

Thermal stress during incubation in an arctic breeding seabird

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ABSTRACT

Arctic breeding seabirds have experienced dramatic population declines in recent decades. The population of Arctic skuas (*Stercorarius parasiticus*) nesting on the Faroe Islands, North Atlantic, breed near the southern extent of their breeding range and are experiencing some of the largest declines. This is thought to be caused in part by increased warming due to climate change and thus, it is becoming critical to investigate the proximate and ultimate effects of the thermal environment on parental physiology, behaviour and breeding success. Behavioural observations at an Arctic skua long-term monitoring colony were undertaken during the 2016 breeding season to determine the frequencies of thermoregulatory panting, and interrupted incubation events. Incubating Arctic skuas showed thermoregulatory behaviour at air temperatures (T_a) of 9 °C, which suggested that they may be operating near their upper thermal tolerance limit. Arctic skuas spent significantly more time panting as T_a increases, wind speed decreases and sun exposure increases. This relationship was apparent even within the narrow ranges of T_a (7.5–15 °C) and wind speed (0–5 ms^{-1}) recorded. Incubation effort was not continuous with birds leaving the nest for up to 100% of the observation block. While we found no relationship between interrupted incubation and environmental conditions, panting was only observed in birds that were simultaneously incubating eggs. These results highlight the constraints on birds during the incubation phase of breeding, and indicate a potential maladaptive behaviour of maintaining incubation despite the increased cost of thermoregulation under warming temperatures in this species. However, the relationship between thermal stress, nest absence and demographic parameters remains unclear, highlighting the importance of longitudinal and/or high-resolution studies that focus on Arctic specialists and the interrelationships between environmental factors, nest absence rates and productivity.

1. Introduction

The Arctic and subarctic regions are warming faster than the global average (IPCC 2015; Rantanen et al., 2022). These regions provide breeding grounds to an abundance of ecologically diverse top-predators, including globally threatened seabirds (Gaston 2011; Dias et al., 2019). Due to the rapid rate of environmental change, birds breeding at high northern latitudes are increasingly faced with suboptimal environmental conditions (Oswald and Arnold 2012), and the expected adaptive response is challenging and most likely to include phenotypic plasticity (Gilg et al., 2012). These species are generally highly morphologically specialised to retain body heat in cold conditions, making them particularly vulnerable to increasing temperatures (Gilg et al., 2012;

O'Connor et al., 2021). Seabirds are generally good homotherms: they are able to maintain a stable body temperature within a narrow range (38–40 °C; Lustick (1984)). The knowledge gaps from limited empirical information on the thermoregulatory capacity across Arctic seabird species has consequences for our understanding of their vulnerability to climate change.

Multiple thermoregulatory behaviours exist that allow animals to deal with heat and to maintain their body temperature within a narrow window. In birds, panting, an evaporative cooling mechanism dissipating heat from the oral cavity, is common; and the most readily observable physiological response to acute thermal stress (Dawson 1982). Panting has been observed to be consistently initiated at the upper critical temperature (UCT) of a bird's thermonutral zone (TNZ)

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(Scanes 2015; Yahav 2015). The UCT is the ambient temperature above which there is an increasing energetic cost associated with active heat loss and the direct effect of temperature on cellular functions (Scanes 2015).

