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1 **Mind the polar sun: Solar radiations trigger frequent heat stress in breeding**
2 **king penguins, despite relatively cool air temperatures.**

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15

16 **Abstract**

17 Polar and sub-polar animals evolved to thrive in cold climates and may thus be
18 particularly vulnerable to the rising temperatures associated with climate change. Polar and
19 sub-polar penguins may be especially vulnerable due to their dual habitat, alternating between
20 foraging in cold waters and breeding/moulting on an increasingly warm land. Here, we
21 characterized heat stress occurrence in breeding king penguins through behavioural
22 observations and subcutaneous body temperature measurements. We show that heat stress
23 is frequent (> 20% of observations at mid-day) in king penguins breeding in the sub-Antarctic
24 region, and that thermoregulatory mechanisms appear insufficient to maintain stable sub-
25 cutaneous temperature. Air temperature alone was a poor predictor of heat stress occurrence,
26 while the combination of high solar radiations, low wind speed and high temperatures was its
27 best predictor. Importantly, reproductive failure occurred on days warmer than average,
28 suggesting potential significant sublethal effects of heat stress being likely to affect population
29 dynamics.

30

31 *Key words:* thermoregulation, temperature, seabird, climate change, heat wave, behaviour

32 Introduction

33 Heat waves, or extremely “hot” climatic events (Marx *et al.* 2021; Robinson 2001), are
34 increasing in frequency with global warming, which is expected to exert direct thermoregulatory
35 pressure on most living organisms (Piatt *et al.* 2024; Stillman 2019). In endotherms, when
36 ambient temperatures reach the upper limits of their thermoneutral zone (TNZ) (*i.e.* the range
37 of ambient temperatures in which metabolic rate is minimal) (Romanovsky 2007, 2018), the
38 costs of active thermoregulation or the failure to properly thermoregulate may lead to reduced
39 reproductive success or survival (Boyles *et al.* 2011; Danner *et al.* 2021; Pipoly *et al.* 2013).
40 Although no real consensus exists regarding the definition of a ‘heat wave’, climate can be
41 defined as “hot” as soon as it triggers a stress response to maintain or restore body
42 temperature and homeostasis through behavioural and physiological changes (*i.e.* heat stress;
43 Hansen 2009).

44 Studies on heat stress occurrence in wild animals are mostly conducted in species from
45 arid, tropical or temperate regions, because of obvious extreme ambient temperatures (Bryant
46 2008; Conradie *et al.* 2020). Yet, cold-adapted species may be at greater risks of struggling
47 under hot conditions because of a narrower, cold-shifted TNZ and thermoregulatory
48 mechanisms specialized for cold environments (Beaman *et al.* 2024; Choy *et al.* 2021;
49 Grémillet *et al.* 2012; O’Connor *et al.* 2021). Even if maximum temperatures in polar regions
50 are seen as less extreme than in other parts of the globe, polar regions are warming at a faster
51 rate than any other place on earth (Clem *et al.* 2020; Stammerjohn & Scambos 2020; You *et al.*
52 2021). Hence, animals adapted to cold environments may reach a breakpoint in
53 thermoregulation efficacy more rapidly than other species in response to climate anomalies
54 (Beaman *et al.* 2024; Choy *et al.* 2021; O’Connor *et al.* 2021).

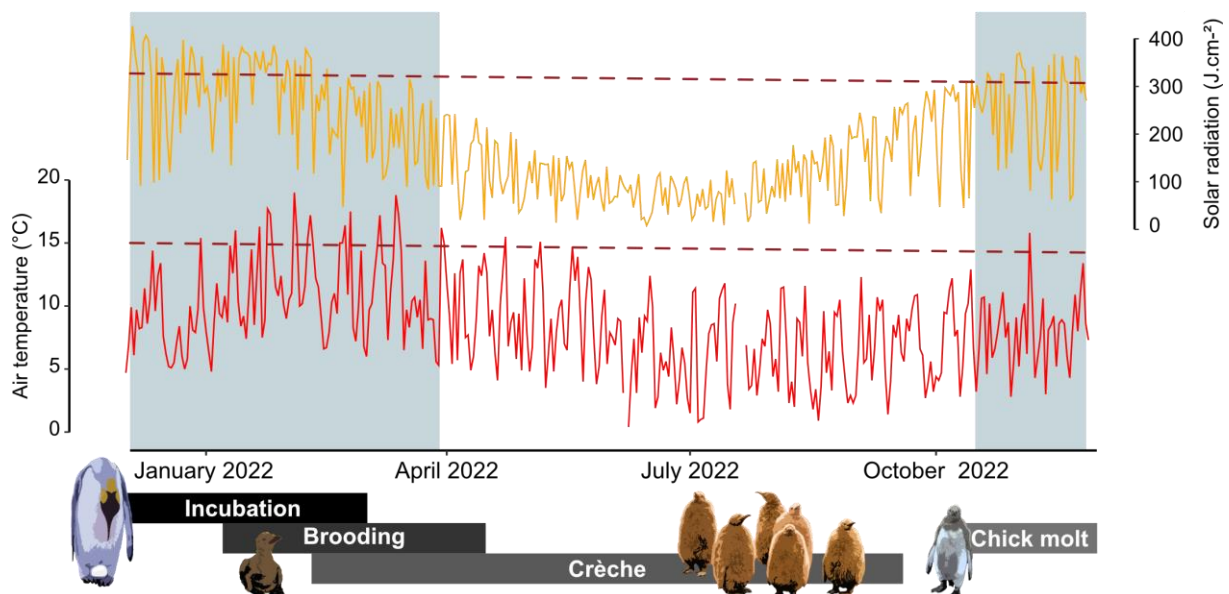
55 Seabirds from polar and subpolar regions are expected to be particularly sensitive to
56 heat stress, because they have to maintain a thick body insulation in order to forage in cold
57 waters (Davis & Darby 2012), but are increasingly exposed to high temperatures on land. It
58 has been suggested that since marine birds have an “easy access” to water to cool down, they
59 are unlikely to suffer much from hot conditions on land (Beaman *et al.* 2024). Yet, this
60 assumption does not consider the high constraints that most seabirds face during reproduction,
61 which is also the timeframe where the heat load is expected to be the highest. For instance,
62 thermoregulatory behaviours such as bathing would directly impact nest attendance, thereby
63 increasing the egg or chick exposure to heat and predators (Olin *et al.* 2023). Direct and
64 indirect (*e.g.* longer foraging times) effects of heat may contribute to decrease reproductive
65 success, leading to a trade-off between thermoregulation and reproduction (or even survival)
66 in breeding adults.

67 Direct observation of thermoregulatory behaviours is an efficient and non-invasive way
68 to study heat stress in free-living animals (Olin *et al.* 2023). Panting is considered a sign of
69 heat stress as it is an energy-expensive evaporative cooling mechanism (Tan & Knight 2018).
70 Panting behaviour has for instance been observed in nesting guillemot (Olin *et al.* 2023), great
71 skuas (Oswald *et al.* 2008) and African penguins (Welman & Pichegru 2022), during days of
72 high air temperature. The use of more passive thermoregulatory behaviours (*i.e.* less
73 energetically costly than panting) has also been described in breeding seabirds, in order to
74 increase convective and/or conductive heat loss for instance through spreading wings (Olin *et*
75 *al.* 2023), bathing (Oswald *et al.* 2008), crouching or standing (Cook *et al.* 2020). To evaluate
76 if thermoregulatory behaviours are sufficient to maintain normal body temperature,
77 measurements of body temperature are required. Various methods exist for measuring body
78 temperature in wild animals (see (McCafferty *et al.* 2015) for a review). For animals being
79 identified using sub-cutaneous pit-tags, the replacement of traditional pit-tag with
80 thermosensitive ones offers the opportunity to collect body temperature (*i.e.* subcutaneous
81 temperature: T_{sc}) while minimizing invasiveness (Andreasson *et al.* 2023; McCafferty *et al.*
82 2015).

