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

Aude Noiret[1,2*], Agnès Lewden[3], Camille Lemonnier[1], Céline Bocquet[1], Marine Montblanc[1], Fabrice Bertile[1], Marine Hoareau[1], Elsa Marçon[1], Jean-Patrice Robin[1], Pierre Bize[4], Vincent A Viblanc[1] & Antoine Stier[1,2,5*]

[1] Université de Strasbourg, CNRS, IPHC UMR 7178, F-67000 Strasbourg, France

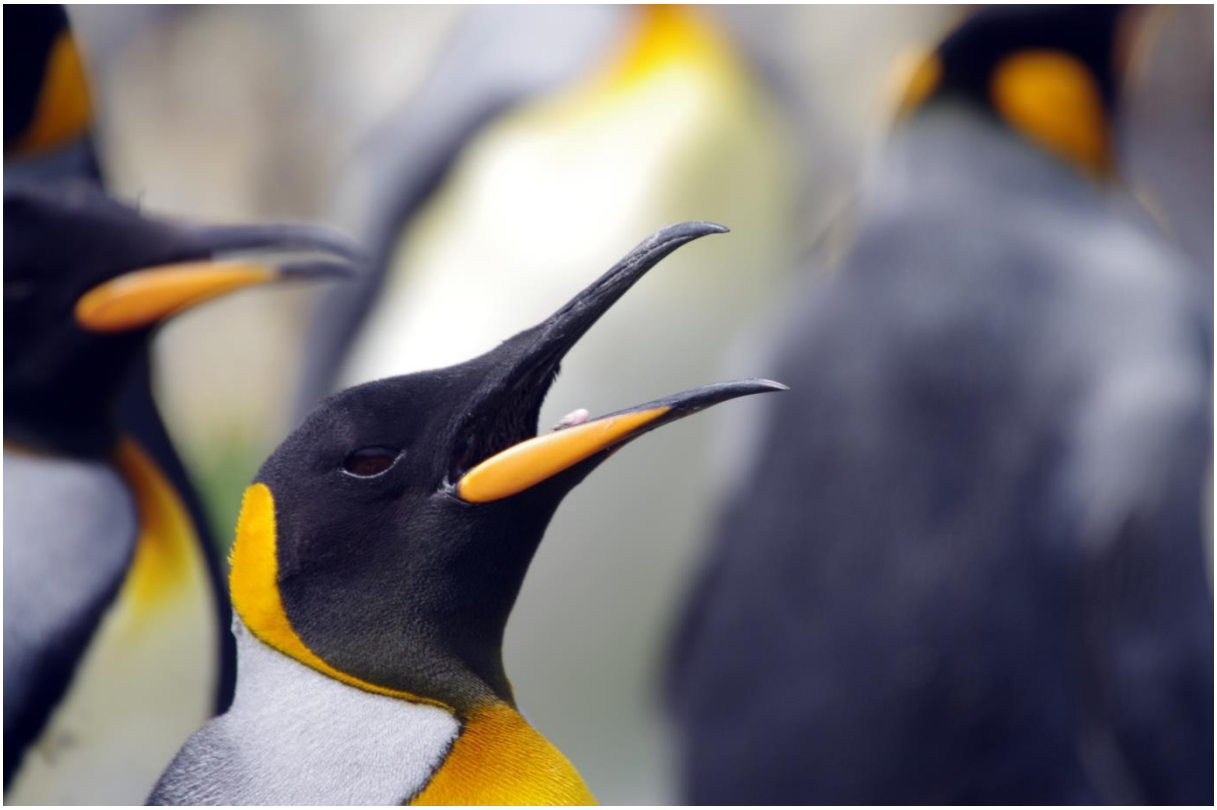
[2]Laboratoire d'Ecologie des Hydrosystèmes Naturels et Anthropisés, CNRS UMR 5023 Université Claude Bernard Lyon 1, Université de Lyon, Lyon, France.

[3] Université de Brest - UMR 6539 CNRS/UBO/IRD/Ifremer, Laboratoire des sciences de l'environnement marin - IUEM - Rue Dumont D'Urville - 29280 - Plouzané