In addition to direct heat dissipation from panting, in the breeding period, a variety of responses to thermal stress are available to birds, such as exposing of tarsi, shade seeking, or bathing (Yahav 2015). An increase in foraging effort to compensate for the additional energetic load of active thermoregulation in temperatures above the TNZ may be observed (Yahav 2015). Alternatively, thermoregulatory behaviours may occur at the expense of essential activities, such as foraging or self-maintenance which could impact body condition and adult fitness (Oswald and Arnold 2012; Cunningham et al., 2015; Nord and Nilsson 2019). Ultimately, for incubating birds this manifests in the momentary to extended cessation of egg incubation or even leaving the territory completely (Oswald et al., 2008). This increases the risk to the clutch, as incubation is crucial for ensuring optimal microclimatic conditions for embryo development as well as protection against UV radiation and predation of the eggs and developing chicks (Webb 1987; Deeming and Reynolds 2015). The latter aspect is particularly critical for ground nesting birds, that do not rely on defensive structures or inaccessibility to deter predation from avian or terrestrial predators, or even conspecifics. Such species are therefore expected to maintain a high incubation consistency, optimally only leaving the eggs exposed for negligible intervals such as during nest defence or the changing of incubation duties. However, the necessity for thermoregulation (e.g. bathing or shade seeking) can result in more frequent or longer interruptions in incubation (Oswald et al., 2008). In addition to the effect of depredation on productivity, there is evidence of prolonged and unmitigated thermal stress in nestlings leading to adverse physiological changes with possible deleterious effects (Webb 1987; Eastwood et al., 2022), or in extreme cases, direct mortality (Salzman 1982; Quintana et al., 2022).

The Arctic skua (*Stercorarius parasiticus*) is a long distance migratory seabird with a breeding range throughout the circumpolar arctic and sub-arctic (Furness 1987). This species is experiencing heavy population declines in the north Atlantic (Paleczny et al., 2015; Perkins et al., 2018), and is considered *endangered* within the European Union (Burfield and van Bommel 2004; van Bemmelen et al., 2021). Declines are most acute at the southern, and warmest, boundary of their range. The Faroe Islands' population, which at the southern extent of the breeding range is potentially most susceptible to climate change, has experienced declines by approximately 60–70% over 4 decades (Bengtson and Bloch 2003; Santos 2018), a similar trend to the UK (another population at the southern margin of the distribution range) where the breeding population has declined 66% between 2015 and 2021 (Burnell et al., 2023). The causes of these declines are likely to be location specific; in the UK and Norway correlations were found with predation of young and food shortages (Perkins et al., 2018; van Bemmelen et al., 2021), while in the Faroe Islands the period of population decline is associated with an increase in adult and immature mortality (Santos et al., 2023) in addition to similar likely disruption to prey abundance (Hátún et al., 2021).

As a long-distance migrant wintering in the tropics, Arctic skuas occupy a range of thermal environments (van Bemmelen et al., 2024). However, the constraints of breeding on physiological and behavioural thermoregulatory plasticity, once the bird is acclimatized to the environment of its breeding range are poorly understood. In order to inform predictions of how climate change may impact already vulnerable birds at a population level, it is important to determine the sensitivity of cold climate breeders to thermal stress under the constraints of the breeding season, identify their optimal thermal window and to understand the strategies with which they combat thermoregulatory challenges. Though physiological adaptations (e.g. metabolic plasticity (McKechnie et al., 2006; Ruuskanen et al., 2021) may allow some bird species to withstand small incremental shifts in climate, and range shifts or morphological changes can be expected in the long term (e.g. (Chen

et al., 2011; Osváth et al., 2018)), modifications of behaviour (short-term) is a likely response to rapidity of warming (Ruuskanen et al., 2021). Here, we hypothesised that thermoregulatory mechanisms of a population at the southern extent of its breeding range, and therefore likely to be sensitive to thermal stress, are a trade-off between physiological and behavioural responses: endothermy is mediated by panting (an innate respiratory mechanism which is also an indicator of associated resource costs), and balanced by high-risk behavioural responses culminating in interrupted incubation. To investigate the proximate and ultimate effects of the thermal environment on the parental physiology, behaviour and breeding potential during the critical period of incubation we determined the frequencies of two thermoregulatory mechanisms (panting and incubation interruption) in Arctic skuas under field conditions in the Faroe Islands in relation to three weather variables underlying a birds general heat balance (Lovette and Fitzpatrick 2016): ambient temperature (T_a), wind speed and solar heat load. If temperatures above the birds' upper critical temperature of their TNZ were encountered we would likely observe the initiation of thermoregulatory panting, modulated by variation in sun exposure and local wind. As such we predicted a logistic relationship between environmental variables and the panting response. In addition, we predicted that increases in heat stress, from increased temperatures, solar radiation and reduced wind speed, would be associated with an increase in interrupted incubation events.

