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Cold adaptation does not handicap warm tolerance in the most abundant Arctic seabird

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Abstract

Arctic birds and mammals are physiologically adapted to survive in cold environments but live in the fastest warming region on the planet. They should therefore be most threatened by climate change. We fitted a phylogenetic model of upper critical temperature (T_{UC}) in 255 bird species and determined that T_{UC} for dovekies (*Alle alle*; 22.4°C) — the most abundant seabird in the Arctic — is 8.8 °C lower than predicted for a bird of its body mass (150 g) and habitat latitude. We combined our comparative analysis with in situ physiological measurements on 36 dovekies from East Greenland and forward-projections of dovekie energy and water expenditure under different climate scenarios. Based on our analyses, we demonstrate that cold adaptation in this small Arctic seabird does not handicap acute tolerance to air temperatures up to at least 15 °C above their current maximum. We predict that climate warming will reduce the energetic costs of thermoregulation for dovekies, but their capacity to cope with rising temperatures will be constrained by water intake and salt balance. Dovekies evolved 15 million years ago, and their thermoregulatory physiology might also reflect adaptation to a wide range of paleoclimates, both substantially warmer and colder than the present-day.

Keywords Animal energetics; Dovekie; Ecophysiology; Evolutionary legacy; Global Warming; Phylogenic analyses.

Introduction

The Arctic is now warming three times as fast as the rest of the planet [1]. Yet, birds and mammals that live and breed in the Arctic exhibit physiological and morphological adaptation to survive low air and water temperatures [2, 3]. Cold adaptation in endothermic animals involves mechanisms that increase heat production and reduce heat loss, which together maintain a high and stable body temperature against a strong thermal gradient [4]. According to the current paradigm, cold adapted endotherms have limited tolerance to even moderately warming air temperatures [5, 6]. Specifically, when air temperature exceeds the upper critical temperature of the thermoneutral zone, evaporative water loss must increase to dissipate excess body heat [7]. At the same time, metabolic heat production also increases as more active forms of evaporative water loss are employed to dissipate heat (e.g., gular fluttering) [8]. When air temperatures remain elevated above thermoneutrality, the cycle of increased water loss and increased heat production can lead to dehydration and hyperthermia. If this current paradigm is accurate and Arctic endotherms have limited tolerance to elevated temperatures, the physiological costs of thermoregulation could render the Arctic region too warm by the end of the century for many endemic species.

To explore how climate warming will affect Arctic endotherms, we studied the thermal physiology and bioenergetics of the dovekie (or little auk, *Alle alle*), the smallest (150 g) diving seabird in the North Atlantic, and most abundant Arctic seabird (40 – 80 million individuals, [9]), that plays a pivotal role in marine and terrestrial trophic flows [10]. We focused on the summer season, while dovekies are breeding in the high Arctic. During this phase, adults spend 54 % of their time on land in underground nest cavities or perched on rocks at the surface of the colony, and 46 % engaged in foraging trips at sea within ca.

100 km from their nests, diving to catch zooplankton within the first 20 meters of the water column [11, 12]. The breeding season is the most energetically demanding period for dovekies [12, 13].

Here, we combined physiological measurements with modelling and phylogenetic analysis to assess whether dovekies will be physiologically challenged by future projected climate scenarios in the Arctic. Dovekies live and breed in cold conditions, with air temperatures frequently around 0 °C at summer breeding grounds, and as low as -10.6°C during inter-breeding (winter) migration in the North Atlantic [13]. The only other study to experimentally examine the thermal physiology of dovekies [14] exposed birds to air temperatures from -20°C up to a maximum of 20 °C, which has since remained the only data from which to estimate the upper critical temperature for the species [15]. Based on the idea that dovekies are putatively cold adapted, combined with limited previous information on their physiological tolerance at warmer temperatures, we expected that dovekies would be poorly equipped to avoid overheating when air temperatures exceed 20 °C; a temperature regularly overshot in summer at the breeding colony we studied in East Greenland (Grémillet et al. *unpublished*).

Methods

Phylogenetic modelling

We fitted phylogenetic mixed models to existing data [15] for upper critical temperature (T_{UC}) in 255 bird species. We added to the data one estimate for T_{UC} for Wilson's storm petrel (*Oceanites oceanicus*) based on data from the literature [16]. We also updated the T_{UC} for dovekies with the observation in the present study, since the existing estimate was based on a single previous study that had too few measurements above 20 °C to reliably

