

Research



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Warming in the land of the midnight sun: breeding birds may suffer greater heat stress at high- versus low-Arctic sites

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Rising global temperatures are expected to increase reproductive costs for wildlife as greater thermoregulatory demands interfere with reproductive activities. However, predicting the temperatures at which reproductive performance is negatively impacted remains a significant hurdle. Using a thermoregulatory polygon approach, we derived a reproductive threshold temperature for an Arctic songbird—the snow bunting (*Plectrophenax nivalis*). We defined this threshold as the temperature at which individuals must reduce activity to suboptimal levels (i.e. less than four-time basal metabolic rate) to sustain nestling provisioning and avoid overheating. We then compared this threshold to operative temperatures recorded at high (82° N) and low (64° N) Arctic sites to estimate how heat constraints translate into site-specific impacts on sustained activity level. We predict buntings would become behaviourally constrained at operative temperatures above 11.7°C, whereupon they must reduce provisioning rates to avoid overheating. Low-Arctic sites had larger fluctuations in solar radiation, consistently producing daily periods when operative temperatures exceeded 11.7°C. However, high-latitude birds faced entire, consecutive days when parents would be unable to sustain required provisioning rates. These data indicate that Arctic warming is probably already disrupting the breeding performance of cold-specialist birds and suggests counterintuitive and severe negative impacts of warming at higher latitude breeding locations.

1. Introduction

Animals frequently experience life-history stages that demand significant increases in their sustained rate of energy expenditure [1–3]. In an era of rapid climate change that is impacting species and ecosystems worldwide [4], understanding energy expenditure limits and their causes is paramount for predicting an organisms response to rising global temperatures [5]. Historically, energetic limits among endotherms have been attributed to intrinsic

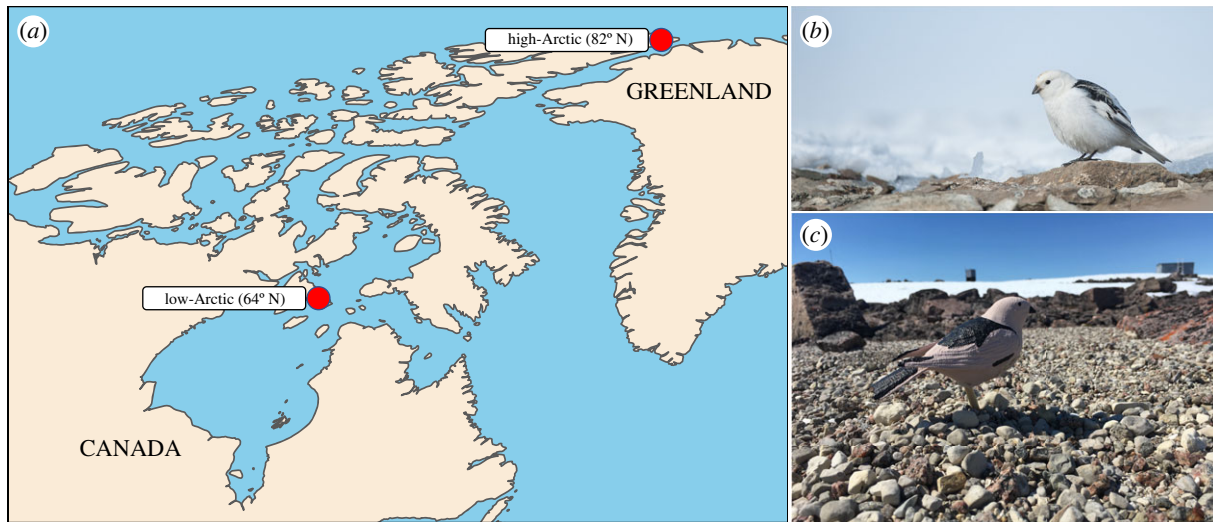


Figure 1. (a) The location of the low-Arctic and high-Arctic study sites examining thermal tolerance in snow buntings (*Plectrophenax nivalis*). (b) A snow bunting in the high-Arctic (photo: F. Vézina). (c) A three-dimensional printed model in the low-Arctic (photo: O.P. Love). (Online version in colour.)

physiological factors (central limitation hypothesis [6]) or constraints in the metabolic capacity of specific peripheral tissues (peripheral limitation hypothesis [1]). Recently, Speakman & Król [7–9] proposed an alternative hypothesis, termed the heat dissipation limit (HDL) theory, which contends that the maximal rate of energy expenditure for an endothermic animal is limited by physiological factors governing heat dissipation capacity and the consequent avoidance of lethal body temperatures. Importantly, whereas the peripheral limitation hypothesis argues that energetic constraints may act on a range of tissues and organs, the HDL theory proposes a universal constraint in the form of heat dissipation and provides a mechanistic link between an animal's physiological capacity to maximize energy expenditure with the interplay between heat dissipation and ambient temperature.