[4] Swiss Ornithological Institute, CH-6204 Sempach, Switzerland

[5] Department of Biology, University of Turku, Turku, Finland

* corresponding authors: aude.noiret@gmail.com & amstie@utu.fi



Abstract

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

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

Introduction

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

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

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

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

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

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

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

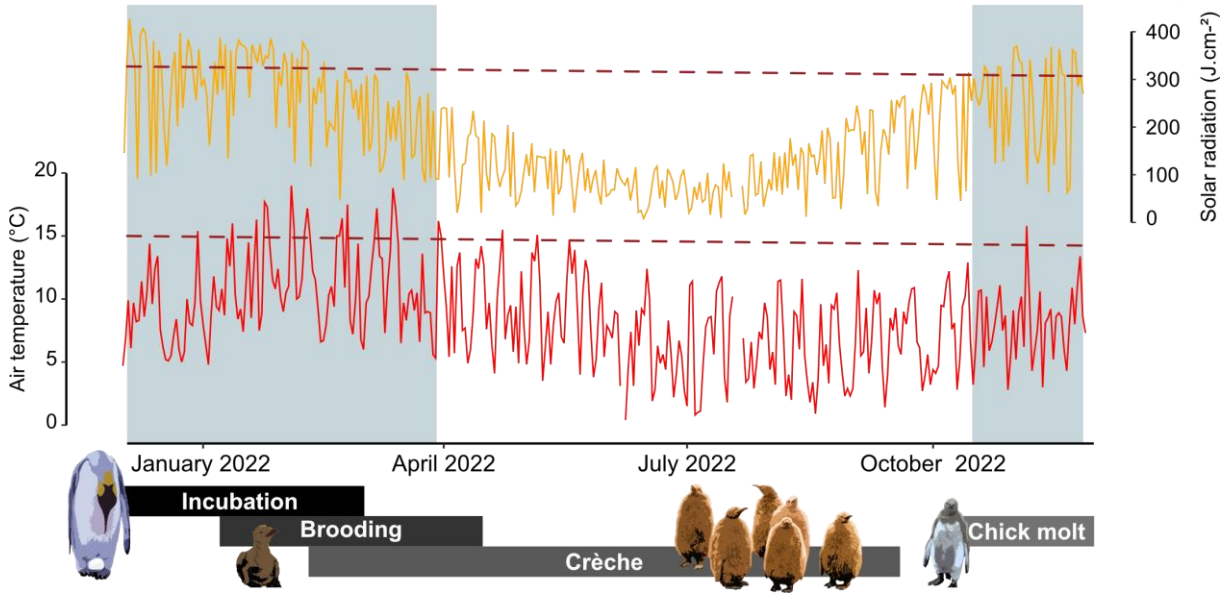


Figure. 1 Breeding cycle and 2022 climatic conditions (daily maximum air temperature (in red) and maximum solar radiation (in orange) of king penguins breeding in Crozet Archipelago.

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

Materials and Methods

Study model and site.

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

Climatic parameters

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

Table 1. Heat indexes computed from air temperature, relative humidity, wind speed and solar radiations using 4 different equations where Tg is the Globe temperature, THI the Temperature-Humidity Index, HLI the Heat Load Index, and WBGT is the Wet-Bulb Globe Temperature. Tnwb is the natural wet-bulb Temperature and can be calculated from Tair, RH and WS using equations in Carter et al. 2020.

Equation 1.	$Tg = 0.01498\,SR + 1.184\,Tair - 0.0789\,RH - 2.739$	*Hajizadeh et al. 2017*
Equation 2.	$THI = Tair + 0.36\,Tw + 41.5$	*Thom et al. 1959; Silva et al. 2007*
Equation 3.	$HLI = 33.2 + 0.2\,RH + 1.2Tg - (0.82WS)0.1 - log\,(0.4\,WS^2 + 0.0001)$	*Ghaugan 2002; Silva et al. 2007*
Equation 4.	$WBGT = 0.7Tnwb \times 0.2Tg \times 0.1Tair$	*Liljegren et al. 2008; Hajizadeh et al. 2017*

We calculated 4 different heat indexes to compare their predictive power to models including raw environmental variables (Table 1). We used the globe temperature (Tg, equation 1, Hajizadeh *et al.* 2017), the Temperature-Humidity Index (THI, equation 2, Thom 1959), the Heat Load Index (HLI, equation 3, Gaughan 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***.

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

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

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

Results

Behavioural thermoregulation

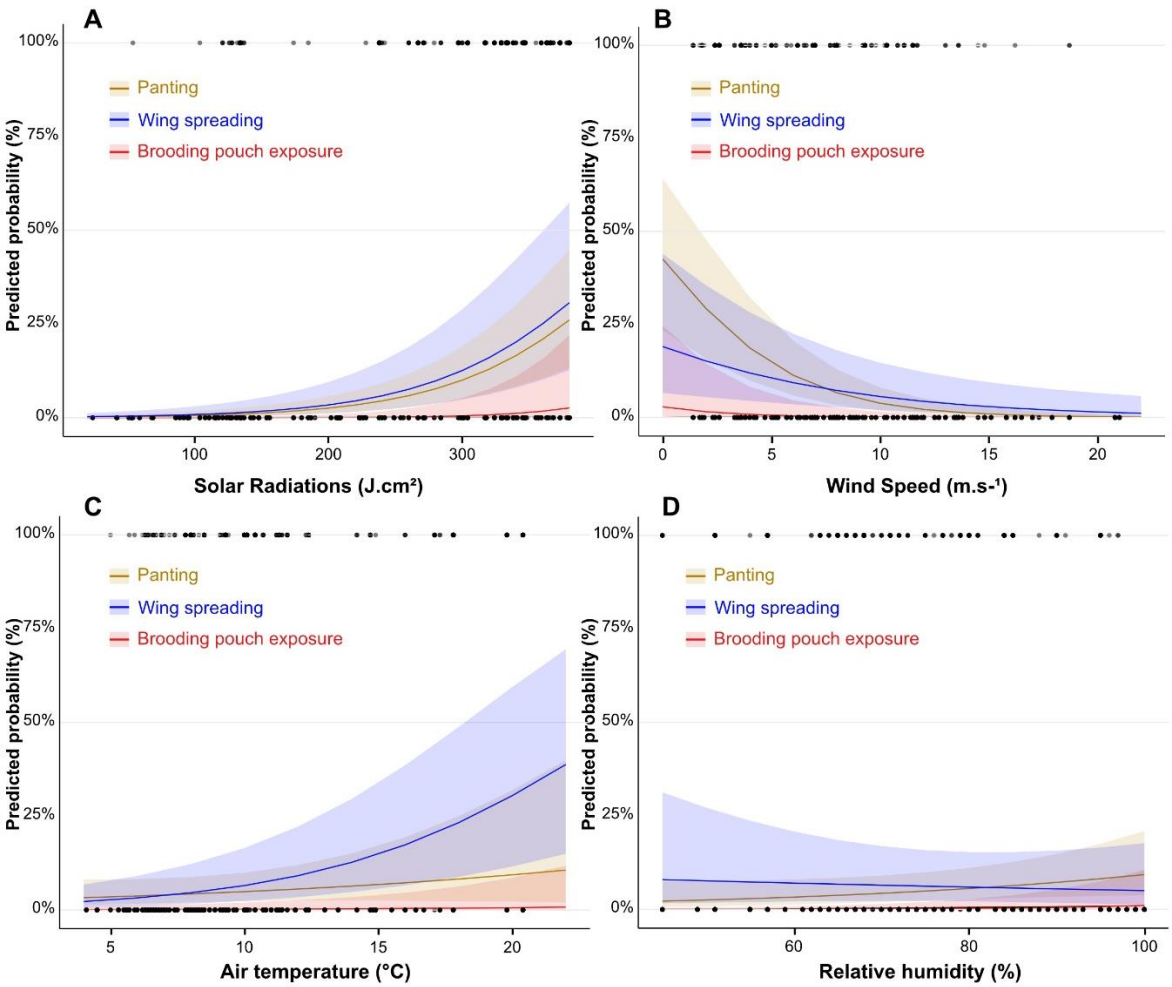


Figure 2. Predicted probabilities of thermoregulatory behaviours (panting (brown), wing spreading (blue) and exposure of the brood pouch (red)) occurrence according to (A) solar radiations, (B) wind speed, (C) air temperature and (D) relative humidity. Predicted probabilities were calculated from generalized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