estimate the inflection point at the T_{UC} ([14]; see below for a description of how we accounted for methodological differences in estimates of T_{UC}). We used the consensus tree for bird species [17] with Grafen's arbitrary branch lengths [18] to fit phylogenetic least squares models to the data for T_{UC} using the *phytools* package [19] in R version 4.1.2 [20]. In addition to the random phylogenetic structure, we fitted fixed effects of log mass and latitude. We also included information on potential sources of variation in T_{UC} estimates due to differences in methodology among studies [21]. Specifically, different studies estimated T_{UC} from respirometric data obtained across different temperature ranges, which potentially influences the precision of estimates of T_{UC}. To account for this potential source of error in T_{UC}, we used the 'data quality' categories proposed by McKechnie et al. (2017) in their examination of the primary data from the Khaliq et al. (2014) dataset. Their categories were 'Good' (i.e., an increase in metabolic rate above thermoneutrality with a clear inflection point defining T_{UC}), 'Insufficient data' (i.e., some evidence of an increase in metabolic rate above thermoneutrality, but based on measurements at too few air temperatures to reliably estimate T_{UC}), 'No T_{UC}' (i.e., no breakpoint in the data, T_{UC} taken as highest measurement temperature), or '------' (i.e., not able to assess the data). Note that McKechnie et al. categorised the previous estimate for dovekies [14] as 'Good', but based on their description of the categories, we thought that it was best defined as 'Insufficient data' due to there being too few measurements above the potential inflection point to reliably estimate $T_{UC.}$ We left all other categorisations as they appear in McKechnie et al. (2017). We included 'data quality' (which we called 'methodology') as a fixed factor (with the four levels described above) in our models. Methodology explained 2.8% of the variance in T_{UC} and the standardized effect sizes (Cohen's *d*) for each methodology category varied between 0.03

and 0.07. In other words, differences in methodology had little to neglible influence on the variance in T_{UC} relative to that associated with latitude and log mass.

Physiological measurements

We performed respirometry on individual dovekies (*Alle alle*, n = 36) captured from a breeding colony at Ukaleqarteq, East Greenland (70° 43' N, 21° 33 W) between 11 July to 8 August 2019 (during the late incubation and chick-rearing period). On each day of measurement, four breeding birds (as indicated by presence of a brood patch) were captured between 8 am and 12:30 pm GMT and mass and morphometrics were recorded at time of capture. Each bird was then kept in a cotton bag in a quiet location for 2 to 3 hours before being placed inside a 5 L plastic respirometry chamber and placed inside a temperature-controlled box. The temperature-controlled box was made from an insulated icebox fitted with a Peltier-thermoelectric air cooler (TE Technology, model AC-027, Traverse City, MI, USA) and temperature controller (TE Technology, model TC-48-20, Traverse City, MI, USA). The temperature-controlled box provided a completely dark space in which to estimate resting metabolic rate and water loss rate in the dovekies exposed to a range of air temperatures. Measurements were completed between ~4 pm and 4 am each day, which corresponds with the period of lowest activity on the colony from which the birds were collected.

The resting metabolic rate and water loss rate of each bird was estimated from the rate of carbon dioxide production ($\dot{V}_{CO_2}$, ml CO_2 h^{-1}) and rate of water vapour production ($\dot{V}_{H_2O}$, ml H_2O h^{-1}), respectively, during open-flow respirometry. Air was drawn from the outside air at the field lab using volumetric flow-controlled pumps (Sensidyne, model Gilian Gilair-5, St. Petersburg, FL, USA) at a flow rate set to 4.5 L min^{-1} and calibrated with a wet-

143 cell air flow calibrator (Sensidyne, Gilibrator-2, St. Petersburg, FL, USA). From the flow-
144 controlled pump, air was delivered directly into the respirometry chambers (5 L plastic
145 container). A subsample of the air leaving the respirometry chambers was passed through
146 CO_2 / H_2O gas analyzers (LI-COR, model LI-840A, Lincoln, NE) interfaced with an analogue-to-
147 digital converter (ADInstruments, model PowerLab 8/30 A/D convertor, Bella Vista, NSW,
148 Australia) that was connected to a laptop computer. We were able to observe our
149 measurements in real-time via the LabChart software (ADInstruments, Bella Vista, NSW,
150 Australia). We measured the excurrent air from chambers containing individual birds, as
151 well as an empty reference chamber to obtain continuous measurements of atmospheric
152 concentrations of CO_2 and H_2O during all measurements. The use of a reference chamber
153 enabled us to mathematically compensate for fluctuations in atmospheric concentrations of
154 CO_2 and H_2O as well as compensate for the effects of fluctuations in atmospheric pressure.
155 The laptop computer was placed outside the room in which birds were being held, to
156 minimize disturbance to the birds and so that respiration of the birds could be observed in
157 real time to monitor welfare of the birds in each trial. We also monitored internal body
158 temperature (T_b) in real time using data loggers (Animals Monitoring, model Anipill, Caen,
159 France) with a data receiver to ensure the birds did not overheat at any point. The Anipill
160 loggers were ingested by birds between capture and being put in the respirometry
161 chambers and recorded body temperature continuously (1 sample min^{-1}). The Anipills are
162 the same as those swallowed by human athletes to monitor their body temperature during
163 activity (e.g. marathons). They are calibrated by the manufacturer, which provided a
164 calibration certificate. In seabirds, the devices reside in the stomach and do not enter the
165 intestine, because the pylorus is extremely small and only let liquid transfer from the
166 stomach into the intestine. The device therefore remains in the stomach until regurgitated