Despite the conceptual gains that the HDL theory has provided in linking heat dissipation capacity with energetic expenditure, our ability to predict the ambient temperatures that will constrain an animal's performance (i.e. sustained rate of energy expenditure) remains a major impediment to assessing species vulnerability to climate change [10]. Although several studies have reported threshold temperatures above which sustained activity and/or reproductive performance were compromised (see [11] and references therein), these studies derived threshold values from *post hoc* analyses on behavioural observations and are therefore not predictive by design. Recently, Rezende & Bacigalupe [12] proposed a predictive analytical tool—the thermoregulatory polygon—for estimating the dimensional space in which thermoregulation is possible given an animal's combined rate of energy expenditure and the environmental temperatures it is operating within. Thermoregulatory polygons are built from commonly measured physiological variables (basal and maximal metabolic rate, and minimum and maximum thermal conductance) to delineate the boundaries in which heat production and dissipation are balanced [12]. Thus, thermoregulatory polygons can help estimate responses to further warming by integrating concepts of the HDL theory to predict the ambient temperatures over which endothermic animals can sustain activity and avoid overheating. Surprisingly, despite their potential as a predictive tool, to our knowledge, only one study has applied thermoregulatory

polygons, using them to predict the energetic consequences of activity time in nocturnal and diurnal mammals [5].

Among endotherms, birds are expected to be particularly sensitive to increasing environmental temperatures [13,14]. The offspring-rearing period for parents with dependent young requires substantial increases in sustained work effort, with adults performing at rates often reported between 4 and 6 times their basal metabolic rate (BMR) [2,3,6], although lower rates can also be observed depending on conditions ([15,16], see [17] for a discussion on this topic). Any excess heat generated as a by-product from foraging and provisioning must ultimately be dissipated, or birds risk overheating. Indeed, birds often decrease activity on days with warmer ambient temperatures, probably a thermoregulatory response to avoid heat stress [18,19]. When a bird's capacity to dissipate heat is increased (e.g. by experimentally removing insulative feathers), provisioning adults can sustain higher levels of activity and invest more in both their current and future reproductive efforts [20–23]. Thus, reproductive performance can be constrained by a bird's capacity to dissipate body heat produced during essential breeding activities, suggesting that increasing environmental temperatures could significantly impact reproductive success.

Here, we apply a thermoregulatory polygon to snow buntings (*Plectrophenax nivalis*; figure 1b), an Arctic-breeding songbird, to investigate how environmental temperature affects the interaction between thermoregulation and sustained energy expenditure. Applying thermoregulatory polygons to Arctic endotherms is pertinent and valuable for predicting how increasing temperatures under climate change will impact certain life-history stages via heat constraints on behaviour. Many Arctic animals are cold specialists and have evolved physiological adaptations for minimizing heat loss [24,25]. Consequently, high-latitude breeding species are probably vulnerable to even moderate increases in ambient temperature [26–29]; an alarming fact given that the Arctic has warmed faster than the global average and is expected to continue outpacing the global average over the twenty-first century [4]. Additionally, O'Connor *et al.* [26] recently showed that buntings become heat-stressed at moderate air temperatures and have an extremely limited evaporative cooling capacity. Consequently, highly active,

breeding buntings exposed to constant solar radiation and modest rises in air temperature would be more likely to depend on behavioural thermoregulatory strategies (e.g. reducing provisioning effort) rather than physiological mechanisms (e.g. sustained increases in evaporate water loss rates) to dissipate body heat and avoid overheating.

Our goal was to estimate how sensitive buntings' performance may be to increasing Arctic temperatures, given their limited heat dissipation capacity. We first used thermal physiological data to construct a thermoregulatory polygon and predict the threshold temperatures at which sustainable performance would be expected to decline in buntings maintaining thermal balance (i.e. heat produced = heat dissipated). We then compared the thermoregulatory polygon prediction to operative and air temperatures measured in the field at two breeding sites separated by 18° of latitude, representing the general southern and northern limits of this species breeding range, to evaluate how heat constraints on bunting performance (i) differed between a low- and high-Arctic region, and (ii) could translate into site-specific impacts on reproductive performance and success.

2. Material and methods

(a) Operative and air temperature measurements

We measured operative (T_e) and air (T_a) temperatures during the bunting breeding period at two sites in northern Canada representing the low-Arctic (East Bay Island; 64°01' N, 81°47' W) and high-Arctic (Alert; 82°30' N, 62°20' W; figure 1a). Operative temperature represents the temperature of the thermal environment as perceived by an individual and integrates the physical properties of the animal with the thermal properties of the local environment [30]. To measure T_e perceived by buntings at our two sites, we used three-dimensional-printed, hollow plastic bird models (hereafter three-dimensional models; [31,32]; figure 1c). We printed the three-dimensional models to match the size and shape of an adult bunting (see the electronic supplementary material, figure S1 in appendix S1). Additionally, we painted the three-dimensional models to match the spectral properties of male buntings in breeding plumage. We focused on males given their simplified monochromatic breeding plumage (figure 1b) [33] and because males actively provision offspring at similar rates to females [34]. We used a spectrophotometer (Ocean Optics Jaz spectrometer) to measure the spectra of the black ($n = 16$ birds) and white ($n = 27$ birds) feather regions of male buntings. We used the *pavo* package in R [35] to convert the spectra wavelengths to a red: green: blue (R:G:B) colour combination. We then used an R:G:B-to-paint converter (<https://www.e-paint.co.uk/convert-rgb.asp>) to acquire a paint that best matched the R:G:B colour combination of male bunting feathers. We opted to paint the three-dimensional models instead of placing the skin and plumage of a male bunting over the models as this optimized our experimental design by allowing us to record T_e in numerous models simultaneously across a broader geographical area [36]. Additionally, multiple studies (e.g. [37,38]) suggest that rough approximations of the study animal can be adequate for estimating operative temperature, and therefore, we felt comfortable using numerous painted operative temperature models over a few models covered with the feathers and skin of a male bunting.