83 The heat load faced by wild animals depends on multiple climatic parameters, including
84 ambient temperature (T_{air}), humidity, solar radiations (SR) and wind speed (WS), but the vast
85 majority of studies focusing on heat stress have tested for air temperature as the sole climatic
86 variable, or in combination with relative humidity (RH) (Mitchell *et al.* 2024). While microclimatic
87 conditions measured as close as possible to the animal are the best way to quantify the heat
88 exchange between an animal and its environment (Mitchell *et al.* 2024), such information is
89 not always available and researchers often rely on climatic data from meteorological services.
90 Using such data, various thermal indexes can be computed from climatic parameters (Ioannou
91 *et al.* 2022), and could be useful to determine a threshold above which an animal would be
92 impacted by “hot” conditions, especially in a complex natural environment.

93 Here, we suggest that king penguins (*Aptenodytes patagonicus*), the second largest
94 penguin species, may be particularly sensitive to heat and thus used as an early sentinel
95 regarding the risk of sub-polar and polar seabirds to suffer from heat stress on land in the
96 context of climate change. Indeed, king penguins are very well adapted to the cold, with a
97 performant body insulation for deep-diving and important fat stores (Davis & Darby 2012).
98 Modifying this insulation during breeding on land is however impossible, as penguins must
99 alternate between incubating/brooding on land during spring/summer at fluctuating ambient
100 temperatures (see Fig. 1, numerous days with maximum temperature $> 15^{\circ}\text{C}$), and foraging at
101 sea in *ca.* 4°C water (Stonehouse 1960). The risks of heat stress are further accentuated as
102 breeders reproduce on volcanic beaches with no access to shade, and must remain on land

103 while fasting for prolonged periods, around 2-3 weeks during egg incubation and around 1
104 week during chick rearing (Weimerskirch *et al.* 1992). During their stay on land, king penguins
105 breed in a dense colony, establishing a small territory against aggressive conspecifics (Côté
106 2000; Lemonnier *et al.* 2024) from which they cannot move or leave their egg/chick unattended
107 without very high risks of reproductive failure due to predation (Descamps *et al.* 2005). This
108 further accentuates the risk of heat stress by limiting access to cooling substrate (*i.e.* water)
109 and triggering frequent antagonistic interactions. Although behavioural signs of heat stress
110 have been observed in polar and sub-polar penguin species (Stier & Lewden, *pers. obs.*), this
111 phenomenon remains to be investigated in details in sub-Antarctic and Antarctic species.
112



113
114 **Figure. 1 Breeding cycle and 2022 climatic conditions (daily maximum air temperature (in red) and**
115 **maximum solar radiation (in orange) of king penguins breeding in Crozet Archipelago.**
116

117 In this study, we investigated the occurrence of heat stress in free-living king penguins.
118 To this end, key parameters were examined : 1. the occurrence of heat stress by studying
119 thermoregulatory behaviours; 2. the biological (*i.e.* breeding stage, sex and fasting duration)
120 and environmental (*i.e.* ambient temperature, solar radiations, relative humidity and wind
121 speed) factors triggering heat stress; 3. the efficacy of thermoregulatory behaviours in
122 maintaining normal (subcutaneous) body temperature under hot climatic conditions; 4. the
123 performance of different thermal indexes in predicting heat stress occurrence; and 5. the
124 climatic conditions associated with reproductive failure.

125 **Materials and Methods**

126 ***Study model and site.***

127 We studied king penguins breeding in the “Baie du Marin” colony on Possession Island
128 in the Crozet Archipelago (46°25’S; 51°52’E). Data were collected over two breeding seasons,
129 2021-2022 and 2022-2023. During breeding, male and female partners alternate between
130 periods of foraging at sea with periods on land caring for the egg or chick (Figure 1). After
131 laying a single egg, females return to forage at sea while males take care of the first incubation
132 shift. Alternated guard continues throughout incubation (ca. 53 days) and brooding until the
133 chicks reach thermoregulatory independence (ca. 35 days) (Davis & Darby 2012). In this study,
134 we monitored 72 breeding pairs (20 during 2021-2022 and 52 during 2022-2023). For each
135 breeding pair, male and female parents were individually marked during courtship using hair-
136 dye (Schwarzkopf Palette Deep Black) and monitored daily throughout incubation and
137 brooding. The number of days on land (D_{land}), from the return of the birds on land until the day
138 of observation, was also considered in the analysis. The first incubation shift of males was
139 excluded from the analysis as they fast 2-3 weeks longer than females, which influences
140 greatly their physiology (Ancel *et al.* 2013; Cherel *et al.* 1988; Gauthier-Clerc *et al.* 2001).

141 ***Climatic parameters***

142 Climatic data were provided by Météo France through a weather station located ca.
143 1km from the penguin colony (Station 98404004, 46°25’S; 51°51’E). The station provided air
144 temperature under shelter (T_{air} , °C), solar radiations (SR, J/cm²), wind speed (WS, m/s) and
145 relative humidity (RH, %) every hour.

146

147 **Table 1. Heat indexes computed from air temperature, relative humidity, wind speed and solar radiations**
148 **using 4 different equations where T_g is the Globe temperature, THI the Temperature-Humidity Index, HLI**
149 **the Heat Load Index, and WBGT is the Wet-Bulb Globe Temperature. T_{nwb} is the natural wet-bulb Temperature**
150 **and can be calculated from T_{air} , RH and WS using equations in Carter *et al.* 2020.**

Equation 1. $T_g = 0.01498 SR + 1.184 T_{air} - 0.0789 RH - 2.739$ [Hajizadeh et al. 2017](#)

Equation 2. $THI = T_{air} + 0.36 T_w + 41.5$ [Thom et al. 1959; Silva et al. 2007](#)

Equation 3. $HLI = 33.2 + 0.2 RH + 1.2 T_g - (0.82 WS) 0.1 - \log(0.4 WS^2 + 0.0001)$ [Ghaugan 2002; Silva et al. 2007](#)

Equation 4. $WBGT = 0.7 T_{nwb} \times 0.2 T_g \times 0.1 T_{air}$ [Liljegren et al. 2008; Hajizadeh et al. 2017](#)

151

152

153 We calculated 4 different heat indexes to compare their predictive power to models
154 including raw environmental variables (Table 1). We used the globe temperature (T_g , equation
155 1, Hajizadeh *et al.* 2017), the Temperature-Humidity Index (THI, equation 2, Thom 1959), the
156 Heat Load Index (HLI, equation 3, Gaugan 2002; Silva *et al.* 2007) and the Wet-Bulb Globe

157 Temperature (WBGT, equation 4, Hajizadeh *et al.* 2017; Liljegren *et al.* 2008), which are either
158 a practical metric of dry heat load to which the biological responses of wild animals should be
159 assessed (Tg, Mitchell *et al.* 2024), the most used indexes to predict heat stress occurrence
160 in humans (THI, WBGT, Budd 2008), or the indexes that have been described to better predict
161 heat stress in humans and farm animals (HLI and WBGT; Carter *et al.* 2020; Liljegren *et al.*
162 2008; Silva *et al.* 2007).