by the bird, usually after a few days. Regurgitation is a natural process in seabirds, to feed chicks and/or to evacuate undigested hard parts of prey, such as fish otoliths. All birds survived the respirometry trials and flew away upon release at the end of each trial. Several birds on which respirometry had been performed were re-sighted at the colony in the following days, and some of those were observed with full gular pouches, meaning they had returned to feeding behavior and attending to their chicks at the nest. The period of time between when an individual was first caught and when it was released and had the opportunity to return to the nest was 17 hours. Dovekies exhibit biparental care, with both male and female adults provisioning their chick with food, meaning that chicks would not have been without food during the time the other parent was in captivity.

Upon being introduced to the respirometry chambers, birds were given 3.5 hours to settle at a temperature between 4 and 10 ℃ (mean air temperature at the colony during our study was 7.5 ℃) before the temperature in the temperature-controlled box was changed. It took approximately 1.5 hours for air temperature to stabilize at each new test temperature, after which birds were held at that temperature for approximately 1 hour. Hence, the first measurement period occurred at 5 hours after birds were introduced to the respirometry chamber, and birds were kept in respirometry chambers for approximately 14 hours and exposed to 4 – 5 acute test temperatures (in total 184 measurements from 36 individual birds). Estimates for resting metabolic rate, water loss rate and internal body temperature were obtained from measurements taken during the 1-hour test period when air temperature was stable. We used a custom algorithm that searched for a 30-minute period corresponding to the lowest mean value of metabolic rate within the 1-hour measurement period. While each individual was exposed to 4 – 5 test temperatures, we randomised the test temperatures that individuals were exposed to between 5 °C and 35 °C.

We randomised test temperatures to maximise the spread of samples across the continuous range of ambient temperatures rather than arbitrarily 'binning' all individuals to a subset of 4 – 5 temperatures, which would reduce the precision of the fit of the regression model to the data. We also randomised the order in which were exposed to test temperatures so that any potential changes in the contribution of stress over the 14-hour measurement period were randomly distributed across the range and order of test temperatures in our study. Temperature was recorded separately inside each respirometry chamber with a temperature data logger (OneTemp, model Hobo MX2201, Adelaide, South Australia, Australia), which was connected via Bluetooth to a smart phone (Apple, model iPhone 6, Cupertino, California, US) and temperatures could be tracked in real time.

No birds that were used for respirometry were observed with full gular pouches when captured prior to respirometry. This does not rule out that the birds might have fed recently prior to the trial but at least birds had not fed immediately prior to capture.. Even if birds had fed immediately prior to capture, the initial phase of the specific dynamic action response (during which time metabolic rate is elevated due to the energetic cost of digestion) would have passed prior to measurement of metabolic rate, which occurred at least 7 hours after capture. To the extent that it is possible in wild birds, our measurement protocols sought to minimise inter-individual variation in metabolic rate associated with energy expenditure on activities other than that required for thermoregulation, including digestion and stress.

Statistical modelling for physiological measurements

We fitted nonlinear least-squares regression models to our data for $\dot{V}_{CO_2}$ and $\dot{V}_{H_2O}$ using the *minpack.lm* package [22] in R. Our goal was to estimate nonlinear function relating $\dot{V}_{CO_2}$ and

215 $\dot{V}_{H_2O}$ to temperature, but we also need to account for the effect of body mass on each
216 response variable. We were unable to achieve convergence for models fitted with
217 parameters describing the effects of both temperature and body mass, so we had to mass-
218 adjust the data prior to fitting models for temperature. We did this by fitting linear models
219 relating log $\dot{V}_{CO_2}$ or log $\dot{V}_{H_2O}$ to log body mass to estimate the allometric scaling exponent.
220 We then divided $\dot{V}_{CO_2}$ and $\dot{V}_{H_2O}$ by mass raised to the allometric exponent to calculate mass-
221 specific rates. We also adjusted our estimates of $\dot{V}_{CO_2}$ and $\dot{V}_{H_2O}$ to account for potential
222 measurement time (order) effects. To do this, we fitted a segmented regression model to
223 $\dot{V}_{CO_2}$ estimates, with air temperature and measurement order (1 – 5) fitted as fixed effects.
224 We estimated the difference between the mean of the final test period (at which point the
225 birds had the longest time to settle since the beginning of the trial) and the mean of each
226 test period preceeding it. We then subtracted that difference in means from each individual
227 trait value according to the order of the test period. The biggest difference was between the
228 first measurement and the final measurement, with the difference between subsequent
229 measurements and the final measurement declining until there was no difference between
230 the last and second last measurement periods. We calculated respiratory exchange ratio
231 (RER) for each individual as a way to identify and exclude any estimates with clearly
232 unrealistic RER values outside the range of 0.45 – 1.2 (a RER near 0.65 indicates fat as the
233 predominant metabolic fuel source and a RER near 1 indicates carbohydrate as the
234 predominant fuel source).
235