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

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

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

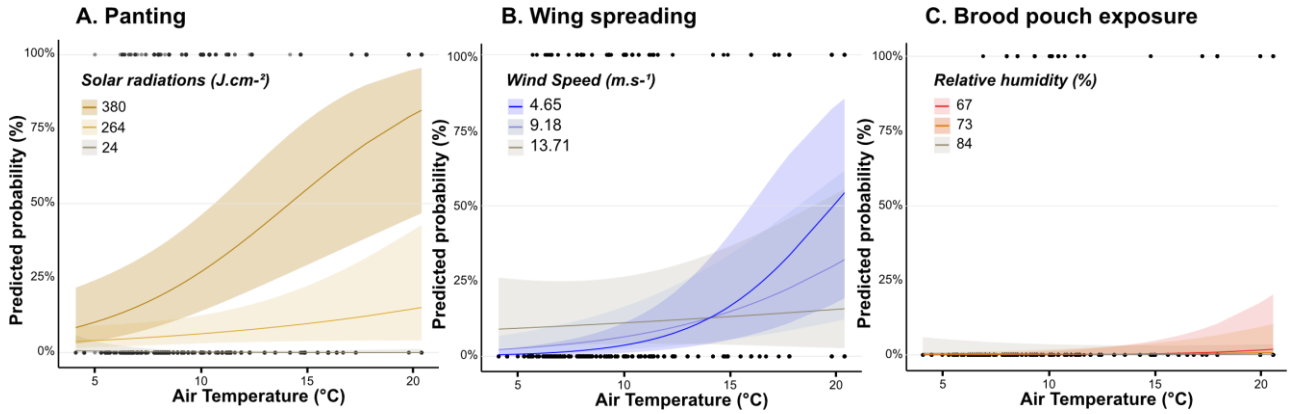


Figure 3. Predicted probability of (A) Panting depending on air temperature and solar radiations; solar radiations are represented as maximum (380), median (264) and minimum (24) registered during behavioural scans; (**B) wing spreading according to air temperature and wind speed** (2nd quartile (4.65),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

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

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

Table 2. Summaries of the most parsimonious generalized linear mixed models predicting thermoregulatory behaviours and subcutaneous temperature: **(A) panting**, **(B) wing spreading**, (**C) exposure of the brood pouch** and **(D) sub-cutaneous temperatures** according to climatic parameters (air temperature: T_{air}: solar radiation: SR; wind speed: WS; relative humidity: RH), their interactions, and biological parameters (sex [Male vs Female], season [2021-2022 vs. 2022-2023], reproductive stage [incubating vs. brooding], and days spent on land 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*
(Intercept)	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} x *WS*				1.69	1.12 – 2.57	**0.013**				-0.22	-0.31 – -0.14	**<0.001**
SR × *WS*	0.67	0.44 – 1.03	0.068									
SR x RH	2.06	1.34 – 3.15	**0.001**	1.98	1.14 – 3.45	**0.016**						
WS x 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^2m/ R^2c	0.684 / 0.729			0.646 / NA			0.479 / 0.839			0.369 / 0.430		

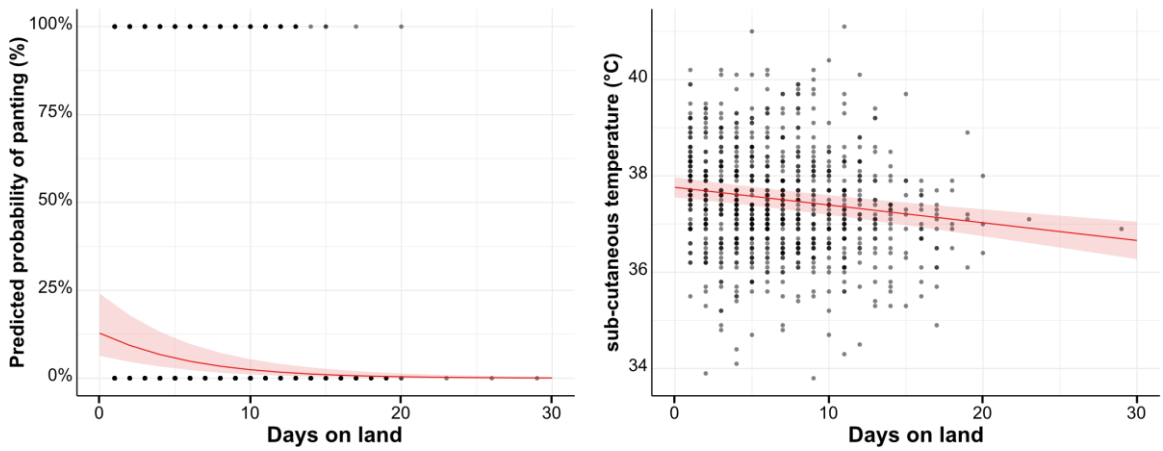


Figure 4. Evolution of (A) panting probability and (B) subcutaneous temperature along the duration of the shift on land. Values are predicted from linear mixed models presented in Table 2. N = 143, n = 1123 for panting; N = 140, n = 856 for T_{sc}.