163 ***Thermoregulatory behaviours***

164 Penguins' thermoregulatory behaviours were recorded using scan sampling every 3
165 days over a period of 40 minutes with an observation recorded every 2 minutes (maximum 21
166 observations per scan). The scans were performed during midday (mean= 14:35 ± 1 hour and
167 35 minutes). We gathered a total number of 1175 scans, scattered over 60 days (from 28th
168 November 2021 to 8th March 2022 and 4th December 2022 to 26th February 2023). The total
169 number of scans per individual (mean of 9 ± 3 scans) varied with the duration of their shift on
170 land and the survival of their offspring. We focused on 3 behaviours considered to have a
171 thermoregulatory function, *i.e.* panting, wing spreading and exposure of the brood pouch (*i.e.*
172 a highly vascularized and featherless area that may serve as a thermal window to dissipate
173 heat; Handrich *et al.* 1997), and analysed their occurrence in terms of presence/absence
174 during the scan (1/0 respectively). Observations were carried out by 11 observers during 2 field
175 seasons.

176 ***Sub-cutaneous temperature***

177 We recorded sub-cutaneous temperature (T_{sc}) using thermosensitive pit-tags
178 (BioTherm13 tag, Biomark) used for individual identification and placed in the upper back of
179 the individuals (Oswald *et al.* 2018). T_{sc} was recorded every 3 days during shifts on land ($n =$
180 856), just after behavioural scans and without handling of the animals. In our study species,
181 T_{sc} changes have been shown to mirror changes in core body temperature relatively well while
182 on land (Eichhorn *et al.* 2011; Lewden *et al.* 2017), and our own unpublished data reveal a
183 significant correlation between T_{sc} and core body temperature in incubating adults ($n = 37$, $r =$
184 0.62, $p < 0.001$).

185 ***Reproductive failure***

186 Survival of the egg or chick was monitored daily throughout the entire breeding season,
187 and the day of egg abandonment or chick disappearance was recorded. However, the exact
188 cause of reproductive failure remained unknown in the vast majority of cases.

189 ***Statistical analysis.***

190 Penguins' observations (behavioural scans and T_{sc}) were merged with climatic
191 parameters by the closest time of the day, with a maximum delay of 30 minutes. The statistical
192 analysis was performed in R version 4.3.2 (R Core Team 2023). The effects of T_{air} , SR, WS
193 and RH on the probability of displaying the 3 thermoregulatory behaviours during the scans
194 were analysed using generalised linear mixed models (R package 'lme4', version 1.1-35.1),
195 assuming a binomial distribution (link=logit) and after scaling of the climatic parameters. Linear
196 mixed models with a normal distribution were used to assess the effects of climatic parameters
197 on T_{sc} . As individuals were measured several times over the breeding season, bird identity was
198 included as a random effect, as well as the identity of the observers (except for T_{sc} , recorded
199 by a pit-tag reader and therefore not subject to inter-observer variation). Year (2021-22 vs.
200 2022-23), sex (Male vs. Female), reproductive stage (Incubation vs. Brooding) and day of the
201 shift ('D_{land}') were included as fixed effects in the models. T_{sc} was further analysed depending
202 on the presence or absence of panting behaviour for each individual during the preceding
203 behavioural scan. Breakpoint analysis of T_{sc} against T_{air} , SR and HLI was performed using the
204 *segmented* package (version 2.0-2). A Davies test was used to test for the significance of a
205 change in slope in each linear model (Muggeo 2008).

206 Models including all variables but no interaction terms (*i.e.* No-interaction models) were
207 compared to two-ways interaction models between environmental variables (*e.g.* T_{air} *SR or
208 WS*RH), and to a null model, using corrected Akaike's information criterion (AICc). The
209 models presented in the results are the best fitted models from model comparison. To assess
210 model fit, 'DHARMA' package was used (version 0.4.6). Variance inflation factors from the No-
211 interaction models were all under 3, suggesting no substantial bias from collinearity between
212 predictor variables (namely climate parameters) occurred (see Zuur *et al.* 2010). Conditional
213 and marginal R^2 were used to compare the predictive power of each model (*i.e.* No-interaction
214 model, Interaction model, heat indexes).

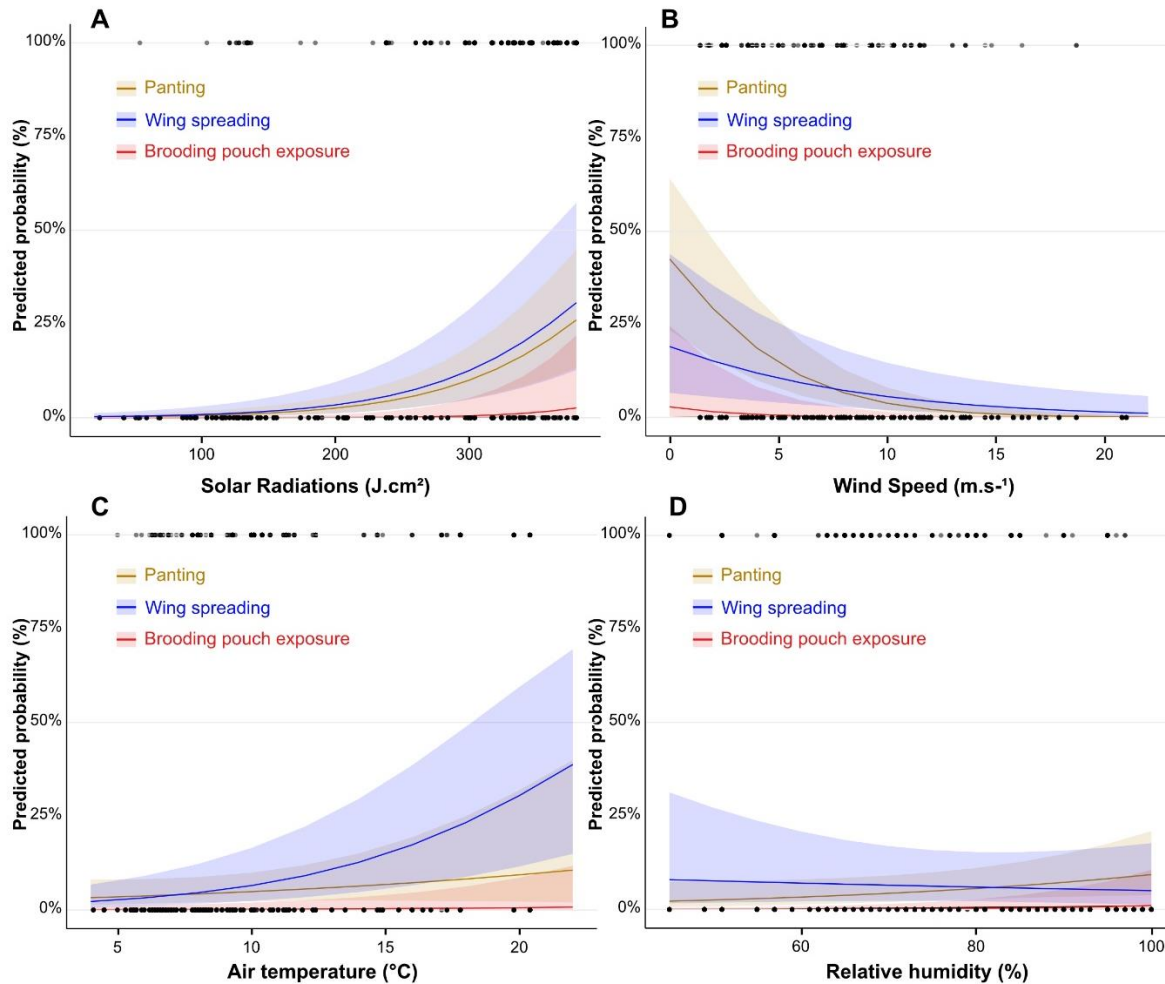
215 Non-parametric Wilcoxon tests were used to analyse the differences in climatic
216 conditions during days in which egg or chick mortality was observed, compared to days where
217 no reproductive failure was recorded (in terms of maximum T_{air} , maximum SR and maximum
218 HLI).

