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

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

3  
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24 **Abstract**

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

40

41

42 **Keywords** Animal energetics; Dovebie; Ecophysiology; Evolutionary legacy; Global Warming;  
43 Phylogenetic analyses.

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47

## 48 **Introduction**

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

65 To explore how climate warming will affect Arctic endotherms, we studied the  
66 thermal physiology and bioenergetics of the dovekie (or little auk, *Alle alle*), the smallest  
67 (150 g) diving seabird in the North Atlantic, and most abundant Arctic seabird (40 – 80  
68 million individuals, [9]), that plays a pivotal role in marine and terrestrial trophic flows [10].  
69 We focused on the summer season, while dovekies are breeding in the high Arctic. During  
70 this phase, adults spend 54 % of their time on land in underground nest cavities or perched  
71 on rocks at the surface of the colony, and 46 % engaged in foraging trips at sea within ca.

72 100 km from their nests, diving to catch zooplankton within the first 20 meters of the water  
73 column [11, 12]. The breeding season is the most energetically demanding period for  
74 dovekies [12, 13].

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

88

## 89 **Methods**

### 90 *Phylogenetic modelling*

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

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



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

121

### 122 *Physiological measurements*

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

138 The resting metabolic rate and water loss rate of each bird was estimated from the  
139 rate of carbon dioxide production ( $\dot{V}_{CO_2}$ , ml  $CO_2$   $h^{-1}$ ) and rate of water vapour production (  
140  $\dot{V}_{H_2O}$ , ml  $H_2O$   $h^{-1}$ ), respectively, during open-flow respirometry. Air was drawn from the  
141 outside air at the field lab using volumetric flow-controlled pumps (Sensidyne, model Gilian  
142 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<sub>2</sub> / H<sub>2</sub>O 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<sub>2</sub> and H<sub>2</sub>O during all measurements. The use of a reference chamber  
153 enabled us to mathematically compensate for fluctuations in atmospheric concentrations of  
154 CO<sub>2</sub> and H<sub>2</sub>O 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<sup>-1</sup>). 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

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

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

191 We randomised test temperatures to maximise the spread of samples across the continuous  
192 range of ambient temperatures rather than arbitrarily ‘binning’ all individuals to a subset of  
193 4 – 5 temperatures, which would reduce the precision of the fit of the regression model to  
194 the data. We also randomised the order in which were exposed to test temperatures so that  
195 any potential changes in the contribution of stress over the 14-hour measurement period  
196 were randomly distributed across the range and order of test temperatures in our study.  
197 Temperature was recorded separately inside each respirometry chamber with a  
198 temperature data logger (OneTemp, model Hobo MX2201, Adelaide, South Australia,  
199 Australia), which was connected via Bluetooth to a smart phone (Apple, model iPhone 6,  
200 Cupertino, California, US) and temperatures could be tracked in real time.

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

211

### 212 *Statistical modelling for physiological measurements*

213 We fitted nonlinear least-squares regression models to our data for  $\dot{V}_{CO_2}$  and  $\dot{V}_{H_2O}$  using the  
214 *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 preceding 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

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

239

$$240 \quad \frac{\dot{V}_{CO_2}}{mass^b} = BMR + C_{min} \times (T_{crit} - temp_{<T_{crit}}) + H \times (temp_{>T_{crit}} - T_{crit}) \quad (1)$$