The best fitting model of the thermal dependence of $\dot{V}_{CO_2}$, $\dot{V}_{H_2O}$ and T_b was a four-parameter function relating mass-adjusted $\dot{V}_{CO_2}$ (or $\dot{V}_{H_2O}$, or T_b) to temperature according to the following equation:

$$\frac{\dot{V}_{CO_2}}{mass^b} = BMR + C_{min} \times (T_{crit} - temp_{<T_{crit}}) + H \times (temp_{>T_{crit}} - T_{crit}) \quad (1)$$

where *b* is the allometric scaling exponent for the relationship between log $\dot{V}_{CO_2}$ and log mass, *BMR* is the minimum rate of $\dot{V}_{CO_2}$, C_{min} is the slope estimate for the thermal dependence of $\dot{V}_{CO_2}$ at temperatures below the critical temperature (T_{crit}), and *H* is the slope estimate for the thermal dependence of $\dot{V}_{CO_2}$ at temperatures above the critical temperature (T_{crit}). Typically, BMR falls within a thermoneutral zone bounded by an upper (T_{UC}) and lower critical temperature (T_{LC}) as estimated using Scholander-Irving models [3]. However, our data exhibited only a single critical temperature when $\dot{V}_{CO_2}$ was lowest, and below that temperature $\dot{V}_{CO_2}$ increased with decreasing temperature and above that temperature $\dot{V}_{CO_2}$ increased with increasing temperature. The same was true for the data for $\dot{V}_{H_2O}$ and T_b.

We were not able to account for repeated measures on individual birds by fitting nonlinear mixed effects models as these models did not converge, likely due to an issue with overparameterization. We decided to continue with nonlinear least-squares regression to obtain confidence intervals on our parameter estimates for the future scenarios modelling (see below), which we obtained using the *confint2* function in the *nlstools* package [23]. We also modelled the data using linear mixed effects models for the data above and below T_{UC}

(i.e., the breakpoint in the data) and obtained the same results as those obtained from nonlinear least squares (nls) models described above.

Modelling dovekie physiology under future climate scenarios

We used one of the best performing climate models for the Arctic climate (HadGEM2-ES; [24]) to extract land surface air temperatures every 3 hours for the summer months (June – August) at our study site at Ukaleqarteq, East Greenland (70° 43' N, 21° 33 W). We extracted 3 hourly summer air temperatures each year for a decade during an historical baseline (1996 – 2005), as well as mid-century (2036 – 2045) and a late-century (2090-2099). In the mid- and late-century decades, summer air temperatures were considered under both low (RCP2.6) and high (RCP8.5) radiative forcing scenarios, creating a total of five climatic conditions (one baseline, mid-century low and high global greenhouse gas emissions, and late century low and high global greenhouse gas emissions). Combining those air temperature data and empirical physiological data, we calculated the total amount of energy expended ($CO_{2\ total}$) and water lost ($H_2O_{\ total}$) by an average individual over the summer breeding season. To examine how $CO_{2\ total}$ and $H_2O_{\ total}$ might also be sensitive to changes in the T_{UC} parameter of the thermoregulatory function (either via evolution or plasticity), we modelled energy and water costs across a range of T_{UC} values from 5 to 35 °C. We then calculated the factorial change in $CO_{2\ total}$ and $H_2O_{\ total}$ under future climate scenarios relative to the baseline scenario.