219

220 **Results**

221 ***Behavioural thermoregulation***

222



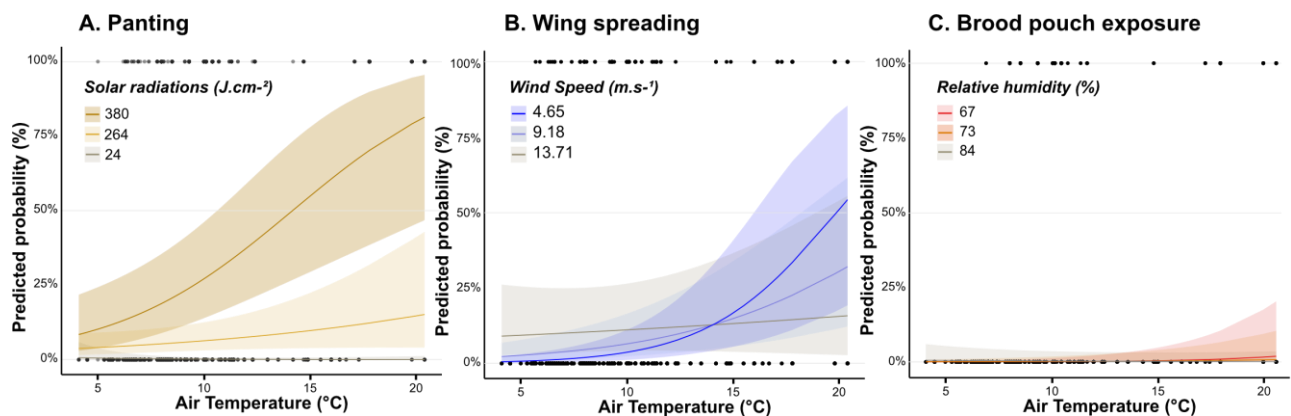
223

224 **Figure 2. Predicted probabilities of thermoregulatory behaviours (panting (brown), wing spreading (blue)**
225 **and exposure of the brood pouch (red)) occurrence according to (A) solar radiations, (B) wind speed, (C)**
226 **air temperature and (D) relative humidity. Predicted probabilities were calculated from generalized linear mixed**
227 **models; N = 144, n = 1175.**

228 Independently of climatic conditions, panting was the most frequently observed
229 thermoregulatory behaviour (23.4% of behavioural scans included panting behaviour),
230 followed by wing spreading (9.7%) and exposure of the brood pouch (7.7%). Over the 60 days
231 with behavioural scans, there were 27 days where at least one individual was observed panting
232 (26 days for wing spreading and 16 days for brood pouch exposure).

233 The probability of observing panting behaviour was mainly explained by solar radiations
234 (SR) and wind speed (WS), while air temperature (T_{air}) and relative humidity (RH) did not
235 significantly impact panting as main effects (Table 2A, Fig 2). Four two-ways interactions

236 significantly explained panting probability, with the most notable being the interaction between
237 T_{air} and SR, revealing that panting only increased with increasing T_{air} when SR were moderate
238 to high (Fig 3; see ESM for details on other interactions). Males tended to display panting
239 behaviour more frequently than females ($p = 0.067$), but the probability to observe panting
240 behaviour did not significantly vary with reproductive stage or between the two breeding
241 seasons we studied (Table 2A). Panting probability significantly decreased with the time spent
242 on land (D_{land}), meaning that the birds' susceptibility to suffer from heat stress gradually
243 decreased after returning from the sea (Table 2A, Fig 4A).



244

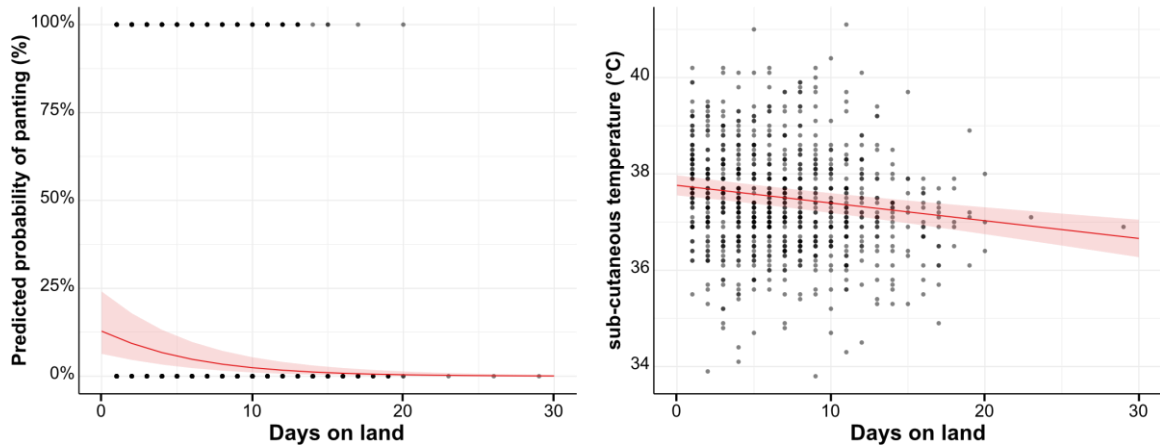
245 **Figure 3. Predicted probability of (A) Panting depending on air temperature and solar radiations;** solar
246 radiations are represented as maximum (380), median (264) and minimum (24) registered during behavioural
247 scans; **(B) wing spreading according to air temperature and wind speed** (2nd quartile (4.65), median (9.18), 3rd
248 quartile (13.71)); **(C) Brood pouch exposure according to air temperature and humidity** (2nd quartile (67),
249 median (73), 3rd quartile (84)). Predicted probabilities were calculated from generalized linear mixed models; $N =$
250 143 $n = 1123$

251 The probability of observing wing spreading increased under high solar radiations, high
252 T_{air} and low wind speed, while relative humidity had no significant impact on this behaviour (Fig
253 2C, Table 2B). Three two-ways interactions also significantly explained wing spreading
254 probability, with the most notable being the interaction between T_{air} and WS (Table 2B),
255 revealing that wing spreading increased with increasing temperature when wind speed was
256 low to moderate (Fig 3B; see ESM Figure S1 for details on other interactions). Males
257 significantly spread their wings more often than females and brooding birds more than
258 incubating ones, but the probability to spread wings did not significantly change along the time
259 spent on land nor between the two breeding seasons we studied (Table 2B).

260 The probability of observing the brood pouch lifted increased with SR, T_{air} , RH and
261 decreased with WS (Fig 2B, Table 2C). The interaction between T_{air} and RH was also
262 significant, revealing that brood pouch exposure only increased with increasing T_{air} when RH
263 was low (Table 2C, Fig 3C). Sex, breeding season and the time spent on land did not
264 significantly influence the probability of exposing the brood pouch, but brooding individuals
265 were more likely to exhibit this behaviour than incubating ones (Table 2C).

266 **Table 2. Summaries of the most parsimonious generalized linear mixed models predicting thermoregulatory**
 267 **behaviours and subcutaneous temperature: (A) panting, (B) wing spreading, (C) exposure of the brood**
 268 **pouch and (D) sub-cutaneous temperatures** according to climatic parameters (air temperature: T_{air} : solar
 269 radiation: SR; wind speed: WS; relative humidity: RH), their interactions, and biological parameters (sex [Male vs
 270 Female], season [2021-2022 vs. 2022-2023], reproductive stage [incubating vs. brooding], and days spent on land
 271 D_{land}).