Subcutaneous temperature

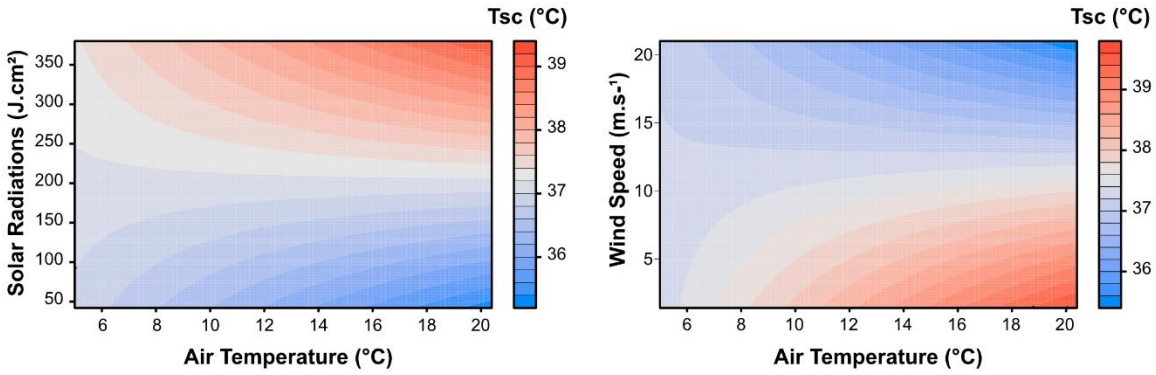


Figure 5. Breeding king penguins' sub-cutaneous temperatures (T_{sc}) according to (A) the interaction between air temperature and solar radiations, and (B) air temperature and wind speed. Values are predicted from the linear mixed model presented in Table 2D; *N = 140, n = 856.*

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

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

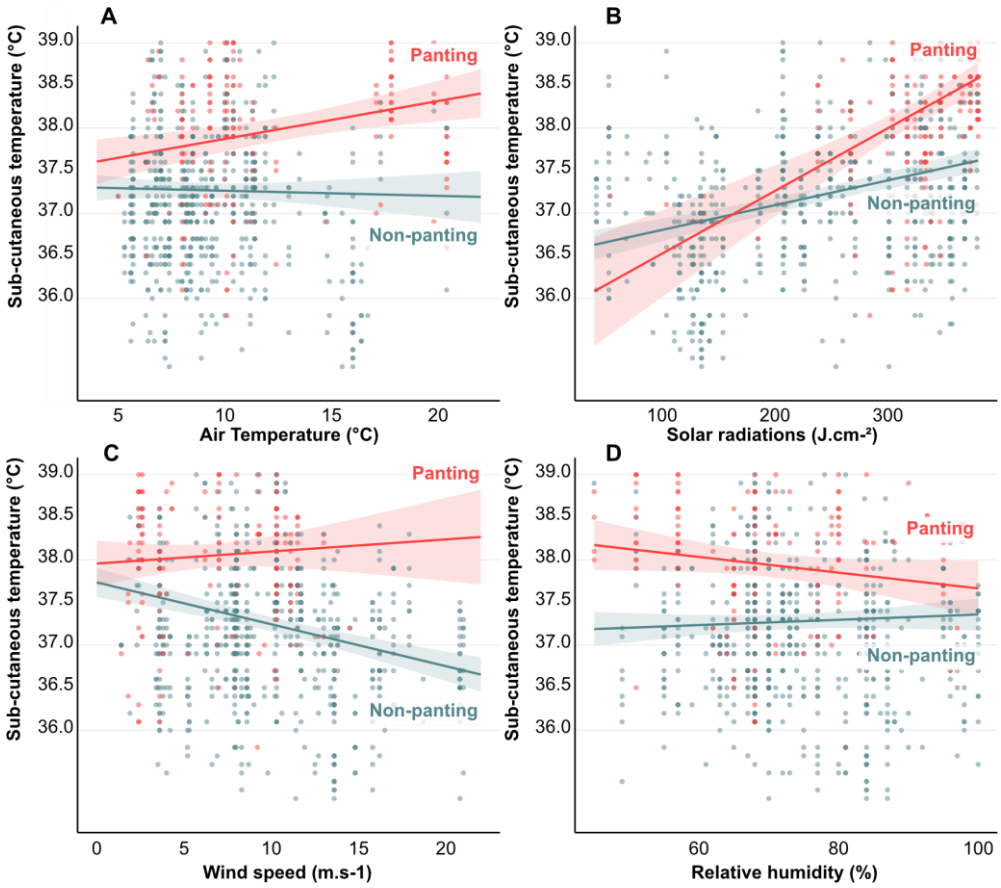


Figure 6. Relationship between air temperature (A), solar radiations (B), wind speed (C) or relative humidity (D) and king penguin's sub-cutaneous temperature according to the use of panting as a thermoregulatory behaviour. *N = 140, n = 856.*

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

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

heat indexes (Globe temperature (Tg), Temperature-Humidity (THI), Heat Load Index (HLI) and Wet-Bulb Globe Temperature (WBGT) explained less variance in thermoregulatory behaviours and T_{sc} than models (with or without interactions) including T_{air}, RH, SR and WS as explanatory variables (Table 3). THI explained the least of all heat index for each explained variables (marginal R^2 were ~0.2 point lower than the other heat indexes).

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

Table 3. Model comparison for the prediction of panting, wing spreading, brood pouch exposure and Tsc based on Akaike's information criterion (AICc), marginal R^2 (R^2m) and conditional R^2 (R^2c). The best predictive model with interactions ('Inter.') between all 4 climatic parameters (Tair, SR, WS and RH), is compared to a model without interactions ('Total'), a model with only Tair or SR and 4 models including Heat indexes: globe temperature (Tg), Temperature-Humidity Index (THI), Wet-Bulb Globe Temperature (WBGT) and Heat Load Index (HLI).