Results and discussion

We performed a phylogenetic analysis of existing data [15] for upper critical temperature (T_{UC}) in 256 bird species spanning in body sizes from 3 grams to 11 kg, from the tropics to the Arctic, to examine the evidence for cold adaption in dovekies. We found that T_{UC} decreases towards the poles ($F_{(1, 249)} = 29.49$, $P < 0.001$) and decreases with log body mass ($F_{(1,249)} = 12.34$, $P < 0.001$), which is consistent with the long-standing assumption that polar species are potentially heat-stressed under warming conditions [2-6]. Dovekies thereby appear to be putatively adapted to cold conditions, with an observed T_{UC} (22.4 °C, this study) that is 8.8 °C lower than predicted (31.2 °C) by our statistical model that included the effects of phylogeny, body mass and habitat latitude (**Figure 1**). To account for potential methodological sources of error in T_{UC} estimates we included a fixed factor in our models based on the 'data quality' categories proposed by McKechnie et al. (2017) in their examination of the primary data from the Khaliq et al. (2014) dataset. Their categories were 'Good', 'No T_{UC}' (i.e., no breakpoint in the data, T_{UC} taken as highest measurement temperature), 'Insufficient data', or '------' (meaning they were not able to assess the data). Data quality explained only 2.8% of the variance in T_{UC}. We included 'data quality', which we called 'methodology', as a fixed factor (with the four levels described above) in our models. Methodology explained 2.8% of the variance in T_{UC} and the standardized effect sizes (Cohen's *d*) for each methodology category varied between 0.03 and 0.07 (very little effect). In other words, variation associated with methodological error (2.8%) was much smaller than that associated with latitude and body mass, and thus does not obfuscate the large-scale signals of latitude and body mass – an argument that has been previously discussed in the physiological and macro-ecological literature [25-27].

The presumed cold adaptation of dovekies is consistent with the only previous experimental study of physiological cold adaptation in this species [14], which estimated that the basal rate of heat production (177.9 kJ day^{-1}) was more than twice that predicted (84.2 kJ day^{-1}) for a non-passerine bird of the same size (153 g) [28]. That same study also found that dovekies have low thermal conductance, meaning that – at cold temperatures below thermoneutrality – they retain heat more effectively than other temperate-zone seabirds of similar size, such as the Georgian diving petrel (*Pelecanoides georgicus*) [14, 29, 30]. Given the phylogenetic and physiological evidence in support of cold adaptation in dovekies, we expected that they would be prone to acute hyperthermia when exposed to warmer temperatures above thermoneutrality. This is coherent with dovekie morphology, notably with an extremely dense plumage which provides highly efficient thermal insulation both in air and water [13].

In this context, we estimated resting metabolic rate ($\dot{V}_{CO_2}$), rate of water loss ($\dot{V}_{H_2O}$) and internal body temperature (T_b) in dovekies from a breeding colony at Ukaleqarteq, East Greenland (70° 43' N, 21° 33 W). Contrary to our expectations based on previous investigations [14], we found that dovekies exhibited a remarkable capacity for thermoregulation at high temperatures. Energy expenditure while resting was lowest at 22.4 °C (95 % C.I. 19.8 – 25.0, $t_{(133)}$ = 16.37, P < 0.0001; **Figure 2A**) and there was only a marginal increase in energy expenditure as ambient temperature increased from 22 up to 35 °C (4.93 ml CO_2 hr^{-1} $°C^{-1}$, 95 % C.I. 1.70 – 8.16, $t_{(133)}$ = 3.02, P < 0.05 ; **Figure 2A**). Heat dissipation mechanisms allowed mean body temperatures to remain stable at temperatures up to 24.3 °C (95 % C.I. 22.3 – 26.2, $t_{(94)}$ = 24.8, P < 0.0001; **Figure 2C**), above which mean body temperature rose by 0.16 °C with every 1 °C increase in ambient temperature (95 % C.I. 0.11 – 0.21, $t_{(94)}$ = 6.1, P < 0.0001; **Figure 2C**). Yet these increases in body temperature

were not uncontrolled, since the rate of increase in T_b (ΔT_b) during high temperature exposure was essentially insensitive to ambient temperature variation (the slope of $\Delta T_b \sim T_a$ was 0.048 °C h^{-1}, **Figure 2D**). This suggests that dovekies engage in facultative hyperthermia to reduce the thermal gradient between their body and the air, and to reduce water loss at higher temperatures. Indeed, rates of water loss show only a gradual and largely passive increase between 5 and 31.6 °C, at which point there is a distinct increase in rates of water loss above 31.6 °C (95 % C.I 30.1 – 33.1, $t_{(131)} = 42.2$, $P < 0.0001$; **Figure 2B**).

We used our physiological measurements and future climate projections for our study site to model how the energetic and water costs of thermoregulation are expected to change under future climate warming. Our modelling predicts that the energetic costs of thermoregulation (while at rest) will be reduced in dovekies under future climate warming scenarios (**Figure 3**). While initially surprising, this result is consistent with the fact that, in dovekies at least, the energetic cost of heat production is greater than the energetic cost of heat dissipation. In other words, it is more energetically costly to maintain a high and stable body temperature at cold air temperatures than it is to dissipate excess body heat at warmer temperatures. Rather than being constrained by energy expenditure, the challenge faced at air temperatures above T_{UC} is water conservation: active mechanisms of evaporative water loss become increasingly important for maintaining core body temperature and preventing lethal hyperthermia. Indeed, our modelling predicts that the water cost of thermoregulation will increase under all future climate scenarios. Across a wide range of plausible values of T_{UC} (current estimate of 22.4 ± 7 °C), our modelling predicts that water costs of thermoregulation will increase by a factor between 1.1 and 2 by 2100.