	(A) Panting			(B) Wing spreading			(C) Brood pouch exposure			(D) Tsc		
	OR	CI	p	OR	CI	p	OR	CI	p	Est.	CI	p
<i>(Intercept)</i>	0.15	0.07–0.32	<0.001	0.07	0.02–0.20	<0.001	0.00	0.00–0.03	<0.001	37.71	37.50–37.92	<0.001
T_{air}	1.26	0.82–1.94	0.283	1.96	1.53–2.50	<0.001	1.55	1.03–2.33	0.037	0.08	0.00–0.15	0.037
RH	1.42	0.99–2.03	0.059	0.89	0.53–1.49	0.666	2.53	1.63–3.93	<0.001	0.09	0.02–0.16	0.017
SR	4.32	2.84–6.55	<0.001	4.15	2.75–6.28	<0.001	7.98	4.25–14.96	<0.001	0.45	0.39–0.52	<0.001
WS	0.27	0.18–0.40	<0.001	0.54	0.37–0.81	0.003	0.24	0.14–0.41	<0.001	-0.32	-0.39–-0.26	<0.001
Season [2]	1.57	0.77–3.21	0.216	0.46	0.20–1.09	0.079	5.14	0.97–27.34	0.055	-0.05	-0.23–0.13	0.595
Sex [M]	1.57	0.97–2.54	0.067	1.81	1.12–2.92	0.015	0.71	0.39–1.29	0.259	0.09	-0.06–0.24	0.241
D_{land}	0.84	0.79–0.89	<0.001	1.00	0.94–1.06	0.996	0.98	0.91–1.06	0.635	-0.04	-0.05–-0.02	<0.001
Repro. St [Incub.]	0.96	0.61–1.49	0.845	0.32	0.19–0.55	<0.001	0.12	0.06–0.25	<0.001	-0.20	-0.33–-0.07	0.002
$T_{air} \times RH$	0.34	0.22–0.52	<0.001				0.37	0.23–0.58	<0.001			
$T_{air} \times SR$	1.57	1.04–2.38	0.033							0.25	0.18–0.31	<0.001
$T_{air} \times WS$				1.69	1.12–2.57	0.013				-0.22	-0.31–-0.14	<0.001
SR \times WS	0.67	0.44–1.03	0.068									
SR \times RH	2.06	1.34–3.15	0.001	1.98	1.14–3.45	0.016						
WS \times RH	1.82	1.21–2.73	0.004	1.80	1.09–2.94	0.020						
Random effects												
σ^2	3.29			3.29			3.29			0.68		
$\tau_{00 ID bird}$	0.46			0.00			0.05			0.07		
$\tau_{00 ID observer}$	0.09			1.18			7.31					
ICC	0.14						0.69			0.10		
$N_{ID bird}$	143			143			143			140		
$N_{ID observer}$	11			11			11					
N Obs.	1123			1123			1123			856		
R^2_m / R^2_c	0.684 / 0.729			0.646 / NA			0.479 / 0.839			0.369 / 0.430		

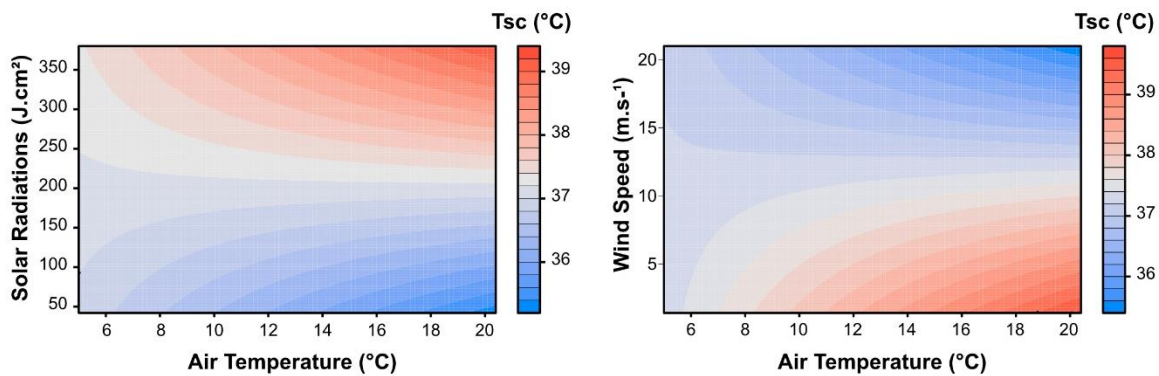


273

274 **Figure 4. Evolution of (A) panting probability and (B) subcutaneous temperature along the duration of the**
275 **shift on land.** Values are predicted from linear mixed models presented in Table 2. $N = 143$, $n = 1123$ for panting;
276 $N = 140$, $n = 856$ for T_{sc} .

277

278 **Subcutaneous temperature**

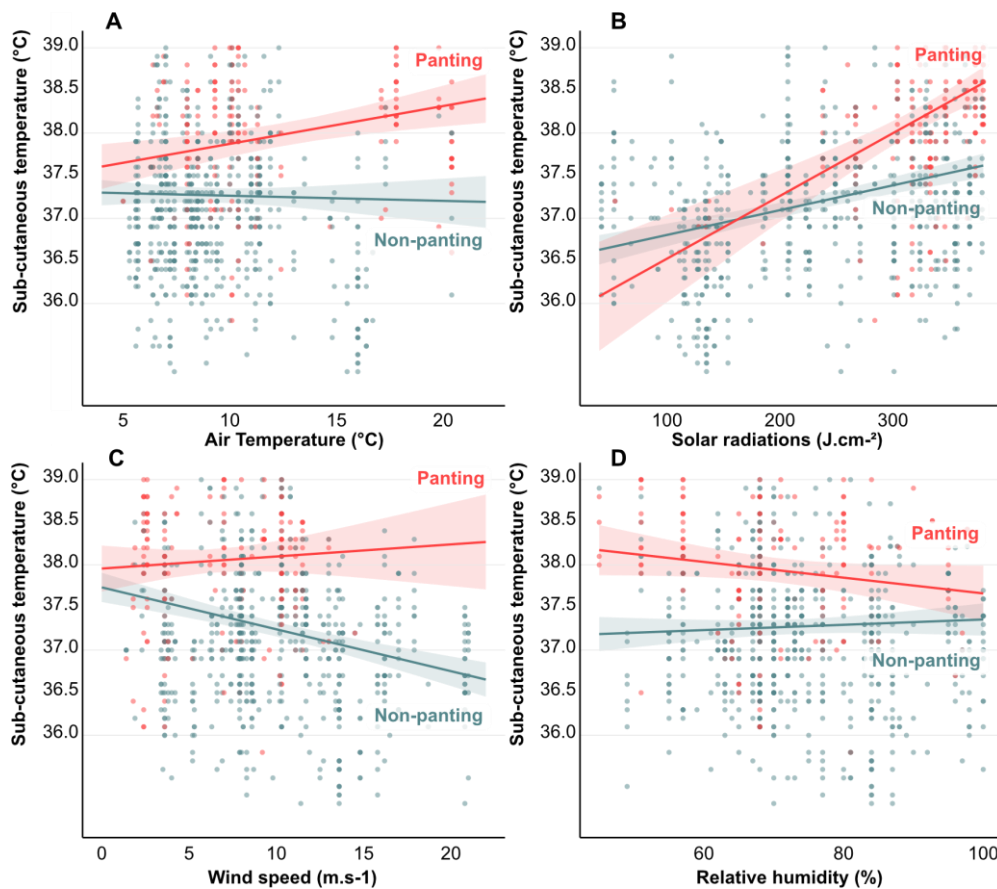


279

280 **Figure 5. Breeding king penguins' sub-cutaneous temperatures (T_{sc}) according to (A) the interaction**
281 **between air temperature and solar radiations, and (B) air temperature and wind speed.** Values are predicted
282 from the linear mixed model presented in Table 2D; $N = 140$, $n = 856$.