We measured the internal temperature of each three-dimensional model by placing a temperature logger in the centre of each model. At the high-Arctic site, we drilled a hole in the belly and secured an iButton (model DS1921G-F5, Maxim Integrated, San Jose, CA USA; resolution = 0.5°C) in the

approximate centre (electronic supplementary material, figures S2 and S3 in appendix S1) by gluing it to the end of a wooden dowel surrounded by a rubber stopper, creating an airtight seal around the drill-hole (electronic supplementary material, figure S4 in appendix S1). At the low-Arctic site, models were similarly set up except for using Hobo data loggers (Pendant model, MX2201, Onset Inc., Bourne, MA USA; resolution = 0.1°C) instead of iButtons, which we secured with silicone caulking. At both sites, the three-dimensional-printed models were secured to a wooden plank by gluing a wooden dowel to a notch in the three-dimensional model (electronic supplementary material, figures S3 and S4 in appendix S1). We cut the wooden dowels to approximate the height of a standing bunting. We covered each plank in the field using the substrate beneath the models to mimic the thermal properties of buntings' natural environment (electronic supplementary material, figure S5 in appendix S1).

At each site, we deployed three-dimensional models within representative breeding territories and across naturally occurring habitats to adequately capture the thermal heterogeneity experienced by buntings. In the high-Arctic, we deployed 68 three-dimensional models and recorded T_e every 5 min from 22 May to 7 September 2019. Models were deployed over six separate periods, each lasting approximately 7 days (owing to iButton memory limitations). After 7 days, we downloaded the T_e data and redeployed the three-dimensional models to a new location. In the low-Arctic, we deployed 13 three-dimensional models and recorded T_e continuously from 11 June to 19 July 2019 at 2 min intervals.

At both study sites, we collected T_a data to compare against operative temperatures. In the high-Arctic, meteorological data was measured at the National Oceanic and Atmospheric Administration's (NOAA) broadband radiation station located adjacent to the Global Atmospheric Watch Observatory (82°28' N, 62°30' W). These data are 1 min averages of T_a obtained at a height of 3 m above the ground using an aspirated Vaisala HMP-235 (PT100 sensor). In the low-Arctic, we collected T_a values every 30 min from six Kestrel weather meters (model 5500, Boothwyn, PA, USA) placed 2–3 m above ground level at separate locations across the study site.

(b) Thermoregulatory polygon parameters and construction

We calculated the BMR ($n = 28$ birds), minimum wet thermal conductance (C_{\min} ; $n = 20$ birds) and maximum dry thermal conductance (C_{\max} ; $n = 21$ birds) using physiological data collected on a wild population of buntings at our high-Arctic site from 2 June to 25 July 2018. All physiological data were derived from previously published research [26,39] approved by the animal care committee of the Université du Québec à Rimouski (CPA-71-17-194, CPA-54-13-130 and CPA-71-17-195) and conducted under scientific (NUN-SCI-15-05 and SC-48) and banding permits (10889 and 10889E) from Environment and Climate Change Canada. Information on gas analysers, experimental protocol, body and air temperature measurements, and equations used for calculating metabolic rates are described in detail in Le Pogam *et al.* [39–41] and O'Connor *et al.* [26]. Briefly, we measured BMR overnight on fasted individuals resting inside a darkened metabolic chamber at thermoneutral temperatures (mean $T_a = 26.2 \pm 0.8^\circ\text{C}$; note, $T_a = T_e$ inside metabolic chambers [30]). For C_{\min} , we measured metabolic rates on individuals at a constant T_a below their lower critical temperature of 10°C ([24]; mean $T_a = -19.0 \pm 1.8^\circ\text{C}$). We did not measure rates of evaporative water loss during our C_{\min} runs and therefore for each bird we calculated minimum wet thermal conductance as

$$C_{\min} = \frac{MR}{T_b - T_a} \quad (2.1)$$

where MR represents metabolic rate in Watts, and T_b and T_a are the mean body and air temperatures, respectively. At T_a below the lower critical temperature, evaporative heat loss is minimal and thus its inclusion has little influence on C_{\min} [42]. During metabolic measurements for C_{\min} , we measured T_b at the start and end of each run and used the mean value for our calculations.

We determined C_{\max} by exposing birds to gradually increasing T_a [26]. We only included birds that tolerated T_a above 31.5°C, representing the mean T_a minus the s.d. at which buntings started panting [26], as we assumed that birds that had initiated panting had reached their C_{\max} [43]. This resulted in the removal of one bird from the dataset. At higher T_a , evaporative heat loss becomes significant and must be accounted for in the calculation of C_{\max} [42]. We thus calculated maximum dry thermal conductance for each bird as

$$C_{\max} = \frac{(MR - EHL)}{(T_b - T_a)}, \quad (2.2)$$

where EHL represents evaporative heat loss measured during respirometry trials [26]. During C_{\max} experiments, we measured T_b continuously and therefore could calculate an average T_b over the same 5 min time window that metabolic rates were calculated [26].

To build the thermoregulatory polygon, we calculated a combined mean across birds for each parameter (i.e. BMR, C_{\min} , C_{\max} and T_b). The BMR mean became the bottom boundary of the thermoregulatory polygon. The C_{\min} and C_{\max} means became the slopes of the left and right boundaries, respectively. We calculated the y-intercepts for the C_{\min} and C_{\max} slopes using the equation:

$$MR = C(T_a) + b, \quad (2.3)$$

where C represents the combined C_{\min} or C_{\max} mean across birds and b is the y-intercept. We assumed $T_a = T_b$ when $MR = 0$ [42] and used the combined T_b mean across birds during C_{\min} (41.0 ± 0.4°C) and C_{\max} (42.6 ± 0.7°C) measurements.