2. Methodology

The study was conducted at an Arctic skua breeding colony at Kirkjuhagi (62.324°N 6.312°W) on the island of Fugloy, Faroe Islands in 2016. The site is situated on a large, open, south facing slope, where early and late in the day some territories are shaded by cliffs. Early in the breeding season all nests were located and mapped, and observation positions ($n = 9$) were identified to monitor multiple territories simultaneously with the aid of binoculars or a telescope. The colony consisted of 41 territories containing an active nest, at a density ca. 60 territories per km^{-2} . We collected observational data between June 4th and July 1st. Observation positions were rotated as best as practical to fit with other fieldwork obligations. Territories were often monitored several times each day, and a full schedule is included in SM Fig. 1. Variation in coverage between territories was due to time/resource limitations, weather conditions and concurrent biotelemetry fieldwork at the colony. Up to 6 territories were observed concurrently, but the total number of territories clearly visible from an observation position ranged from 1 to 8 and typically 3 were observed simultaneously.

We obtained observational data from 27 territories, totalling 577 observation blocks of 15-min duration, and 16 were excluded due to incomplete sampling (incomplete observation blocks due to periods where fieldworkers disturbed the birds were excluded). Complete observation blocks ranged from 2 to 50 per territory, mean 21.3. Occurrences of panting and interrupted incubation events were recorded at 1-min resolution during continuous observation blocks. We standardised observations at a resolution of 1-min interval (if a behaviour was observed at any point during that minute it was recorded) to allow monitoring of several nests simultaneously. Panting was defined as having a continuously open bill for more than 10 s (we used this definition as we may miss very short panting episodes when monitoring multiple territories), although panting observed exclusively lasted substantially longer (typically several minutes continuously) and extremely short periods of less than 10 s were expected to be extremely rare based on observations. Interrupted incubation was defined as any instance where the bird was not sitting on the nest within that 1-min interval. Potentially extremely short interruptions may have been missed, however compared to the more subtle behaviour of panting we don't believe this is likely for experienced observers. Panting and interrupted incubation data were aggregated as the sum per observation block (values 0–15). To avoid observer effect, observations were made from vantage

points with partial observer cover (e.g., large rock) up to 200 m distance, and observation blocks were not initiated during nest absences (this occurred in 4 instances: birds returned to nest after 1–6 min, after which observations were initiated). Observations were conducted in all daylight hours between 6am and 10pm (SM Fig. 1).

For the duration of the study period weather data were logged every minute with a locally synchronized Automatic Weather Station (HOBO U30, Onset Computers) placed ca. 400 m downhill from the lower colony border. We recorded ambient temperature (T_a ; °C) and wind speed (ms^{-1}) at 1.5 m above ground level (SM Fig. 2), and rainfall at ground level. We used the mean values per observation block in analysis. No rain occurred throughout the study, so this metric was excluded. Furthermore, we assigned solar heat load as a sun exposure index to each individual nest site. To capture the variation in shading between territories we categorically recorded sun exposure at 1-min intervals during observation blocks as None (full cloud cover or shading; 0), Intermediate (intermittent cloud cover; 1) or Full (no cloud cover; continuous sunshine; 2). Cloud cover varied between territories, for example, broken cloud may result in some incubating birds being exposed to direct sun, while a neighbouring territory being shaded; similarly, some territories can be shaded by cliffs. The sun exposure index (SM Fig. 2c) was summed for each observation block (values 0–30).