283 Subcutaneous temperature (T_{sc}) increased under high T_{air} , SR and RH, and decreased in
284 response to high WS (Table 2D). The best predictive model included significant interactions
285 between T_{air} and SR and between T_{air} and WS (Figure 5, Table 2D), revealing that king
286 penguin's T_{sc} was especially elevated when T_{air} and SR increased concomitantly, along with a
287 decrease in WS. Males and females did not show significant differences in their T_{sc} , but
288 brooding individuals had a higher T_{sc} than incubating ones (Table 2D). T_{sc} also significantly
289 decreased along the shift on land (Figure 4B, Table 2D). Breakpoint analyses showed that T_{sc}
290 significantly increased with T_{air} when a threshold of 16.0 ± 1.1 °C was reached (Davies test: p
291 = 0.005; Figure S2A), or when SR reached 125.3 ± 11.7 J.cm⁻² (Davies test: $p < 0.001$; Figure
292 S2B). However, no significant change of slope was found using the heat load index (HLI)
293 (breakpoint 56.12 ± 2.5 ; Davies test: $p = 0.18$; Figure S2C).

294 T_{sc} was significantly higher in panting than non-panting individuals (37.8°C vs. 37.2°C ,
295 $\chi^2= 48.1$, $p < 0.001$), and increased with T_{air} and SR in panting individuals while this was not
296 the case or less pronounced for non-panting animals (χ^2 Panting* $T_{air} = 7.5$; $p = 0.006$; Figure
297 6A; χ^2 Panting*SR = 14.3; $p < 0.001$; Figure 6B). Moreover, the increase of WS was not
298 sufficient to decrease T_{sc} in panting individuals compared to non-panting birds (χ^2 Panting* T_{air}
299 = 10.2; $p = 0.001$; Figure 6C). Relative humidity had no effect on T_{sc} as a main effect, but the
300 T_{sc} of panting individuals slightly decreased with increasing RH (χ^2 Panting*RH = 4.3; $p = 0.038$
301 Figure 6D).



302

303 **Figure 6. Relationship between air temperature (A), solar radiations (B), wind speed (C) or relative humidity**
304 **(D) and king penguin's sub-cutaneous temperature according to the use of panting as a thermoregulatory**
305 **behaviour. $N = 140$, $n = 856$.**

306 ***Evaluating the relevance of T_{air} and heat indexes in predicting heat stress occurrence***

307 Models only including T_{air} poorly explained the occurrence of thermoregulatory
308 behaviours or variation in T_{sc} , with R^2 ranging from 0.07 to 0.23 (Table 3). Solar radiations
309 always performed better than T_{air} in predicting heat stress occurrence, with $R^2 > 0.24$ (Table
310 3). Models containing T_{air} , RH, SR and WS as main effects (R^2 ranging from 0.30 to 0.67) and
311 models including these 4 variables and their two-ways interactions (R^2 ranging from 0.37 to
312 0.68) were the best predictive models for all explained variables (Table 3). Models including

313 heat indexes (Globe temperature (T_g), Temperature-Humidity (THI), Heat Load Index (HLI)
 314 and Wet-Bulb Globe Temperature (WBGT) explained less variance in thermoregulatory
 315 behaviours and T_{sc} than models (with or without interactions) including T_{air}, RH, SR and WS
 316 as explanatory variables (Table 3). THI explained the least of all heat index for each explained
 317 variables (marginal R² were ~0.2 point lower than the other heat indexes).

318

	<i>Panting</i>			<i>Wing spreading</i>			<i>Brooding pouch exposure</i>			<i>Tsc</i>		
	AICc	R ² m	R ² c	AICc	R ² m	R ² c	AICc	R ² m	R ² c	AICc	R ² m	R ² c
<i>Tair</i>	1067.6	0.23	0.30	659.82	0.14	0.29	517.69	0.15	0.58	2514.05	0.071	0.10
<i>SR</i>	928.96	0.49	0.52	601.93	0.33	0.45	462.88	0.42	0.69	2343.39	0.24	0.28
<i>Total</i>	740.06	0.67	0.71	554.86	0.44	0.59	401.65	0.50	0.80	2277.08	0.30	0.35
<i>Inter.</i>	695.47	0.68	0.73	545.37	0.57	0.69	382.09	0.48	0.84	2181.49	0.37	0.43
<i>Tg</i>		0.44	0.51		0.28	0.46		0.29	0.65		0.20	0.24
<i>TH</i>		0.21	0.28		0.13	0.27		0.14	0.58		0.062	0.092
<i>WBGT</i>		0.45	0.52		0.37	0.56		0.29	0.66		0.19	0.23
<i>HLI</i>		0.47	0.54		0.28	0.46		0.30	0.68		0.20	0.24

319

320 **Table 3. Model comparison for the prediction of panting, wing spreading, brood pouch exposure and Tsc**
 321 **based on Akaike's information criterion (AICc), marginal R² (R²m) and conditional R² (R²c).** The best
 322 predictive model with interactions ('Inter.') between all 4 climatic parameters (T_{air}, SR, WS and RH), is compared
 323 to a model without interactions ('Total'), a model with only T_{air} or SR and 4 models including Heat indexes: globe
 324 temperature (T_g), Temperature-Humidity Index (THI), Wet-Bulb Globe Temperature (WBGT) and Heat Load Index
 325 (HLI).

326 ***Climatic conditions and reproductive failure***

327 Over the two breeding seasons, 72 eggs were laid, 65 hatched and 53 chicks survived
 328 until thermal emancipation, resulting in a 26.4% rate of reproductive failure. The days where
 329 reproductive failure occurred (17 dates where parents were not found, or the chick was found
 330 dead) were significantly hotter than the days where no death was observed. This was true
 331 considering maximum T_{air} (T_{air} = 10.8 ± 3.3 °C, n = 166 for normal days vs. 12.6 ± 3.2 °C, n = 17
 332 for days with reproductive failure, W=2103.5, p = 0.002), and maximum HLI (63.5 ± 6.2 vs.
 333 65.5 ± 5.7, W = 2474, p = 0.004). Maximum SR did not differ between days with or without
 334 reproductive failure (SR = 283.8 ± 95.2 J.cm⁻² vs. 293.1 ± 73.5 J.cm⁻², W=3065, p=0.54)

335 Discussion

336 Sub-Antarctic islands are expected to warm by 2.3 to 2.9°C over the next 100 years
337 (Nel *et al.* 2023), and these trends for mean temperature do not take into account the frequency
338 and magnitude of climate anomalies such as heat waves. Heat waves will likely become more
339 frequent in the coming decades (Piatt *et al.* 2024; Stillman 2019), especially during the austral
340 spring and summer, *i.e.* the breeding season of many endemic species (Chambers *et al.* 2014).
341 Although sub-Antarctic or Antarctic penguins were never previously described panting in the
342 literature, our study unambiguously show that king penguins do experience heat stress while
343 breeding on land, at a frequency being far from anecdotal, with >20% of the behavioural
344 scans including heat stress.