(c) Estimating sustainable performance in the high-Arctic and low-Arctic

We conducted all analyses in R v. 4.0.4 [44]. In the high-Arctic, we recorded a total of 843 773 individual T_e values from 68 three-dimensional models and a total of 107 092 T_a values. In the low-Arctic, we recorded 405 000 individual T_e values from 13 models and a total of 10 803 T_a values. We used these raw temperature data to create a time series of T_e and T_a for each site averaged at 1 h intervals using the *timeAverage* function in the *openair* package [45].

The discontinuous sampling protocol in the high-Arctic (e.g. downloading data and redeploying models) resulted in 643 1 h gaps in our T_e time series. To estimate the percentage of time on a given day that buntings would have been behaviourally constrained from heat (see below), it was necessary to fill these gaps. We filled the T_e gaps by fitting an artificial neural network [46] with the *neuralnet* package [47] to predict T_e based on seven radiative and meteorological variables observed at the NOAA broadband radiation station (see the electronic supplementary material, appendix S2 for details). The neural network predicted hourly operative temperatures with an average mean square error of 1.8°C (range = 1.2 to 2.7°C).

We used the C_{\max} slope to estimate the maximum sustainable energy expenditure of buntings maintaining thermal balance under either T_a or T_e . As the provisioning period is one of the most energetically expensive life-history stages for birds [3], we focused on the maximal sustainable performance possible for buntings during this period. At the high-Arctic site, adult

buntings are typically observed provisioning from 4 July to 25 July (A. Le Pogam 2016-2019, personal observations) and at the low-Arctic site from 3 July to 24 July [33,34]. We thus used these respective periods to represent the typical provisioning period at each site. We defined performance as a multiple of BMR and assumed that four-time BMR is the minimum sustainable performance required for adult buntings to adequately provision nestlings [2,3]. Although lower levels of daily energy expenditure during provisioning have been reported for other species [17], we believe four-time BMR to be a plausible minimum sustainable performance requirement for snow buntings given that: (i) they produce a single clutch during the breeding season, (ii) they have a very short-time window for breeding, and (iii) nestlings grow fast and have a short growth period (approx. 13 days) for a passerine of their size [48]. Therefore, we defined four-time BMR as the energetic threshold for 'optimal performance', and we calculated the percentage of time on a given day that buntings could work at either optimal (greater than or equal to four-time BMR) or suboptimal (less than four-time BMR) performance levels based on either T_e or T_a . However, we did include a continuous colour scheme into our figures to illustrate the discrepancy around our four-time BMR threshold value, thereby introducing a gradual transition into a darker red zone representing a more serious impact on sustainable performance. Lastly, we assumed buntings rested and reduced provisioning rates for 3 h a day [49], and we therefore only used temperature values measured between 01.00 and 22.00 when calculating the daily percentage of time that buntings could work at optimal or suboptimal performance levels.

3. Results

(a) Thermoregulatory polygon

All values reported are mean ± s.d. The mean BMR of buntings was 0.564 ± 0.076 W. Mean thermal conductance varied threefold, with a calculated minimum wet thermal conductance of 0.023 ± 0.005 W/°C and a maximum dry thermal conductance of 0.073 ± 0.023 W/°C (figure 2a). The thermoregulatory polygon bounded by these parameters predicted that buntings could maintain thermal balance and sustain optimal performance (i.e. greater than four-time BMR) at operative temperatures (T_e) of up to 11.7°C (figure 2b). Once T_e exceeds 11.7°C, we expect buntings to become behaviourally constrained by heat and forced to perform at suboptimal levels to avoid overheating.

(b) Estimated sustainable performance in the high-Arctic and low-Arctic

At the high-Arctic site, T_e and air temperatures (T_a) increased steadily from the beginning of the breeding period until peaking during the nestling-provisioning period and then gradually declined towards the post-fledging period (electronic supplementary material, figure S1a in appendix S3). Operative temperatures experienced by buntings frequently exceeded T_a , and on average were 3.5 ± 3.1°C warmer (range of differences between T_e and T_a = -4.9°C to 14.5°C; electronic supplementary material, figure S1b in appendix S3).

At the high-Arctic site, T_e , but not T_a , exceeded the predicted thermoregulatory polygon threshold value of 11.7°C before 5 July (figure 3a). However, from 5 July to 5 August, both T_a and T_e periodically exceeded 11.7°C (figure 3a), suggesting that buntings would have had to regularly perform at suboptimal levels below four-time BMR during this