Statistical analyses and visualisations were performed in R (version 4.2.2 (R Core Team 2017);) using RStudio. We evaluated correlation between predictor variables using package *corrplot*. Package *pscl* (Zeileis et al., 2008; Jackman 2010) was used to fit zero-inflated and hurdle models and package *MASS* (Venables and Ripley 2002) for negative binomial models. As the count data for both panting and interrupted incubation is likely to be zero-inflated we first assessed the fit of 6 models with differing distributional assumptions (Poisson, negative binomial, zero-inflated Poisson, zero-inflated negative binomial, Poisson logit hurdle and negative binomial logit hurdle), by AIC (Loeys et al., 2012). The zero-inflated negative binomial and negative binomial hurdle model were equally supported: we chose to present zero-inflated negative binomial models only. For each response, panting and interrupted incubation, we tested air temperature (T_a), wind speed and sun exposure as main effects individually and their interaction, and used likelihood ratio test (LRT) to jointly test the effect of the count- and zero-components (package *lmtree*; Zeileis and Hothorn (2002)) by comparing the models with and without the main effects. 95% confidence intervals were calculated from the model predictions using the package *boot* (Canty and Ripley (2021); $R = 100$), and strictly for comparison between models, we report a pseudo- R^2 measure for zero-inflated models, a measure of explained variation, package *performance* (Lüdtke et al., 2021). We evaluated potential heat built-up and radiation from the ground as the interaction with T_a of time since sunrise, package *suncalc* (Agafonkin and Thieurmél 2017) to quantify daylight duration at the start of the observation block (SM Appendix 1); and present the seasonal influence on the environmental predictor variables and observed responses (SM Figs. 3–5). For the response variable of interrupted incubation, we also included panting as an additional predictor term, but we found no support for this as a confounding factor with interrupted incubation events. As zero-inflated and hurdle models could not account for random effects, we further tested the panting and interrupted incubation datasets as a binary response (at the observation block level) with a logistic model (package *lme4* (Bates et al., 2015);) to include Territory ID as a random effect with the same explanatory variables (T_a , wind speed and sun exposure) and evaluated based on AIC.

3. Results

For the 577 observation blocks at the Kirkjuhagi Arctic skua colony, birds were not incubating 3.8% of the time. They were observed panting in 432 min, an estimate of 5% of the total observation time and 5.2% of

the time incubating. When individuals were not actively incubating (recorded as an interrupted incubation event) they were generally standing within their territory, but short flights, preening, bathing in local pools and interactions with their mate were recorded. For the observation blocks T_a ranged between 7.7 and 14.6 °C, mean 10.4 °C; wind speed ranged between 0 and 4.9 ms^{-1} , mean 2.2 ms^{-1} ; and mean sun exposure index was 10.9 (SM Figs. 2 and 3), which was representative of the study period (SM Fig. 3).

Zero-inflated negative binomial models of individual predictor variables showed significant variation in instances of panting in Arctic skuas to be explained by T_a (LRT $\chi^2 = 62.53$, $p < 0.001$, pseudo- $R^2 = 0.55$), wind speed (LRT $\chi^2 = 22.44$, $p < 0.001$, pseudo- $R^2 = 0.30$), and sun exposure (LRT $\chi^2 = 9.43$, $p = 0.009$, pseudo- $R^2 = 0.17$) (Fig. 1, Table 1, SM Fig. 6). Assessment of the interactions of main effects by likelihood ratio test indicated that there was no overall significance of the interaction terms ($p > 0.05$). Backwards stepwise variable elimination of the full joint zero-inflated model retained only T_a as significant in the zero-inflated binomial model: a conservative interpretation is that the other main effects may only be significant because they have some correlation with T_a and each other (SM Fig. 5). Panting occurred at temperatures as low as 9.2 °C and significantly increased with T_a (from the predicted overall model estimates (Fig. 1a) panting occurs in 2.5% of the observation intervals 95% CI [1.2%, 3.6%] at the mean T_a experienced (10.4 °C)). Panting increased as windspeed decreased and sun exposure increased (Fig. 1, SM Fig. 6). With the inclusion of the interaction term daylight duration as a proxy of heat build-up, backwards elimination of the full zero-inflated model, all predictor variables were retained (SM Appendix 1) corroborating individual models.