Climatic conditions and reproductive failure

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

Discussion

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

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

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

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

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

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

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

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

Data availability

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

Author's contribution

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

Ethical note

All the procedures were approved by the French Ethical Committee (*APAFIS#31268-2021042117037897 v3*) and the Terres Australes et Antarctiques Françaises (Arrêtés TAAF A-2021-49 and A-2022-69).

Acknowledgments

We are grateful to the French Polar Institute (IPEV) and the Terres Australes et Antarctiques Françaises for providing financial and logistical support for this study through the polar program #119 (ECONERGY). We are grateful to Mathilde Lejeune, Thomas Faulman, Nina Cossin-Sevrin, Robin Dardel, Laetitia Vuibert and the entire Alfred Faure field station for their help in the field. This study is part of the long-term Studies in Ecology and Evolution (SEE-Life) program of the CNRS. We wish to thank the Zone Atelier Antarctique et Terres Australes (ZATA) from the CNRS for financial support, and the members of the Alfred Faure field station for their help and support in the field. AL was supported by ISblue project, Interdisciplinary graduate school for the blue planet (ANR-17-EURE-0015) and co-funded by a grant from the French government under the program "Investissements d'Avenir" embedded in France 2030. AS was supported by a 'Turku Collegium for Science and Medicine' Fellowship, a Marie Sklodowska-Curie Postdoctoral Fellowships (#894963) and AN was funded by an IdEx grant from the Université de Strasbourg (*HotPenguin*) granted to AS. CB, MM, MH and EM were funded by the French Polar Institute.

References

Ancel, A., Beaulieu, M. & Gilbert, C. (2013). The different breeding strategies of penguins: A review. *Comptes Rendus Biologies*, 336, 1–12.

Andreasson, F., Rostedt, E. & Nord, A. (2023). Measuring body temperature in birds – the effects of sensor type and placement on estimated temperature and metabolic rate. *Journal of Experimental Biology*, 226, jeb246321.

Arriagada, M. (2023). King penguin mortality related to heat wave events in 2019 and 2020 at Bahía Inútil, Tierra del Fuego. In: *11th International Penguin Congress*.

Beaman, J.E., White, C.R., Clairbaux, M., Perret, S., Fort, J. & Grémillet, D. (2024). Cold adaptation does not handicap warm tolerance in the most abundant Arctic seabird. *Proc. R. Soc. B.*, 291, 20231887.

Boyles, J.G., Seebacher, F., Smit, B. & McKechnie, A.E. (2011). Adaptive Thermoregulation in Endotherms May Alter Responses to Climate Change. *Integrative and Comparative Biology*, 51, 676–690.

Bryant, D.M. (2008). Heat stress in tropical birds: behavioural thermoregulation during flight. *Ibis*, 125, 313–323.

Budd, G.M. (2008). Wet-bulb globe temperature (WBGT)—its history and its limitations. *Journal of Science and Medicine in Sport*, 11, 20–32.

Carter, A.W., Zaitchik, B.F., Gohlke, J.M., Wang, S. & Richardson, M.B. (2020). Methods for Estimating Wet Bulb Globe Temperature From Remote and Low-Cost Data: A Comparative Study in Central Alabama. *GeoHealth*, 4, e2019GH000231.

Chambers, L.E., Dann, P., Cannell, B. & Woehler, E.J. (2014). Climate as a driver of phenological change in southern seabirds. *Int J Biometeorol*, 58, 603–612.

Chappell, M.A. & Souza, S.L. (1988). Thermoregulation, gas exchange, and ventilation in Adelie penguins (Pygoscelis adeliae). *J Comp Physiol B*, 157, 783–790.

Cherel, Y., Robin, J.P., Walch, O., Karmann, H., Netchitailo, P. & Le Maho, Y. (1988). Fasting in king penguin. I. Hormonal and metabolic changes during breeding. *American Journal of Physiology-Regulatory, Integrative and Comparative Physiology*, 254, R170–R177.

Choy, E.S., O'Connor, R.S., Gilchrist, H.G., Hargreaves, A.L., Love, O.P., Vézina, F., *et al.* (2021). Limited heat tolerance in a cold-adapted seabird: implications of a warming Arctic. *Journal of Experimental Biology*, 224, jeb242168.

Clem, K.R., Fogt, R.L., Turner, J., Lintner, B.R., Marshall, G.J., Miller, J.R., *et al.* (2020). Record warming at the South Pole during the past three decades. *Nat. Clim. Chang.*, 10, 762–770.

Conradie, S.R., Woodborne, S.M., Cunningham, S.J. & McKechnie, A.E. (2019). Chronic, sublethal effects of high temperatures will cause severe declines in southern African arid-zone birds during the 21st century. *Proc. Natl. Acad. Sci. U.S.A.*, 116, 14065–14070.

Conradie, S.R., Woodborne, S.M., Wolf, B.O., Pessato, A., Mariette, M.M. & McKechnie, A.E. (2020). Avian mortality risk during heat waves will increase greatly in arid Australia during the 21st century. *Conservation Physiology*, 8, coaa048.

Cook, T.R., Martin, R., Roberts, J., Häkkinen, H., Botha, P., Meyer, C., *et al.* (2020). Parenting in a warming world: thermoregulatory responses to heat stress in an endangered seabird. *Conservation Physiology*, 8, coz109.

CôTé, S.D. (2000). Aggressiveness in king penguins in relation to reproductive status and territory location. *Animal Behaviour*, 59, 813–821.

Danner, R.M., Coomes, C.M. & Derryberry, E.P. (2021). Simulated heat waves reduce cognitive and motor performance of an endotherm. *Ecol. Evol.*, 11, 2261–2272.