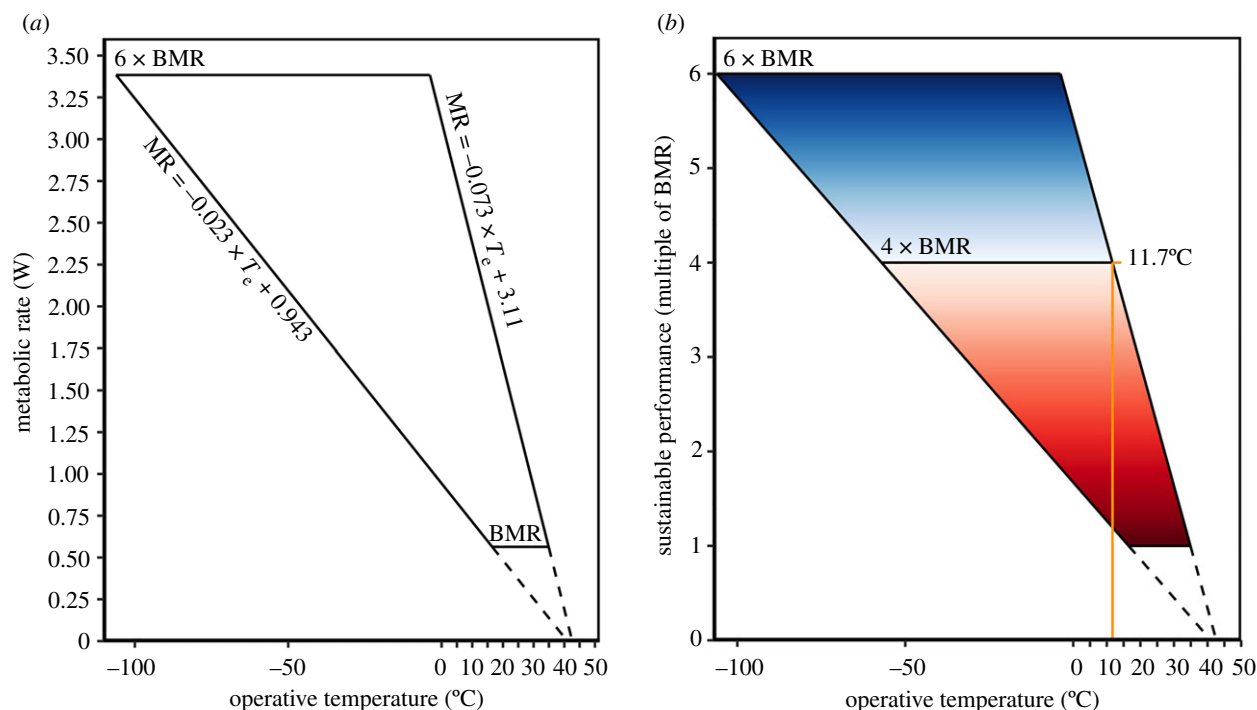


Figure 2. (a) Snow bunting (*Plectrophenax nivalis*) thermoregulatory polygon bounded by BMR (0.564 W), minimum wet thermal conductance (0.023 W/°C), maximum dry thermal conductance (0.073 W/°C) and maximal sustained metabolic rate set at 6 × BMR. (b) Sustainable performance (expressed as a multiple of BMR) is possible for buntings under thermal balance. At operative temperatures below 11.7°C, buntings can maintain thermal balance and sustain optimal performance (i.e. performance $\geq 4 \times$ BMR). As operative temperatures increase, buntings must reduce activity, and concomitantly metabolic rate, to maintain thermal balance, resulting in a suboptimal performance (i.e. performance less than 4 × BMR). Optimal performance is defined as the sustained level of work required by adults to sufficiently rear nestlings. The continuous colour scheme signifies the transition into more detrimental impacts on sustainable performance at higher temperatures (i.e. dark red zone). The black dashed lines are the extrapolation of the minimum and maximum thermal conductance slopes to the average body temperature recorded during laboratory measurements. (Online version in colour.)

period. Within the nestling-provisioning period at the high-latitude site (i.e. 4 July–25 July), buntings experienced multi-day periods where they could have either performed at optimal levels for their entire active period (i.e. 01.00–22.00) or they would have been heat constrained and forced to work at suboptimal levels (figure 4a). For example, under T_e , there were two periods of consecutive days (9–11 July and 19–22 July) where we predict that buntings could have worked at optimal performance levels for their entire active period (figure 4a). However, there were two periods of consecutive days (6–8 July and 13–17 July) when T_e exceeded 11.7°C for their entire active period, and we predict that buntings would have had to reduce their provisioning rates to lower metabolic heat production and avoid overheating. From 13 to 19 July, buntings experienced only 5 h with T_e that we predict allowed them to both maintain thermal balance and sustain a performance level greater than or equal to four-time BMR. Overall, under T_e at the high-Arctic site, the percentage of time each day that buntings would have been behaviourally constrained from heat during their active period ranged from a minimum of 19% (4 h) to a maximum of 100% (21 h; figure 4a).

At the low-Arctic site, average hourly temperatures were relatively consistent across the study period (electronic supplementary material, figure S2a in appendix S3). The overall mean difference between T_e and T_a was 4.0 ± 4.1 (range = -2.7°C to 15.5°C ; electronic supplementary material, figure S2b in appendix S3). In contrast with the high-Arctic site, where both T_e and T_a exceeded the threshold temperature of 11.7°C, only T_e at the low-Arctic site consistently placed

a heat constraint on buntings' sustainable performance (figure 3b). For example, during the typical nestling-provisioning period in the low-Arctic (i.e. 3 July–24 July), we predict that buntings would have been behaviourally constrained on just 4 days under T_a , whereas T_e values suggest that bunting performance would have been constrained to some degree on 15 out of 17 days (figure 4b). Furthermore, unlike the high-Arctic birds, we predict buntings at the low-Arctic site would not be forced to perform at suboptimal levels for their entire active period, but would instead be forced to alter performance for a portion of each day (figure 4b). Overall, under T_e at the low-Arctic site, the percentage of time that buntings would have been behaviourally constrained from heat on a given day during their active period ranged from a minimum of 5% (1 h) to a maximum of 67% (14 h; figure 4b).