The best supported binomial response logistic regression model was the full model (all 3 predictor variables) but the model with T_a and wind (SM Fig. 7, Table 2) was also well supported ($\Delta\text{AIC} = 1.6$). All other models had $\Delta\text{AIC} > 2$ (Table 2). The full model verified that panting was more likely with increasing temperature (est 0.74 ± 0.17 , $p < 0.001$), sun exposure (est 0.04 ± 0.02 , $p = 0.057$) and decreasing wind speed (est -0.55 ± 0.22 , $p = 0.0012$). AIC values indicate strong support for both T_a and wind speed, but only some support for sun exposure (Table 2).

We found no significant relationship between the behavioural response of interrupted incubation and the three environmental variables (SM Fig. 8). Notably, when the bird was observable, there was no instance when incubation was interrupted and the bird was panting.

4. Discussion

This study provides direct evidence that Arctic skuas on the Faroe Islands experience ambient thermal conditions sufficient to induce thermoregulatory panting for intervals during the incubation period. Despite seeing a clear signal that birds are at the upper threshold of their thermal neutral zone, within the relatively low ambient temperatures encountered, we found no response of interrupted incubation within this range. It is possible that such behavioural mechanisms associated with interrupted incubation can be expected at temperatures greater than those during this study; however, in panting there is an apparent thermal constraint during incubation, which is likely to have consequences for water balance and energy budgets.

Panting was observed at relatively low temperatures (minimum air temperature 9.2 °C) compared to current and expected regional temperatures. The Faroes archipelago consists of 18 small rocky islands buffered by the maritime climate of the north Atlantic current (Fosaa et al., 2004). Ambient temperatures are characterised by low variation and typically range between 3.9 and 15.6 °C, with a mean over all years of 9.3 °C (June data 2000–2022; mean absolute min and max; and mean air temperatures; DMI (2023)) during the breeding period in this region. Conditions in the study year were typical (June data 2000–2022): average temperature 9.5 °C for 2016 and mean for all years 9.3 °C [range 7.8–10.3 °C]; average daily maximum – 11.8 °C for 2016 and

