & Raber, P. (1986). Cutaneous evaporation in heat-stressed
639 spotted sandgrouse. *Condor*, 88(1), 99-100.

640 Martin, R. O., Cunningham, S. J., & Hockey, P. A. (2015). Elevated temperatures drive fine-
641 scale patterns of habitat use in a savanna bird community. *Ostrich*, 86(1-2), 127-135.

642 Mason, T. H., Brivio, F., Stephens, P. A., Apollonio, M., & Grignolio, S. (2017). The
643 behavioral trade-off between thermoregulation and foraging in a heat-sensitive
644 species. *Behavioral Ecology*, 28(3), 908-918.

645 McCullagh, P., & Nelder, J. A. (Eds.). (1989). *Generalized Linear Models* (Second ed. Vol.
646 37): Chapman & Hall.

647 McKechnie, A. E., Gerson, A. R., McWhorter, T. J., Smith, E. K., Talbot, W. A., & Wolf, B.
648 O. (2017). Avian thermoregulation in the heat: evaporative cooling in five Australian
649 passerines reveals within-order biogeographic variation in heat tolerance. *Journal of*
650 *Experimental Biology*, jeb. 155507.

651 McKechnie, A. E., & Wolf, B. O. (2010). Climate change increases the likelihood of
652 catastrophic avian mortality events during extreme heat waves. *Biology Letters*, 6(2),
653 253-256.

654 McNamara, J. M. and A. I. Houston (1992). Evolutionarily stable levels of vigilance as a
655 function of group size. *Animal Behaviour* 43(4), 641-658.

656 Meehl, G. A., & Tebaldi, C. (2004). More intense, more frequent, and longer lasting heat
657 waves in the 21st century. *Science*, 305(5686), 994-997.

658 Noakes, M. J., Wolf, B. O., & McKechnie, A. E. (2016). Seasonal and geographical variation
659 in heat tolerance and evaporative cooling capacity in a passerine bird. *Journal of*
660 *Experimental Biology*, 219(6), 859-869.

661 Puga-Gonzalez, I., Ostner, J., Schülke, O., Sosa, S., Thierry, B., & Sueur, C. (2018).
662 Mechanisms of reciprocity and diversity in social networks: a modeling and
663 comparative approach. *Behavioral Ecology*, 29(3), 745-760.

664 R-Core-Team. (2016). R: A language and environment for statistical computing (Version
665 3.4). Vienna, Austria.

666 Romano, V., Shen, M., Pansanel, J., MacIntosh, A. J., & Sueur, C. (2018). Social
667 transmission in networks: global efficiency peaks with intermediate levels of
668 modularity. *Behavioral Ecology and Sociobiology*, 72(9), 154.

669 Rubenstein, D. I. (1992). The greenhouse effect and changes in animal behavior: effects on
670 social structure and life-history strategies. In R. L. Peters (Ed.), *Global warming and*
671 *biological diversity* (pp. 180-192): Yale University Press.

672 Rubenstein, D. R., & Lovette, I. J. (2007). Temporal environmental variability drives the
673 evolution of cooperative breeding in birds. *Current Biology*, 17(16), 1414-1419.

674 Santee, W. R., & Bakken, G. S. (1987). Social Displays in Red-Winged Blackbirds (*Agelaius*
675 *phoeniceus*): Sensitivity to Thermoregulatory Costs. *The Auk*, 104(3), 413-420.
676 doi:10.2307/4087538

677 Shen, S. F., Emlen, S. T., Koenig, W. D., & Rubenstein, D. R. (2017). The ecology of
678 cooperative breeding behaviour. *Ecology Letters*, 20(6), 708-720.

679 Silk, M. J. (2018). The next steps in the study of missing individuals in networks: a comment
680 on Smith et al.(2017). *Social Networks*, 52, 37-41.

681 Smit, B., Harding, C., Hockey, P. A., & McKechnie, A. E. (2013). Adaptive
682 thermoregulation during summer in two populations of an arid-zone passerine.
683 *Ecology*, *94*(5), 1142-1154.

684 Smit, B., Whitfield, M. C., Talbot, W. A., Gerson, A. R., McKechnie, A. E., & Wolf, B. O.
685 (2018). Avian thermoregulation in the heat: phylogenetic variation among avian
686 orders in evaporative cooling capacity and heat tolerance. *Journal of Experimental*
687 *Biology*, jeb. 174870.