Davis, L.S. & Darby, J.T. (2012). *Penguin Biology*. Elsevier.

Descamps, S., Gauthier-Clerc, M., Le Bohec, C., Gendner, J.-P. & Le Maho, Y. (2005). Impact of predation on king penguin Aptenodytes patagonicus in Crozet Archipelago. *Polar Biol*, 28, 303–310.

Eichhorn, G., Groscolas, R., Le Glaunec, G., Parisel, C., Arnold, L., Medina, P., *et al.* (2011). Heterothermy in growing king penguins. *Nat Commun*, 2, 435.

Gaughan, J. (2002). *Validation of the Heat Load Index for use in the feedlot industry* (No. 9781741918069).

Gauthier-Clerc, M., Le Maho, Y., Gendner, J.-P., Durant, J. & Handrich, Y. (2001). State-dependent decisions in long-term fasting king penguins, Aptenodytes patagonicus, during courtship and incubation. *Animal Behaviour*, 62, 661–669.

Grémillet, D., Meslin, L. & Lescroël, A. (2012). Heat dissipation limit theory and the evolution of avian functional traits in a warming world. *Funct Ecol*, 26, 1001–1006.

Grunst, M.L., Grunst, A.S., Grémillet, D., Kato, A., Gentès, S. & Fort, J. (2023). Keystone seabird may face thermoregulatory challenges in a warming Arctic. *Sci Rep*, 13, 16733.

Hajizadeh, R., Farhang Dehghan, S., Golbabaei, F., Jafari, S.M. & Karajizadeh, M. (2017). Offering a model for estimating black globe temperature according to meteorological measurements. *Meteorological Applications*, 24, 303–307.

Handrich, Y., Bevan, R.M., Charrassin, J.-B., Butler, P.J., Ptz, K., Woakes, A.J., *et al.* (1997). Hypothermia in foraging king penguins. *Nature*, 388, 64–67.

Hansen, P.J. (2009). Effects of heat stress on mammalian reproduction. *Phil. Trans. R. Soc. B*, 364, 3341–3350.

Holt, K.A. & Boersma, P.D. (2022). Unprecedented heat mortality of Magellanic Penguins. *Ornithological Applications*, 124, duab052.

Ioannou, L.G., Ciuha, U., Fisher, J.T., Tsoutsoubi, L., Tobita, K., Bonell, A., *et al.* (2023). Novel Technological Advances to Protect People Who Exercise or Work in Thermally Stressful Conditions: A Transition to More Personalized Guidelines. *Applied Sciences*, 13, 8561.

Ioannou, L.G., Mantzios, K., Tsoutsoubi, L., Notley, S.R., Dinas, P.C., Brearley, M., *et al.* (2022). Indicators to assess physiological heat strain – Part 1: Systematic review. *Temperature*, 9, 227–262.

Knoch, S., Whiteside, M.A., Madden, J.R., Rose, P.E. & Fawcett, T.W. (2022). Hot-headed peckers: thermographic changes during aggression among juvenile pheasants (*Phasianus colchicus*). *Phil. Trans. R. Soc. B*, 377, 20200442.

Kriesell, H.J., Aubin, T., Planas-Bielsa, V., Benoiste, M., Bonadonna, F., Gachot-Neveu, H., *et al.* (2018). Sex identification in King Penguins *Aptenodytes patagonicus* through morphological and acoustic cues. *Ibis*, 160, 755–768.

Lemonnier, C., Schull, Q., Stier, A., Boonstra, R., Delehanty, B., Lefol, E., *et al.* (2024). Social, not genetic, programming of development and stress physiology of a colonial seabird. *Proceedings of the Royal Society B: Biological Sciences*, 291, 20240853.

Lewden, A., Enstipp, M.R., Picard, B., Van Walsum, T. & Handrich, Y. (2017). High peripheral temperatures in king penguins while resting at sea: thermoregulation versus fat deposition. *Journal of Experimental Biology*, jeb.158980.

Liljegren, J.C., Carhart, R.A., Lawday, P., Tschopp, S. & Sharp, R. (2008). Modeling the Wet Bulb Globe Temperature Using Standard Meteorological Measurements. *Journal of Occupational and Environmental Hygiene*, 5, 645–655.

Marx, W., Haunschild, R. & Bornmann, L. (2021). Heat waves: a hot topic in climate change research. *Theor Appl Climatol*, 146, 781–800.

McCafferty, D.J., Gallon, S. & Nord, A. (2015). Challenges of measuring body temperatures of free-ranging birds and mammals. *Anim Biotelemetry*, 3, 33.

Mitchell, D., Maloney, S.K., Snelling, E.P., Carvalho Fonsêca, V.D.F. & Fuller, A. (2024). Measurement of microclimates in a warming world: problems and solutions. *Journal of Experimental Biology*, 227, jeb246481.

Muggeo, V. (2008). segmented: an R Package to Fit Regression Models with Broken-Line Relationships.

Nel, W., Hedding, D.W. & Rudolph, E.M. (2023). The sub-Antarctic islands are increasingly warming in the 21st century. *Antarctic Science*, 35, 124–126.

O'Connor, R.S., Le Pogam, A., Young, K.G., Robitaille, F., Choy, E.S., Love, O.P., *et al.* (2021). Limited heat tolerance in an Arctic passerine: Thermoregulatory implications for cold-specialized birds in a rapidly warming world. *Ecol. Evol.*, 11, 1609–1619.

Olin, A., Dück, L., Berglund, P., Karlsson, E., Bohm, M., Olsson, O., *et al.* (2023). Breeding failures and reduced nest attendance in response to heat stress in a high-latitude seabird. *Mar. Ecol. Prog. Ser.*, HEAT.

Oswald, K.N., Evlambiou, A.A., Ribeiro, Â.M. & Smit, B. (2018). Tag location and risk assessment for passive integrated transponder-tagging passerines. *Ibis*, 160, 453–457.