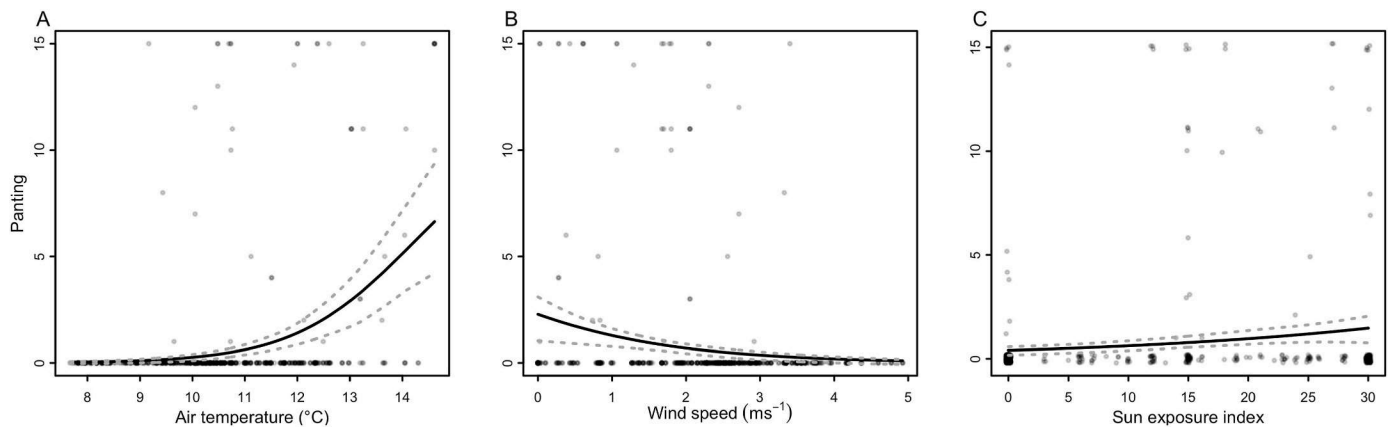


Fig. 1. Relationship between Arctic skua panting and weather variables Individual panting response count data (points; $n = 577$) and reduced zero-inflated negative binomial model predicated overall mean (line, 95% CI dashed lines) in response to A) air temperature (T_{a} ; °C) and B) wind speed (ms^{-1}) at 1.5 m above ground level, and C) sun exposure index. (note raw sun exposure index data plotted with jitter).

Table 1

Panting response estimated parameters (with standard Error), log-likelihood value and likelihood ratio test for zero-inflated negative binomial (ZINB) models with Temp (mean ambient temperature), Wind (mean wind speed), and sun exposure index as the main effect.

	Air temperature (°C)	Wind Speed (ms^{-1})	Sun exposure index
<i>Count component</i>			
(intercept)	2.042 ± 0.686	2.358 ± 0.174	2.129 ± 0.173
Parameter estimate	0.023 ± 0.056	-0.024 ± 0.101	0.012 ± 0.009
Log(theta)	1.361 ± 0.360	1.352 ± 0.361	1.424 ± 0.370
<i>Zero component</i>			
(intercept)	12.374 ± 1.479	1.291 ± 0.276	2.993 ± 0.253
Parameter estimate	-0.879 ± 0.124	0.658 ± 0.144	-0.034 ± 0.012
df	5	5	5
Log L	-250.9	-271.0	-277.4
LRT Chisq	62.325	22.164	9.426
P	<0.001	<0.001	0.009

Table 2

AIC and ΔAIC values for binomial logistic regression models of panting response for the main effects of Temp (mean ambient temperature), Wind (mean wind speed), and SunE (sun exposure index) and territory ID as a random factor; and number of estimated parameters (K). The null model is an intercept only model. The best supported models are highlighted in bold.

model	K	AIC	ΔAIC
Temp + Wind + SunE	5	236.2	0
Temp + Wind	4	237.8	1.6
Temp	3	239.4	3.2
Temp + SunE	4	240.8	4.6
Wind + SunE	4	259.3	23.1
Wind	3	278.2	42.0
SunE	3	285.0	48.8
Intercept only	2	292.2	56.0

mean $11.6\text{ }^{\circ}\text{C}$ [$9.8\text{--}12.7\text{ }^{\circ}\text{C}$] across years. At the study site temperatures were greater than the panting threshold of $9.2\text{ }^{\circ}\text{C}$ for 61.8% of the time, including multiple nights (SM Fig. 3). While instances of panting during the observations were relatively few, the cumulative impact of panting over the incubation period, and its likely indication that the UCT has been exceeded, the cost of thermoregulation could have consequences for the overall energy budget during breeding. Furthermore, the

pressure of increased evaporative water loss is expected in connection with elevated temperatures and panting behaviour (Song and Beissinger 2020).

We found that the panting response was modulated in a predictable direction by both wind and solar irradiance: panting decreased with increasing wind speed and increased with sun exposure. Furthermore, we reported that panting was no longer observed at wind speeds above 3.5 ms^{-1} , which is equivalent to a gentle breeze (Beaufort Wind Scale) and generally typical of coastal marine habitats (mean June wind speed 5.1 ms^{-1} ; DMI (2023)). The relationship to sun exposure in our study was the smallest in magnitude with limited statistical support, yet indicated a significant positive slope, corroborating other studies (Lustick et al., 1978; Olin et al., 2023). The response to all three environmental variables tested were consistent with heat transfer mechanisms expected to impact a bird's body temperature. Although we acknowledge that some inherent correlation exists between the three weather variables which poses difficulties in attributing the relative importance of each driver, the panting response can be attributed to the physiological processes governing thermoregulation (Lustick 1984).