345 While many studies on heat stress in wild animals focus on air temperature alone, the
346 heat load experienced by wild animals depends markedly on other climatic factors (Mitchell *et*
347 *al.* 2024). Here we show that the use by breeding king penguins of thermoregulatory
348 behaviours indicative of heat stress was influenced, in order of magnitude, by solar radiations,
349 wind speed, air temperature and humidity. Additionally, several interactions between climatic
350 factors were significant in explaining the occurrence of heat stress, even if models without
351 interactions were only slightly less predictive of heat stress occurrence than models including
352 interactions (Table 3). Panting behaviour was the most observed thermoregulatory behaviour,
353 and increased in frequency under high solar radiation and low wind speed, as well as under
354 high air temperature when solar radiations were moderate to high. Wing spreading was the
355 second most observed thermoregulatory behaviour, and was more likely to be observed under
356 high solar radiation, high air temperature and low wind speed. Exposing the brood pouch was
357 the least observed behaviour, which can likely be explained by a trade-off between evacuating
358 heat and protecting the egg/chick against predators. Yet, this behaviour was more frequent
359 under high heat load (*i.e.* high solar radiations, high humidity, low wind speed and high air
360 temperature), which supports our hypothesis regarding its potential use as a thermal window.
361 High T_{air} has been reported to trigger heat stress in several seabirds and/or high latitude
362 species (Cook *et al.* 2020; Holt & Boersma 2022; O'Connor *et al.* 2021; Olin *et al.* 2023;
363 Welman & Pichegru 2022). While an increase in air temperature as a main effect increased
364 the probability to observe wing spreading or brood pouch exposure in breeding king penguins,
365 it did not for panting. Yet, air temperature in interaction with solar radiation explained panting
366 behaviour frequency, to a point that virtually no bird would show panting around 20°C when
367 solar radiations were low, while *ca.* 20% of the studied population was already observed
368 panting below 10°C if sun exposure was maximal (Figure 3A). These results echo recent
369 findings in Guillemots, which showed an increased probability of panting with T_{air} in sun-

370 exposed individuals around 15°C, compared with individuals in shaded areas in which panting
371 started around 25°C (Olin *et al.* 2023).

372 While behavioural thermoregulation may enable animals to maintain normal body
373 temperature under increasing heat load (Talbot *et al.* 2017), our results on subcutaneous
374 temperature suggest that thermoregulatory mechanisms employed by king penguins were
375 likely insufficient to maintain a stable body temperature. We first showed that subcutaneous
376 temperature rose under increasing heat load (high solar radiation, air temperature and
377 humidity, as well as low wind speed). More importantly, we demonstrated that panting birds
378 have a higher subcutaneous temperature than non-panting ones, and that subcutaneous
379 temperature increased with air temperature only in panting king penguins. Those results also
380 suggest that hyperthermia occurs under hot conditions, but measurements of core body
381 temperature are needed to properly confirm this. Our results contrast with studies in dovekeys
382 (*Alle alle*) suggesting that the core body temperature of this Arctic species is not challenged
383 while attending the breeding colony on land (Grunst *et al.* 2023; maximum $T_a = 13.5^\circ\text{C}$ over 11
384 days) or in a captive setting up to 25°C (*i.e.* substantially above the natural maximal
385 temperature; Beaman *et al.* 2024). Yet, solar radiation was not investigated in the
386 aforementioned studies, and empirical evidence, including in our king penguins, suggest that
387 solar radiation is a key factor conditioning the heat load faced by wild animals (Mitchell *et al.*
388 2024).

389 Taken together, the 4 climatic variables (T_{air} , SR, WS and RH) we used predicted heat
390 stress occurrence more accurately than T_{air} alone, or the four thermal indexes calculated from
391 climatic parameters. These indexes have been established for humans and farm animals
392 (Gaughan 2002; Ioannou *et al.* 2023), which likely explain why they seem less suited for wild
393 seabirds such as penguins. Developing heat indexes specifically for wild endotherms would
394 enable to better predict the response of natural populations to heat waves. Considering the
395 tremendous impact of solar radiation and wind speed on animal heat load, modelling future
396 changes in climatic parameters beyond the sole air temperature seems of critical importance
397 to predict the coping capacity of wild species in the context of climate change. Yet, for many
398 species, macro-climatic conditions may only reflect poorly the micro-climatic conditions
399 experienced by animals, and thus on-site measurement of micro-climate is needed (Mitchell
400 *et al.* 2024).

401 Beyond climatic parameters, biological factors were also important in predicting the
402 risks of king penguins to suffer from heat stress. First, sex did seem to play a role (albeit small)
403 in explaining variation in heat stress occurrence, since males spread their wings more often
404 and had a tendency to pant more than females. This may, at least partly, be linked to the higher

405 size of beak and flipper relative to body mass found in females (Kriesell *et al.* 2018), which
406 likely provides higher heat dissipation capacity through those thermal windows. Second,
407 brooding parents generally suffered more from hot conditions than incubating ones, as they
408 spread their wings and exposed their brood pouch more often, as well as exhibited higher
409 subcutaneous temperature than incubating individuals. Yet, brooding adults were not panting
410 more than incubating ones. Considering that panting is extremely expensive in terms of water
411 (Adélie penguins can lose water up to 0.3% of their body mass per hour while panting; Chappell
412 & Souza 1988), our results may suggest that brooding individuals could limit the use of panting
413 to avoid severe dehydration (Smit *et al.* 2016), especially because breeding king penguins do
414 not seem to drink while fasting on land (Cherel *et al.* 1988). Brooding adults are also known to
415 exhibit higher aggression rates towards conspecifics than incubating ones (Côté 2000), which
416 could result in elevated body temperatures due to both physical activity and stress response
417 (Knoch *et al.* 2022). Finally, king penguins seemed especially sensitive to heat stress when
418 freshly returned from the sea to incubate or brood on land. Indeed, they showed a higher
419 probability to pant and a higher subcutaneous temperature during their first few days on land.
420 This can be due to the progressive switch into the hypometabolic fasting state (2-5 days are
421 needed to reach a stable hypometabolic state; Cherel *et al.* 1988), but also to a progressive
422 thermal acclimation to on-land conditions. The mechanisms involved in such a potential
423 transient thermal acclimation on land remain to be investigated.

424 The impact of heat stress on breeding king penguins in our study was sublethal,
425 contrary to what has been reported in Magellanic (Holt & Boersma 2022) and king penguins
426 (Arriagada 2023) breeding in Argentina. Yet, sublethal effects may have drastic consequences
427 on population dynamics (Conradie *et al.* 2019), especially if reproduction is affected.
428 Reproductive failure may be related or accentuated by hot environmental conditions since
429 parents may abandon reproduction because of heat stress, or be more susceptible to egg/chick
430 predation when suffering from heat stress. Our results show that climatic conditions were hotter
431 during days where reproductive failure occurred, which suggest that heat stress may be an
432 important constraint on reproductive success for king penguins, as this has been demonstrated
433 previously in common Guillemot (Olin *et al.* 2023). Better understanding the sublethal
434 consequences of heat stress in king penguins is thus needed to predict more accurately the
435 changes in population dynamics expected under the various climate change projections.

436

437 **Data availability**

438 The datasets used in this manuscript are available on *FigShare* (Noiret *et al.* (2024). HotKing
439 dataset: heat stress in breeding king penguins. figshare. Dataset.
440 <https://doi.org/10.6084/m9.figshare.26968723.v2>).

441 **Author's contribution**

442 Study design: AS, VAV, AL. Funding acquisition: AS, JPR, PB, VAV. Data collection in the field: CL, CB,
443 MM, MH, FB, EM, VAV, AS. Data analysis: AN. Writing original draft: AN and AS. Writing review and
444 editing: AL, CL, CB, MM, MH, FB, EM, JPR, PB, VAV.