Oswald, S.A., Bearhop, S., Furness, R.W., Huntley, B. & Hamer, K.C. (2008). Heat stress in a high-latitude seabird: effects of temperature and food supply on bathing and nest attendance of great skuas *Catharacta skua*. *Journal of Avian Biology*, 39, 163–169.

Piatt, J., Arimitsu, M., Thompson, S., Suryan, R., Wilson, R., Elliott, K., *et al.* (2024). Mechanisms by which marine heatwaves affect seabirds. *Mar. Ecol. Prog. Ser.*, 737, 1–8.

Pipoly, I., Bókony, V., Seress, G., Szabó, K. & Liker, A. (2013). Effects of Extreme Weather on Reproductive Success in a Temperate-Breeding Songbird. *PLoS ONE*, 8, e80033.

Robinson, P.J. (2001). On the Definition of a Heat Wave. *J. Appl. Meteor.*, 40, 762–775.

Romanovsky, A.A. (2007). Thermoregulation: some concepts have changed. Functional architecture of the thermoregulatory system. *American Journal of Physiology-Regulatory, Integrative and Comparative Physiology*, 292, R37–R46.

Romanovsky, A.A. (2018). The thermoregulation system and how it works. In: *Handbook of Clinical Neurology*. Elsevier, pp. 3–43.

Silva, R.G. da, Morais, D.A.E.F. & Guilhermino, M.M. (2007). Evaluation of thermal stress indexes for dairy cows in tropical regions. *R. Bras. Zootec.*, 36, 1192–1198.

Smit, B., Zietsman, G., Martin, R.O., Cunningham, S.J., McKechnie, A.E. & Hockey, P.A.R. (2016). Behavioural responses to heat in desert birds: implications for predicting vulnerability to climate warming. *Clim Chang Responses*, 3, 9.

Stammerjohn, S.E. & Scambos, T.A. (2020). Warming reaches the South Pole. *Nat. Clim. Chang.*, 10, 710–711.

Stillman, J.H. (2019). Heat Waves, the New Normal: Summertime Temperature Extremes Will Impact Animals, Ecosystems, and Human Communities. *Physiology*, 34, 86–100.

Stonehouse, B. (1960). Breeding behaviour and development. In: *The King Penguin (Aptenodites patagonica) of South Georgia*.

Talbot, W.A., McWhorter, T.J., Gerson, A.R., McKechnie, A.E. & Wolf, B.O. (2017). Avian thermoregulation in the heat: evaporative cooling capacity of arid-zone caprimulgiforms from two continents. *Journal of Experimental Biology*, jeb.161653.

Tan, C.L. & Knight, Z.A. (2018). Regulation of Body Temperature by the Nervous System. *Neuron*, 98, 31–48.

Thom, E.C. (1959). The Discomfort Index. *Weatherwise*, 12, 57–61.

Weimerskirch, H., Stahl, J.C. & Jouventin, P. (1992). The breeding biology and population dynamics of King Penguins *Aptenodytes patagonica* on the Crozet Islands. *Ibis*, 134, 107–117.

Welman, S. & Pichegru, L. (2022). Nest microclimate and heat stress in African Penguins *Spheniscus demersus* breeding on Bird Island, South Africa. *Bird Conservation International*, 1–9.

You, Q., Cai, Z., Pepin, N., Chen, D., Ahrens, B., Jiang, Z., *et al.* (2021). Warming amplification over the Arctic Pole and Third Pole: Trends, mechanisms and consequences. *Earth-Science Reviews*, 217, 103625.

Zuur, A.F., Ieno, E.N. & Elphick, C.S. (2010). A protocol for data exploration to avoid common statistical problems: *Data exploration*. *Methods in Ecology and Evolution*, 1, 3–14.