The UCT for a larger seabird, the herring gull (*Larus argentatus*), was determined to be $30\text{ }^{\circ}\text{C}$ under controlled conditions, but similarly to our study, panting was initiated at much lower temperatures, between 5 and $12\text{ }^{\circ}\text{C}$ under direct sunshine while birds were incubating (Lustick et al., 1978). Common guillemots (*Uria aalge*) initiated panting at ca. $15\text{--}22\text{ }^{\circ}\text{C}$ under full sun conditions but around $10\text{ }^{\circ}\text{C}$ higher in the shade (Olin et al., 2023). In controlled conditions, Brünnich's guillemot (*Uria lomvia*) initiated panting at $26\text{ }^{\circ}\text{C}$ (Choy et al., 2021), but observations in the wild indicate deleterious thermal stress in this species occurs at much lower temperatures (Gaston and Elliott 2013): there is an apparent sizeable mismatch between controlled and field conditions. Nevertheless, Arctic skuas initiate panting at relatively low temperatures compared to other Arctic species of similar body size.

Long-term monitoring of breeding success in Arctic skua colonies on the Faroe Islands (unpublished data & Santos (2018)) revealed years of total or near-total failure. This study indicated a potential cumulative energetic cost over the breeding season. We speculate that local thermal effects, and associated water balance and energetic costs, on the warmer days of the breeding season, may be a potential mechanism that impacts productivity by reduced investment in reproduction. In combination with anticipated bottom-up impact of reduced food availability (Hátún et al., 2021), low productivity could contribute to the observed population declines. There is a clear rationale for studying climate change in the Arctic region in order to gain insights into what may be expected in seabird species elsewhere.

We found a potential energetic cost from the birds' response to their thermal environment through panting at higher temperatures. This may

lead to a carry-over effect on the successful development of the embryo through, for example, increasing parental foraging to offset the increased metabolic costs. Our study did not yield any evidence of behavioural responses to increased temperatures such as the cessation of incubation or abandoning the nest/territory completely. We found no evidence that the rate of interrupted incubation was influenced, either directly or indirectly, by weather conditions. Similar to (Lustick et al., 1978) we report that no instances of panting occurred when the focal bird was not incubating. Even simply standing up can allow birds to lose heat rapidly from the legs; as such, this behavioural signal may not be expected to be proportional to the ambient temperature. Furthermore, birds can utilise convective, conductive and radiative heat loss strategies, in advance of panting or leaving the nest, that are challenging to monitor in the field (Scanes 2015). As such it is possible that cessation of incubation response is not detected within the limitations of the model (including an effect of panting modulating this behavioural response), or this behavioural response is not yet evident in the narrow and relatively low range of temperatures encountered during our study, despite conditions being sufficient to elicit a panting response. Olin et al. (2023) reported that in common guillemots the non-incubating partner spent less time in attendance as temperatures increased, and at around 25 °C birds began to temporarily abandon the egg. For great skuas (*Stercorarius skua*), Oswald et al. (2008) reported a negative relationship between the mean number of birds on territory and temperature, and a positive relationship between the number of birds bathing and temperature over the course of the breeding season; and that as temperature began to exceed *ca.* $T_a = 14$ °C the probability of temporary territory desertion increased to 10%. However, Gaston & Elliott (2013) reported that, in extreme cases, incubating Brünnich's guillemots can die during incubation when exposed to full solar irradiance in daily maximum temperatures of only 16 °C when water loss is exacerbated by mosquito parasitism. In our study, either a critical temperature was not reached or, that while Arctic skuas may interrupt incubation briefly, they will not desert their clutch due to temperature, even when under some degree of thermal stress.