4. Discussion

(a) Using the thermoregulatory polygon to predict thermal constraints

The HDL theory postulates that an animal's maximum sustained energy expenditure scales with its capacity to dissipate body heat [8]. Many factors influence an animal's thermoregulatory ability, including BMR and thermal conductance [50,51]. Given buntings' BMR and maximum dry thermal conductance, the thermoregulatory polygon predicts that at operative temperatures above 11.7°C, snow buntings

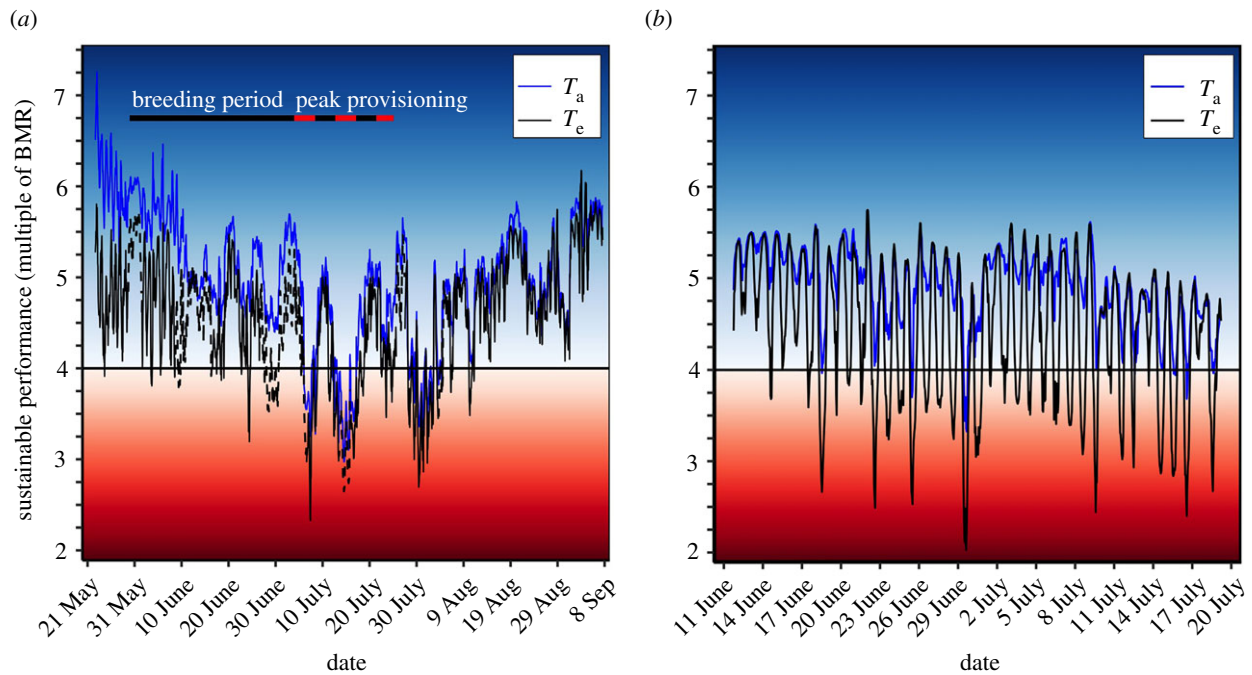


Figure 3. Estimated sustainable performance possible for snow buntings (*Plectrophenax nivalis*) maintaining thermal balance at a (a) high-Arctic and (b) low-Arctic breeding site. The transition into the blue zone represents the times when average hourly operative (T_e) or air (T_a) temperature was below the thermoregulatory polygon threshold temperature of 11.7°C , predicting that buntings could sustain performance levels \geq four-time BMR without altering behaviour. The transition into the red zone represents the times when T_e or T_a exceeded 11.7°C , predicting that buntings would be required to reduce their provisioning behaviour and work below four-time BMR to limit heat production and avoid overheating. Note that the darker the blue colour, the colder the recorded operative temperatures and the darker the red colour, the hotter the operative temperatures. The dashed black lines in (a) represent the predicted T_e values from the artificial neural network (see methods for details). (Online version in colour.)

cannot maintain thermal balance and sustain activity at optimal expenditure rates of four-time BMR. Consequently, when operative temperature exceeds the threshold temperature for extended periods, we would expect to observe a slower growth rate in nestlings, prolonged breeding period and potentially reduced fledging mass as adults reduce provisioning rates to maintain thermal balance [52,53]. Supporting a temperature dependence on provisioning rates among buntings, Hoset *et al.* [54] reported lower parental feeding rates during periods when air temperatures were high (the study did not measure operative temperatures), even though the range of air temperatures was small (e.g. $0\text{--}5^\circ\text{C}$). Similarly, Cunningham *et al.* [55] reported lower provisioning rates at higher ambient temperatures in common fiscals (*Lanius collaris*) and that fledglings were significantly lighter when maximum air temperature frequently exceeded 33°C . The comparatively low-threshold temperature for buntings (11.7°C) probably stems from their physiological adaptations for life in the cold [41]. Consequently, snow buntings' cold specialization appears to come at the cost of not being able to adequately dissipate heat through increases in maximum thermal conductance at even moderate operative temperatures.