ESM

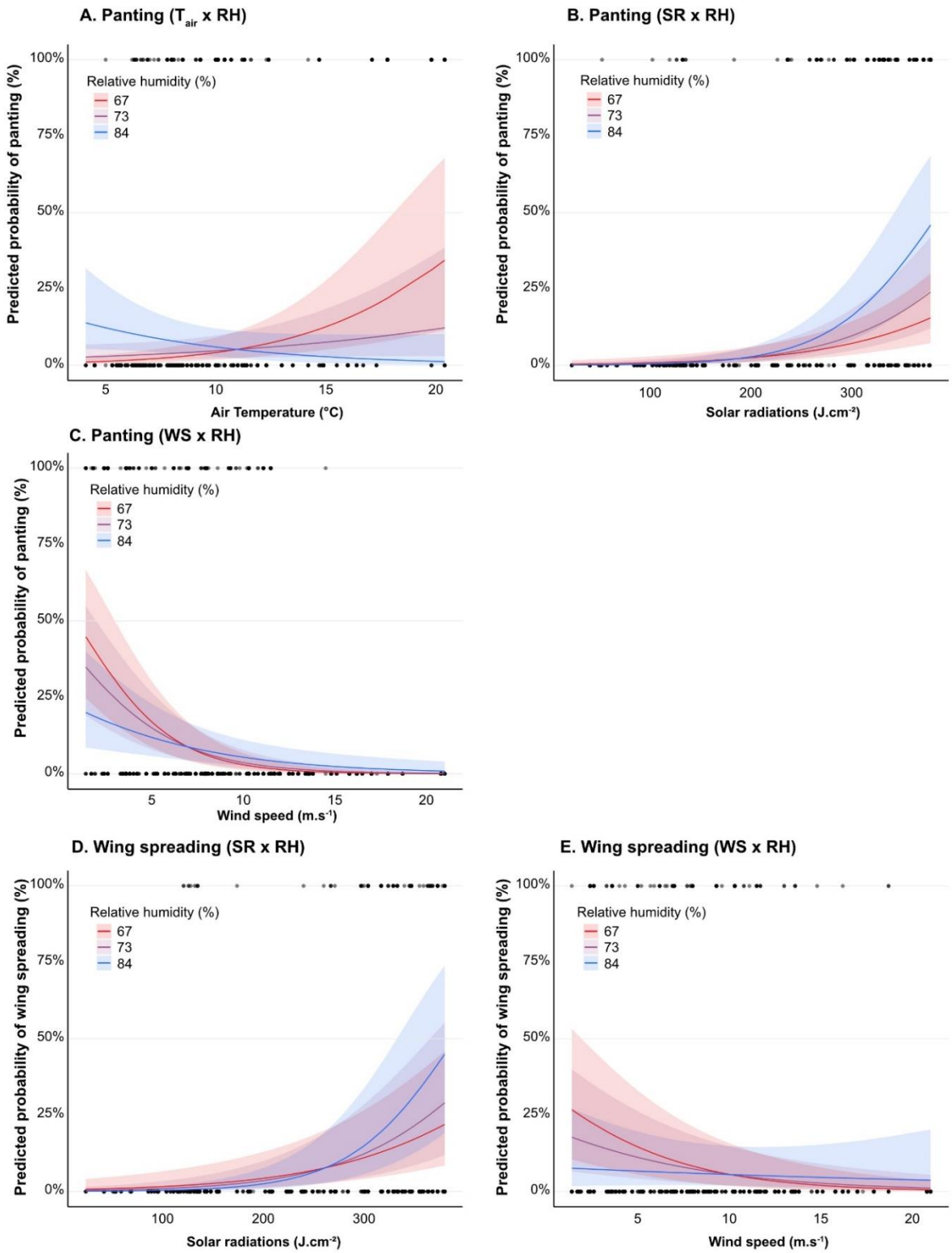


Figure S1. **Predicted probability of (A) Panting depending on air temperature and relative humidity** (**B) panting depending on solar radiations and relative humidity (C) panting depending on wind speed and relative humidity (D) wing spreading depending on solar radiations and relative humidity and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

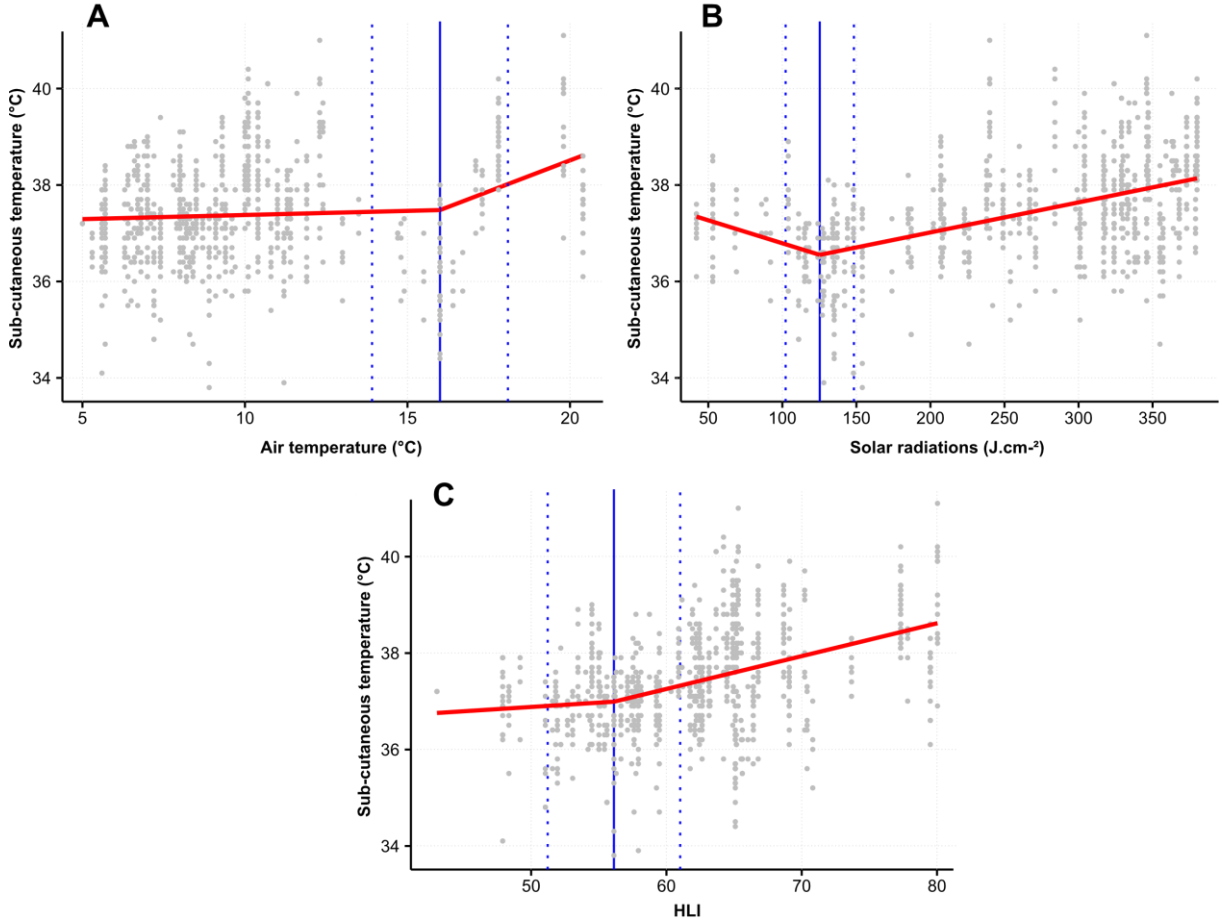


Figure S2. Breakpoint analyses between king penguins' sub-cutaneous temperatures (T_{sc}) and (A) air temperature; (B) solar radiations and (C) heat load index (HLI) computed from **air temperature, solar radiations, wind speed and relative humidity.** Segmented models are shown in red, and estimated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