Arctic skuas are long distance migrants, breeding in the Arctic and subarctic and wintering in tropical and subtropical waters (van Bemelen et al., 2024); this trait suggests a need for rapid acclimatisation to extremely disparate climates. Such seasonal variation in thermoregulatory behaviours and heat exchange (Zuluaga and Danner 2023), or metabolic rates (Wu et al., 2015) have been reported in passerines resident in temperate climates. To observe birds panting in the North Atlantic suggests a profound influence of marine conditions on thermoregulatory capabilities for this species throughout the annual cycle, low phenotypic flexibility to facilitate homeothermy, and highlights the constraints associated with breeding, in particular, egg incubation. As seabirds possess morphological adaptations of insulating feathers and fat, they are likely to be better able to tolerate low temperatures rather than heat (Lustick 1984). Furthermore, the high thermal conductivity of water is associated with a critical thermal stress, considering the extended period that seabirds spend almost exclusively pelagic during the non-breeding season (O'Hanlon et al., 2024). However, in addition to overall warming air temperatures, an increase in the frequency and intensity of marine heatwaves due to climate change is predicted (IPCC 2015; Perkins-Kirkpatrick and Lewis 2020). The acute effects of heatwaves (marine and atmospheric) are expected to be amplified in regions where the climate is inextricably linked to the marine environment (Perkins-Kirkpatrick and Lewis 2020) and in species, such as seabirds, that rely on both terrestrial and marine ecosystems during the breeding period. In conjunction with the indirect effects of marine heatwaves which have been shown to impact lower trophic-level prey abundance, size and quality (Portner and Farrell 2008), these events may ultimately lead to a northward contraction of the Arctic skuas breeding range (see Gilg et al., 2012) or changes in breeding phenology (see Durant et al., 2007). A changing thermal environment is thought to disproportionately affect organisms with a small TNZ, long generation times, and low

genetic diversity (Portner and Farrell 2008) such as the philopatric Arctic skua populations of the north Atlantic (Furness 1987; Hammer et al., 2014).

The gulf between the surprisingly low temperature range under which our study species initiates energetically costly thermoregulatory behaviour (in advance of risky behavioural modifications) and the temperatures reported for panting initiation in seabirds under controlled laboratory conditions, highlights the importance of thermal physiology studies to be conducted under environmentally rich wild settings. The variation may be taxa specific and further studies are needed to elucidate species-specific responses. The miniaturisation of biologging technologies is one such avenue which could permit the quantitative assessment of energetic costs in the field (e.g., heart rate; tri-axial accelerometer derived activity (Bograd et al., 2010)). An important knowledge gap is that we don't yet know how birds respond when temperatures rise beyond those experienced in the study (Flack et al., 2022). Understanding fundamental metabolic processes, together with the nature of the temperature variation experienced (i.e., gradual increase of temperatures overall or an increase in number of heatwaves) is necessary to better inform predictions at a population level (Gallagher et al., 2021). We argue that a better knowledge of thermal capabilities of Arctic species not only allows us to better understand the challenges facing temperate and tropical species in the future, but also responses can be used to model predictions under further changes in the thermal environment. This framework can then be used to assess species persistence and inform conservation management practices across the Polar regions.

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CRediT authorship contribution statement

Katherine R.S. Snell: Writing – review & editing, Writing – original draft, Visualization, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Jón Aldará:** Writing – original draft, Investigation, Data curation. **Sjúrður Hammer:** Writing – review & editing, Resources, Methodology, Conceptualization. **Kasper Thorup:** Writing – review & editing, Supervision, Funding acquisition, Formal analysis.

Declaration of competing interest

The authors have no competing interests to declare.

Data availability

The raw data required to reproduce the above findings are available to download from https://github.com/krssnell/Skua_ThermalTolerance.

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Appendix A. Supplementary data

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