Dovekies, being sea birds, have an abundance of water available in their habitat, and because they possess salt glands in the frontal part of their skulls, they can (and do) drink saltwater and excrete excess salt [32, 33]. Hence, increased water costs to support thermoregulation may not necessarily impose an immediate constraint. Taken together, our bioenergetic and water loss data suggest that dovekies have an unexpectedly high thermoregulatory capacity to survive acute heat exposures at least five times their current habitat average air temperature and ~15 °C above maximum air temperatures. In the 2019 breeding summer season, average air temperature was 7.6 °C ± 5.9 (SD) and maximum recorded air temperature was 20.8 °C (unpublished data, gathered by a weather station at the breeding colony, recording temp each minute).

Our results and their implications primarily concern the resting phase of dovekies, which represents 54% of their time budget during the summer breeding season [12], and 64% during the inter-breeding winter period [34]. During the remaining time, birds engage in energetically demanding activities such as flying and diving (flying: 7.24 × basal metabolic rate; diving: 9.37 × basal metabolic rate [35]), which may lead to overheating. Yet, recent field measurements [36] demonstrated that dovekies efficiently alternate periods spent flying and diving, with resting at sea or at the colony enabling the rapid dissipation of muscular heat and body temperature decline.

Overall, the implication of our study is that the longer-term impacts of climate warming on Arctic endotherms are unlikely to be dictated by direct (i.e., lethal) susceptibility to acute hyperthermia, even during the highly energetically demanding breeding season. Instead, the climate vulnerability of species is more likely to be modulated by indirect climate-change impacts. Notably, previous studies pointed to climate-induced shifts in North Atlantic zooplankton communities, with smaller, less profitable prey invading dovekie

foraging areas [37]. Dovekies buffered this indirect consequence of Arctic warming by increasing their foraging effort, and their breeding performance remained unchanged [38]. Yet, they reached an energetic ceiling [39] and are more sensitive to contaminant exposure [40]. As a consequence, dovekie adult survival declined in Arctic areas most affected by climate warming [41], but overall population consequences of these changes remain unclear.

It is at first surprising that cold adaptation does not preclude warm tolerance in dovekies. It is important to recall, however, that dovekies diversified from ancestral Alcid species 15 million years ago (Ma) [42] during the Middle-Miocene Climatic Optimum (MMCO). The MMCO was a global warming event that occurred 16–14 Ma, when global mean surface temperature was 3–4 °C warmer than today [43, 44], and is associated with major shifts in the global distribution of faunal and floral assemblages [45]. Further, during the Pliocene (2.6–5 Ma), global mean annual temperature was 2–3 °C warmer than today, and the Arctic was estimated to be 19 °C warmer [46]. Following paleoclimatic warm periods, dovekies persisted through ice ages when global temperatures were much colder than the present. For instance, during the Last Glacial Maximum (23–19 thousand years ago), global average temperature was about 6 °C colder compared to modern-day (pre-industrial) temperatures, and up to 15 °C colder at high northern latitudes [47]. During the inter-breeding winter period today, migrating dovekies experience a range of air temperatures between 6.4 °C and -10.7 °C and sea temperatures between 6.3 °C and -1.3 °C (see Table 1 in [13]). Hence, throughout their evolutionary history, dovekies may have been exposed to climates that were both markedly warmer and colder than in the present time. We speculate that the ecophysiology of dovekies has been shaped by a complex climatic legacy, with a resulting blend of cold and warm-adaptive traits. Overall, our study suggests

that we may suffer from evolutionary short-sightedness when assessing the impact of current global warming on endemic Arctic birds and mammals.

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Figure 1. Dovekies exhibit lower T_{UC} than predicted for a bird of its size and habitat latitude. (**A**, map inset) Dovekies (*Alle alle*) are the most abundant seabird in the Arctic. The geographic distribution of dovekies in winter, summer and breeding locations are shown in light green, medium green, and dark green shades, respectively [31]. The light blue and dark blue lines show the present-day maximum and minimum sea-ice extent, respectively [48]. (**B**) Bird species that live at higher latitudes (blue branches on phylogenetic tree) show reduced upper critical temperature (T_{UC}) after accounting for the effects of body mass and phylogeny. Residual T_{UC} is shown by the bars at the tree tips, with bar length (see axis) and color (green, orange) corresponding to deviation from model predictions. Dovekies have a T_{UC} 14.8 °C less than predicted for a bird of its body mass and taxonomy (and 8.8 °C lower than predicted by a model that also includes habitat latitude; see main text for full statistical results).