445

446 **Ethical note**

447 All the procedures were approved by the French Ethical Committee (APAFIS#31268-
448 2021042117037897 v3) and the Terres Australes et Antarctiques Françaises (Arrêtés TAAF A-2021-49 and
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450

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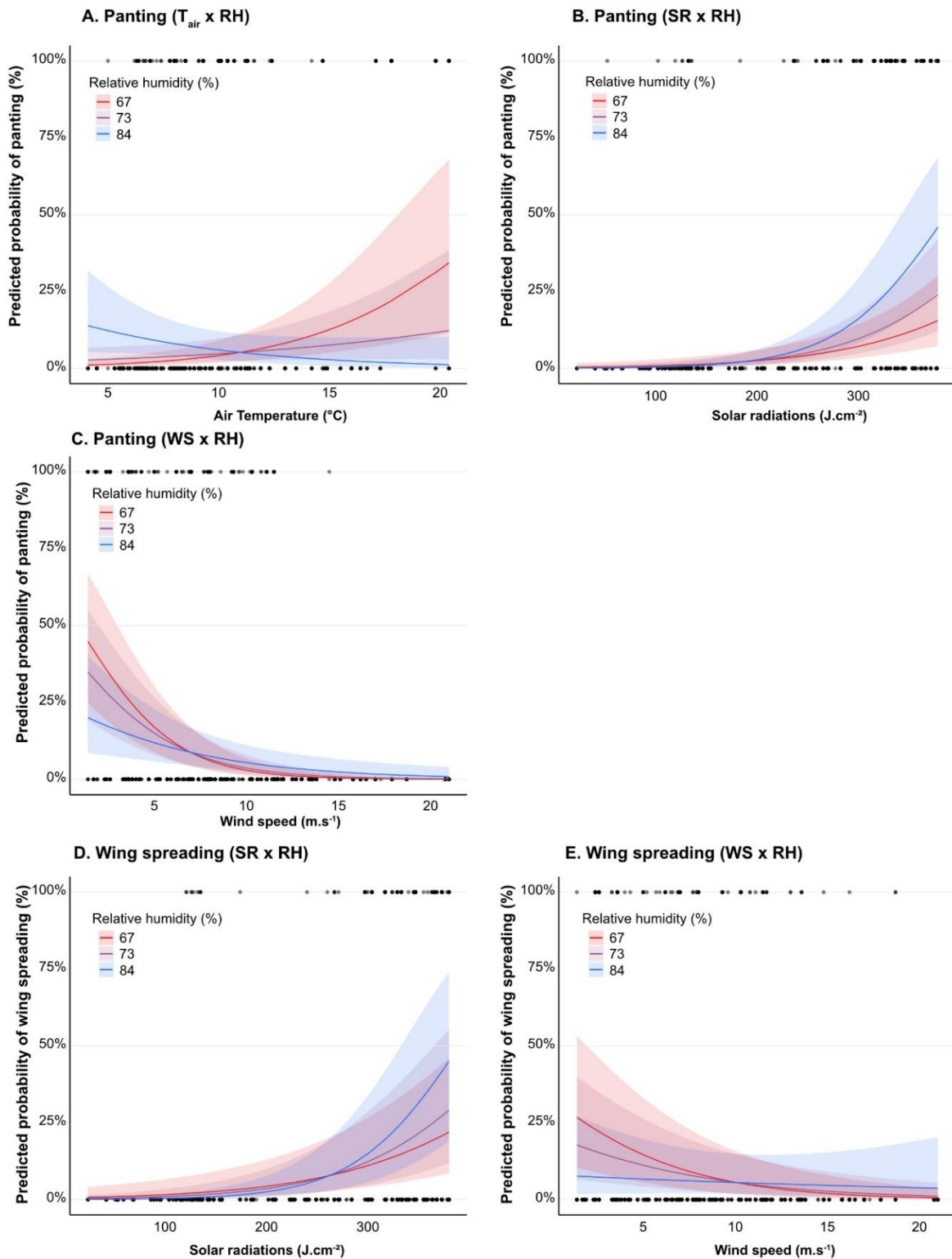
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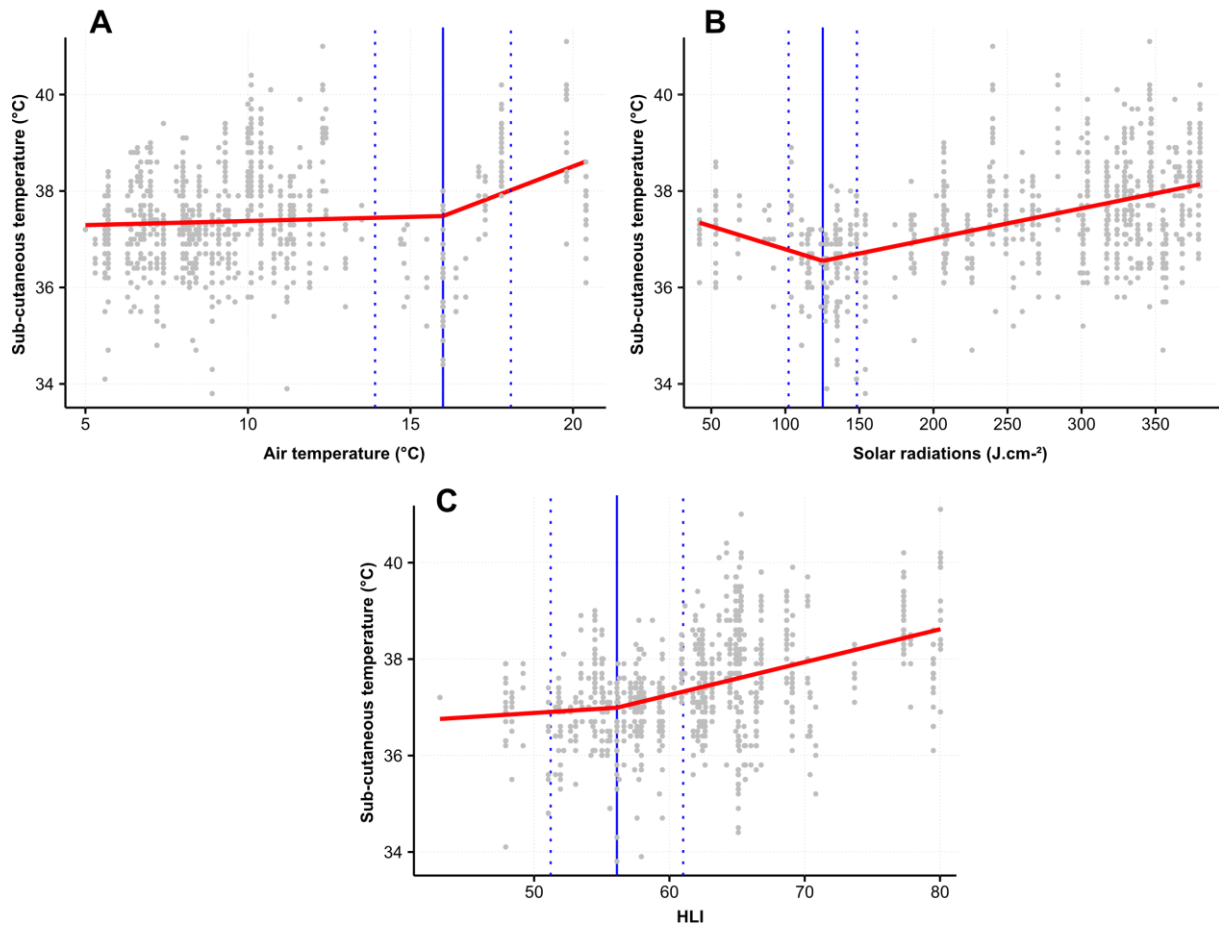
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617 **ESM**



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619 **Figure S1. Predicted probability of (A) Panting depending on air temperature and relative humidity (B)**
620 **panting depending on solar radiations and relative humidity (C) panting depending on wind speed and**
621 **relative humidity (D) wing spreading depending on solar radiations and relative humidity and (E) wing**
622 **spreading depending on wind speed and relative humidity; probabilities were calculated from generalized linear**
623 **mixed models; N = 143, n = 1123 relative humidity (%) is represented as second quartile (67), median (73) and 3rd**
624 **quartile (84) registered during behavioural scans.**



625

626 **Figure S2. Breakpoint analyses between king penguins' sub-cutaneous temperatures (T_{sc}) and (A) air**
627 **temperature; (B) solar radiations and (C) heat load index (HLI) computed from air temperature, solar**
628 **radiations, wind speed and relative humidity. Segmented models are shown in red, and estimated breakpoints**
629 **with confidence intervals are shown in blue. $N = 140$, $n = 856$.**

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