Because the thermoregulatory polygon boundaries are set by the thermal conductance of the animal, they represent the space in which an animal can balance heat loss and gain through non-evaporative pathways. Theoretically, an animal could maintain thermal balance and sustain a high rate of energy expenditure outside its thermoregulatory polygon by continuously dissipating body heat evaporatively. However, O'Connor *et al.* [26] recently showed that the evaporative cooling capacity of buntings is extremely limited,

with most birds unable to evaporatively shed an amount of heat equivalent to their metabolic heat production. Therefore, it is unlikely that snow buntings can rely on evaporative cooling for prolonged periods to sustain activity outside their thermoregulatory polygon limits and, instead, will be highly dependent on behavioural thermoregulation.

(b) Site-specific impacts of thermal constraints on breeding performance and success

Solar radiation is a major driving force of operative temperature and can vary by time of day, year or geographical location [56,57]. Our two sites represent the general southern and northern breeding limits for Arctic-breeding snow bunting populations in Canada [49] and are separated by approximately 18° latitude. This difference leads to distinct amounts of solar radiation reaching the Earth's surface [56], probably producing the significant differences observed in the duration and frequency that operative temperature exceeded the predicted threshold temperature. For example, during the peak nestling-provisioning period, buntings at the high-Arctic site were predicted to frequently experience consecutive days where they would not be able to perform at four times their BMR. By contrast, buntings in the low-Arctic were predicted to experience shorter, but more consistent heat constraints on provisioning activity almost every day. Given that snow bunting nestlings have some of the highest recorded growth rates of any passerine ($11\text{--}13\%$ of adult body mass per day; [48]), these latitudinal differences in constraints suggest that warming will produce different impacts on provisioning behaviour, offspring growth and survival in different populations. For instance, lower latitude

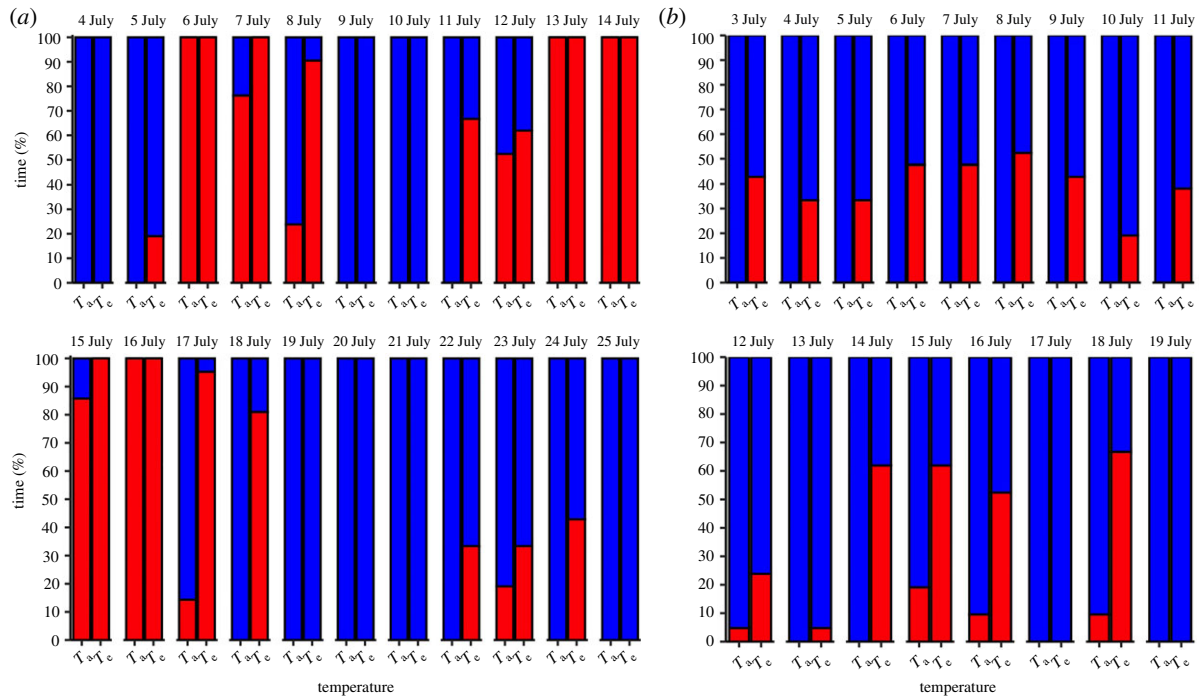


Figure 4. The daily percentage of time during their active period (01.00–22.00) when snow buntings (*Plectrophenax nivalis*) at a (a) high-Arctic and (b) low-Arctic breeding site could either sustain an optimal performance level (blue region) or forced to work at suboptimal performance levels (red region) based on either operative (T_e) or air (T_a) temperature recordings. Optimal and suboptimal performance is defined as the periods when buntings could sustain levels of work \geq four-time BMR or less than four-time BMR, respectively, while maintaining thermal balance. (Online version in colour.)

breeding birds could possibly make up for reduced provisioning opportunities each day by adjusting their activity budget; working harder during the cooler periods to counteract overheating risks during warmer periods [5]. Indeed, under identical heat loads, Tapper *et al.* [23] observed higher feeding rates in wild female tree swallows (*Tachycineta bicolor*) that had their ventral feathers clipped to experimentally increase heat dissipation rates relative to unclipped females. Alternatively, parents breeding at lower latitudes could provision growing nestlings at lower rates per day and possibly extend the developmental period of the growing young. However, this could nonetheless impose survival constraints on nestlings and fledglings given that ground-nesting songbird species have evolved rapid growth rates and shorter in-nest development periods owing to high rates of nest predation [58], as well as the short, ephemeral nature of productivity in insects required for offspring growth [59].