Figure 2. Thermoregulatory physiology of dovekies (*Alle alle*). Basal metabolic rate in our study population coincided with an air temperature of 22.38 °C, and energy expenditure increased less with increasing air temperature than it did with decreasing air temperature (**A**). Rates of evaporative water loss increased passively and gradually from 5 to 31.6 °C, beyond which active mechanisms of evaporative cooling led to a rapid increase in rate of water loss (**B**). Dovekies showed signs of facultative hyperthermia, with increases in body temperature (T_b) at air temperatures above 24.3 °C (**C**) that were controlled, since the rate of increase in T_b (ΔT_b) during high temperature exposure was insensitive to ambient temperature (**D**).

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449 **Figure 3.** Modelling the energetic and water costs of thermoregulation in dovekies under
450 warming Arctic climates. We used one of the best performing climate models for the Arctic
451 climate (HadGEM2-ES; [24]) to extract land surface air temperatures every 3 hours for the
452 summer months (June - August) at our study site at Ukaleqarteq, East Greenland (**A**). We
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454 mid-century (2036 - 2045) and late-century (2090 - 2099) decades, each under low (RCP2.6)
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456 data, we modelled total energy expenditure and water loss for the whole of summer in each
457 year of our climate scenarios (C and D). Energy and water costs were calculated for the
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462 change into the future, plots E and F show the factorial change in total energy and water
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464 (22.4°C).

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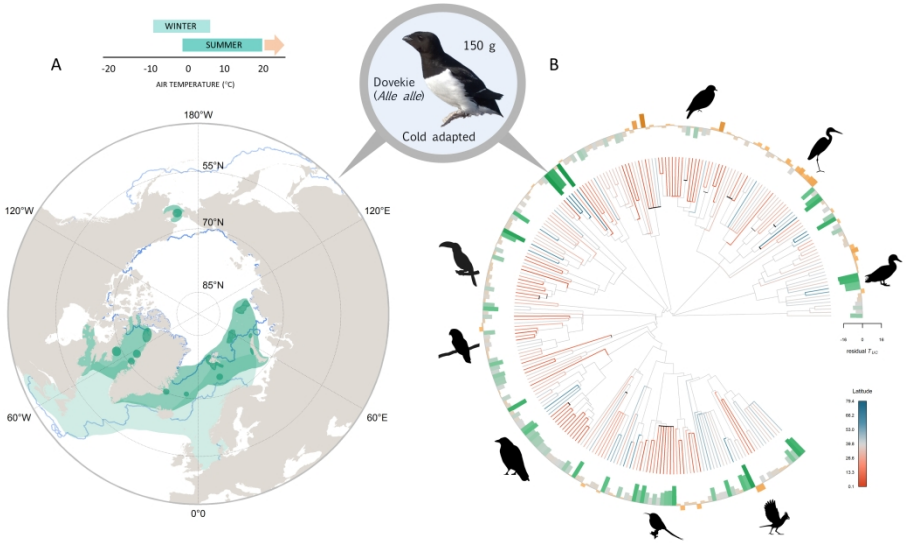

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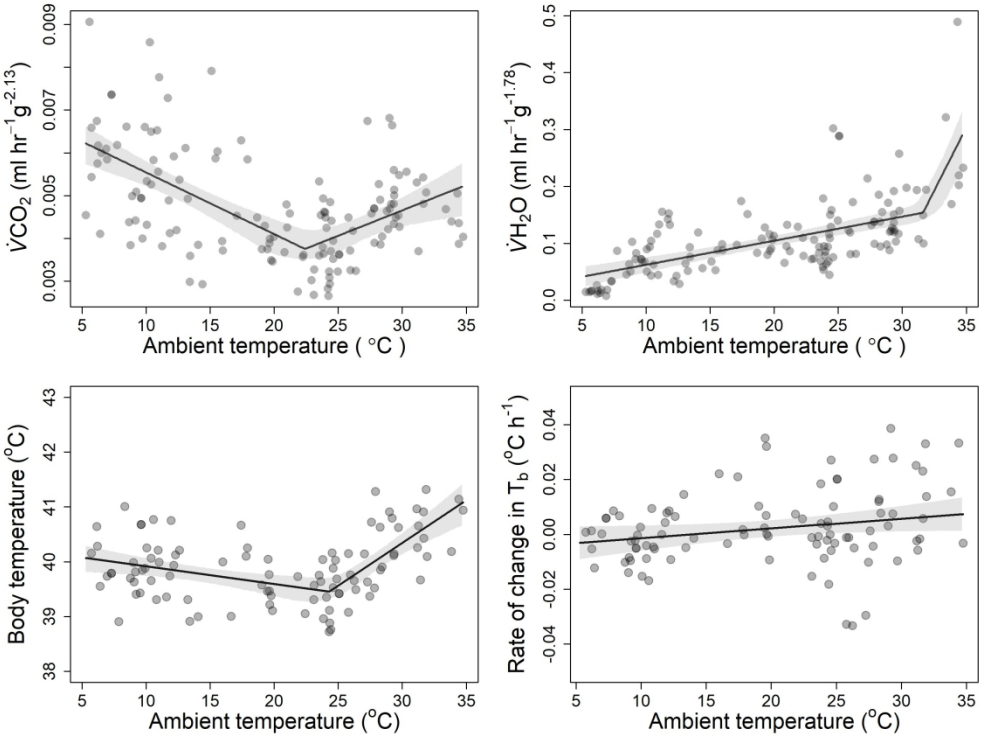