688 Smith, J. A., Moody, J., & Morgan, J. H. (2017). Network sampling coverage II: the effect of
689 non-random missing data on network measurement. *Social Networks*, *48*, 78-99.

690 Spottiswoode, C. N. (2005). Sociable Weaver. In P. A. R. Hockey, W. R. J. Dean, & P. G.
691 Ryan (Eds.), *Roberts Birds of southern Africa*. Cape Town: The Trustees of the John
692 Voelcker.

693 Strobl, C., Boulesteix, A.-L., Kneib, T., Augustin, T., & Zeileis, A. (2008). Conditional
694 variable importance for random forests. *BMC Bioinformatics*, *9*(1), 307.

695 Sueur, C., Romano, V., Sosa, S., & Puga-Gonzalez, I. (2019). Mechanisms of network
696 evolution: a focus on socioecological factors, intermediary mechanisms, and selection
697 pressures. *Primates*, 1-15.

698 Tanner, C. J., & Jackson, A. L. (2012). Social structure emerges via the interaction between
699 local ecology and individual behaviour. *Journal of Animal Ecology*, *81*(1), 260-267.
700 doi:10.1111/j.1365-2656.2011.01879.x

701 Thompson, M., Cunningham, S., & McKechnie, A. E. (2018). Interspecific variation in avian
702 thermoregulatory patterns and heat dissipation behaviours in a subtropical desert.
703 *Physiology & Behavior*.

704 Tyson, P. D., & Crimp, S. J. (1998). The climate of the Kalahari transect. *Transactions of the*
705 *Royal Society of South Africa*, *53*(2), 93-112. doi:10.1080/00359199809520380

706 van de Ven, T. (2017). *Implications of climate change on the reproductive success of the*
707 *southern Yellow-billed Hornbill Tockus leucomelas*. (Ph.D.), University of Cape
708 Town, Cape Town.

709 van Dijk, R. E., Covas, R., Doutrelant, C., Spottiswoode, C. N., & Hatchwell, B. J. (2015).
710 Fine-scale genetic structure reflects sex-specific dispersal strategies in a population of
711 sociable weavers (*Philetairus socius*). *Molecular Ecology*, 24(16), 4296-4311.
712 doi:10.1111/mec.13308

713 van Wilgen, N. J., Goodall, V., Holness, S., Chown, S. L., & McGeoch, M. A. (2015). Rising
714 temperatures and changing rainfall patterns in South Africa's national parks.
715 *International Journal of Climatology*.

716 Vasse, M., Noble, R. J., Akhmetzhanov, A. R., Torres-Barcelo, C., Gurney, J., Benateau, S.,
717 et al. (2017). Antibiotic stress selects against cooperation in the pathogenic bacterium
718 *Pseudomonas aeruginosa*. *Proceedings of the National Academy of Sciences of the*
719 *U.S.A.*, 114(3), 546-551. doi:10.1073/pnas.1612522114

720 Viblanc, V. A., Pasquaretta, C., Sueur, C., Boonstra, R., & Dobson, F. S. (2016). Aggression
721 in Columbian ground squirrels: relationships with age, kinship, energy allocation, and
722 fitness. *Behavioral Ecology*, arw098.

723 Ward, P. and A. Zahavi (1973). The importance of certain assemblages of birds as
724 “information-centres” for food-finding. *Ibis* 115(4): 517-534.

725 Whitehead, H., & Dufault, S. (1999). Techniques for analyzing vertebrate social structure
726 using identified individuals. *Advances in the study of behavior*, 28, 33-74.

727 Whitfield, M. C., Smit, B., McKechnie, A. E., & Wolf, B. O. (2015). Avian thermoregulation
728 in the heat: scaling of heat tolerance and evaporative cooling capacity in three
729 southern African arid-zone passerines. *The Journal of experimental biology*, 218(11),
730 1705-1714.

- 731 Wiley, E. M., & Ridley, A. R. (2016). The effects of temperature on offspring provisioning in
732 a cooperative breeder. *Animal Behaviour*, *117*, 187-195.
- 733 Wolf, B. (2000). Global warming and avian occupancy of hot deserts; a physiological and
734 behavioral perspective. *Revista chilena de historia natural*, *73*, 395-400.
- 735