For higher latitude populations, the accumulation of reduced provisioning opportunities over consecutive days could impose substantial developmental costs on nestlings that may be too high for parents to overcome on cooler days. Chick provisioning in buntings typically lasts 13 days; lowering provisioning rates for 3–4 consecutive days could have major impacts on chick condition at fledging and, consequently, post-fledging survival [11,60,61]. Therefore, as rapid Arctic warming continues [4], the temperature-dependent costs on reproductive performance may be more strongly felt at higher latitudes where climatic and meteorological patterns subject individuals to unique operative temperature cycles, with above threshold temperatures potentially lasting for days at the peak of breeding activities. It is worth noting, however, that our three-dimensional models were painted to match the male colour morph and therefore represent operative temperatures perceived by male snow buntings. During the provisioning period, both

male and female buntings feed young and thus the operative temperatures experienced by females may differ from males leading to different sex constraints on performance. For instance, females lack the full dark back of male buntings and hence may experience lower operative temperatures allowing them to maintain higher provisioning rates than males. Nevertheless, under such a scenario, we would still predict negative impacts on nestling condition and fledgling success as both parents cannot adequately feed young at optimal rates.

5. Conclusion

A growing body of evidence suggests that increasing environmental temperatures associated with climate change will impose reproductive costs on birds via trade-offs between essential breeding behaviours and the need to dissipate body heat and avoid lethal body temperatures [10,11,14,21]. To date, predicting the threshold temperatures that will adversely affect breeding activity has been a limiting factor in forecasting the impacts of anthropogenic climate change on birds. Additionally, studies on how thermoregulatory demands will negatively impact breeding behaviour within birds are overwhelmingly focused on hot, arid climates while studies on Arctic birds are severely lacking.

Using a thermoregulatory polygon approach, we estimated the maximal sustained energy expenditure in an Arctic songbird maintaining thermal balance across a range of environmental temperatures at two field locations representing the southern and northern breeding limits of its breeding populations in Canada. Assuming an optimal performance level of four-time BMR [3], our findings predict that buntings will become heat constrained at operative temperatures above 11.7°C. Above this threshold, buntings

would need to reduce their maximal sustained energy expenditure and provision their offspring at suboptimal performance levels to balance heat loads and avoid overheating. Importantly, our conclusions would remain unchanged even if buntings were found to maintain lower sustained performance rates as reported in other species [17]. For example, assuming buntings operated at three-time BMR, our threshold value would rise to 19.4°C for reduced performance. Indeed, Alert has already been experiencing short periods of air temperatures above 20°C for several years, suggesting even higher levels of operative temperature. However, we acknowledge that the actual sustained working level of provisioning snow buntings remains to be measured empirically.

By examining impacts at both a low- and high-Arctic breeding site, our data reveal site-specific differences in operative temperature, probably linked to latitude and the consequential differences in available sunlight and radiative flux, culminating in site-specific patterns in the heat constraints placed on an animal's maximal sustained energy expenditure. It appears that synoptic-scale (i.e. weather-scale, 2–4 days) influences on local temperature dominate in modulating operative temperatures in the high-Arctic, whereas the diurnal cycle is the dominant factor in the low-Arctic. We also argue that intraspecific differences among bunting populations in heat tolerance may be minimal given that recent genetic evidence suggests mixing between our two study populations [62]. Additionally, recent data show comparable metabolic responses to cold in buntings from Alert before breeding and wintering buntings in eastern Québec, two populations known to breed at different locations [41]. Taken together, a thermoregulatory polygon built upon physiological parameters from our East Bay population may not significantly differ from that presented currently.

Collectively, our results indicate that while Arctic warming will expose all snow bunting populations to more periods above their threshold temperature for sustained optimal performance, high-Arctic birds will probably face greater increases in the duration and magnitude of these periods owing to the suppressed amplitude of the diurnal cycle where the sun is above the horizon continuously from early

April through to early September. The expectation then will be that high-Arctic populations will face greater downstream costs to reproductive performance, and ultimately breeding success, compared to low-Arctic populations.

Ethics. All physiological data were derived from previously published research [26,39] approved by the animal care committee of the Université du Québec à Rimouski (CPA-71-17-194, CPA-54-13-130 and CPA-71-17-195) and conducted under scientific (NUN-SCI-15-05 and SC-48) and banding permits (10889 and 10889E) from Environment and Climate Change Canada.

Data accessibility. Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.vmcvdcnctr> [63].

The data are also provided in the electronic supplementary material [64].

Authors' contributions. R.S.O.: conceptualization, data curation, formal analysis, methodology and writing—original draft; A.L.P.: investigation, writing—review and editing; K.G.Y.: investigation, writing—review and editing; O.P.L.: conceptualization, funding acquisition, methodology, writing—review and editing; C.J.C.: data curation, writing—review and editing; G.R.: investigation, writing—review and editing; F.R.: investigation, writing—review and editing; K.H.E.: conceptualization, funding acquisition, writing—review and editing; A.L.H.: conceptualization, funding acquisition, writing—review and editing; E.S.C.: writing—review and editing; H.G.G.: writing—review and editing; D.B.: writing—review and editing; A.T.: funding acquisition, writing—review and editing; F.V.: conceptualization, funding acquisition, methodology, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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