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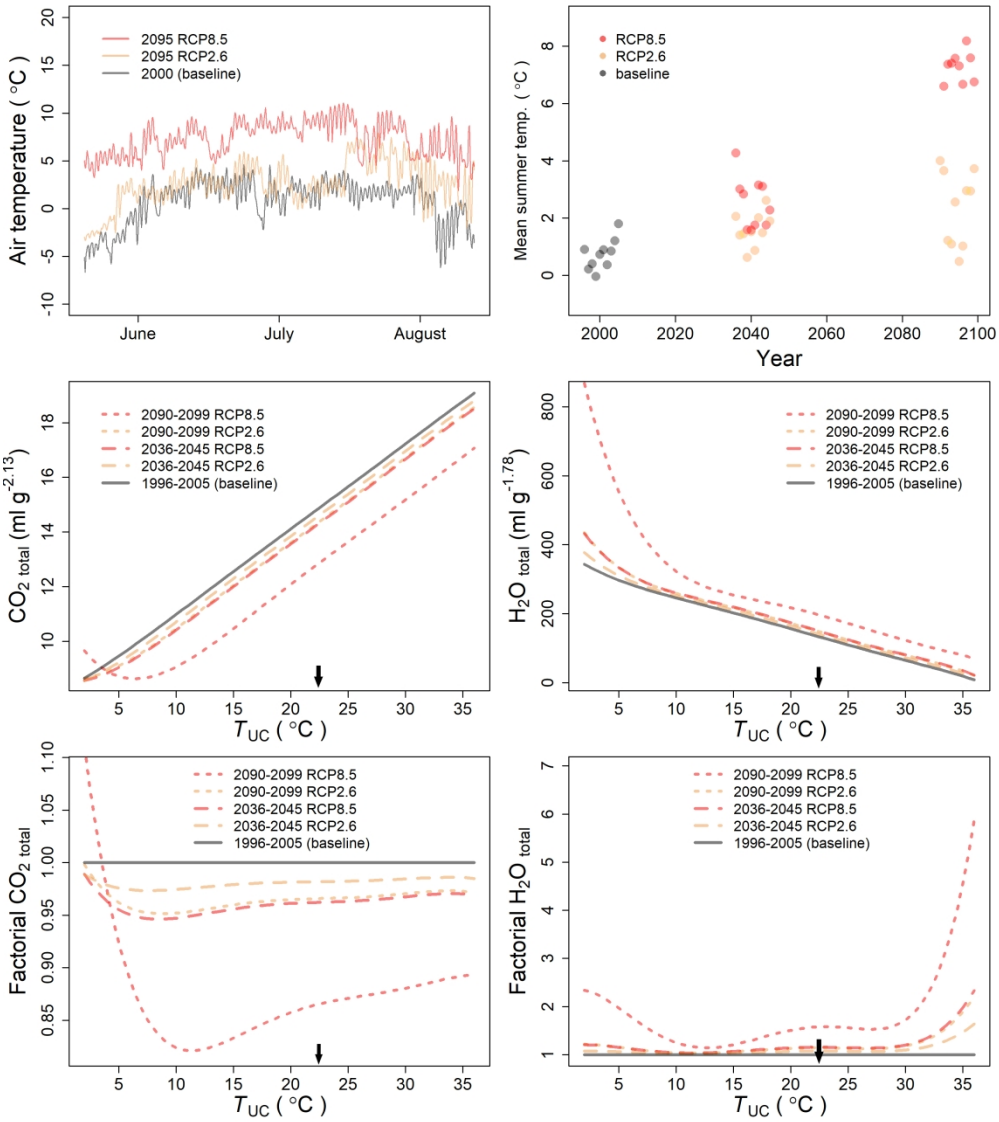

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793x898mm (96 x 96 DPI)