241

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

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

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

260

### 261 *Modelling dovekie physiology under future climate scenarios*

262 We used one of the best performing climate models for the Arctic climate (HadGEM2-ES;  
263 [24]) to extract land surface air temperatures every 3 hours for the summer months (June –  
264 August) at our study site at Ukaleqarteq, East Greenland (70° 43' N, 21° 33 W). We  
265 extracted 3 hourly summer air temperatures each year for a decade during an historical  
266 baseline (1996 – 2005), as well as mid-century (2036 – 2045) and a late-century (2090-  
267 2099). In the mid- and late-century decades, summer air temperatures were considered  
268 under both low (RCP2.6) and high (RCP8.5) radiative forcing scenarios, creating a total of  
269 five climatic conditions (one baseline, mid-century low and high global greenhouse gas  
270 emissions, and late century low and high global greenhouse gas emissions). Combining  
271 those air temperature data and empirical physiological data, we calculated the total amount  
272 of energy expended ( $\text{CO}_2_{\text{total}}$ ) and water lost ( $\text{H}_2\text{O}_{\text{total}}$ ) by an average individual over the  
273 summer breeding season. To examine how  $\text{CO}_2_{\text{total}}$  and  $\text{H}_2\text{O}_{\text{total}}$  might also be sensitive to  
274 changes in the  $T_{UC}$  parameter of the thermoregulatory function (either via evolution or  
275 plasticity), we modelled energy and water costs across a range of  $T_{UC}$  values from 5 to 35 °C.  
276 We then calculated the factorial change in  $\text{CO}_2_{\text{total}}$  and  $\text{H}_2\text{O}_{\text{total}}$  under future climate  
277 scenarios relative to the baseline scenario.

278

279

280

281

## 282 **Results and discussion**

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



305           The presumed cold adaptation of dovebies is consistent with the only previous  
306 experimental study of physiological cold adaptation in this species [14], which estimated  
307 that the basal rate of heat production ( $177.9 \text{ kJ day}^{-1}$ ) was more than twice that predicted  
308 ( $84.2 \text{ kJ day}^{-1}$ ) for a non-passerine bird of the same size (153 g) [28]. That same study also  
309 found that dovebies have low thermal conductance, meaning that – at cold temperatures  
310 below thermoneutrality – they retain heat more effectively than other temperate-zone  
311 seabirds of similar size, such as the Georgian diving petrel (*Pelecanoides georgicus*) [14, 29,  
312 30]. Given the phylogenetic and physiological evidence in support of cold adaptation in  
313 dovebies, we expected that they would be prone to acute hyperthermia when exposed to  
314 warmer temperatures above thermoneutrality. This is coherent with dovebie morphology,  
315 notably with an extremely dense plumage which provides highly efficient thermal insulation  
316 both in air and water [13].

317           In this context, we estimated resting metabolic rate ( $\dot{V}_{CO_2}$ ), rate of water loss ( $\dot{V}_{H_2O}$ )  
318 and internal body temperature ( $T_b$ ) in dovebies from a breeding colony at Ukaleqarteq, East  
319 Greenland ( $70^\circ 43' \text{ N}$ ,  $21^\circ 33' \text{ W}$ ). Contrary to our expectations based on previous  
320 investigations [14], we found that dovebies exhibited a remarkable capacity for  
321 thermoregulation at high temperatures. Energy expenditure while resting was lowest at  
322  $22.4 \text{ }^\circ\text{C}$  (95 % C.I.  $19.8 - 25.0$ ,  $t_{(133)} = 16.37$ ,  $P < 0.0001$ ; **Figure 2A**) and there was only a  
323 marginal increase in energy expenditure as ambient temperature increased from 22 up to  
324  $35 \text{ }^\circ\text{C}$  ( $4.93 \text{ ml CO}_2 \text{ hr}^{-1} \text{ }^\circ\text{C}^{-1}$ , 95 % C.I.  $1.70 - 8.16$ ,  $t_{(133)} = 3.02$ ,  $P < 0.05$ ; **Figure 2A**). Heat  
325 dissipation mechanisms allowed mean body temperatures to remain stable at temperatures  
326 up to  $24.3 \text{ }^\circ\text{C}$  (95 % C.I.  $22.3 - 26.2$ ,  $t_{(94)} = 24.8$ ,  $P < 0.0001$ ; **Figure 2C**), above which mean  
327 body temperature rose by  $0.16 \text{ }^\circ\text{C}$  with every  $1 \text{ }^\circ\text{C}$  increase in ambient temperature (95 %  
328 C.I.  $0.11 - 0.21$ ,  $t_{(94)} = 6.1$ ,  $P < 0.0001$ ; **Figure 2C**). Yet these increases in body temperature

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

336 We used our physiological measurements and future climate projections for our  
337 study site to model how the energetic and water costs of thermoregulation are expected to  
338 change under future climate warming. Our modelling predicts that the energetic costs of  
339 thermoregulation (while at rest) will be reduced in dovekeys under future climate warming  
340 scenarios (**Figure 3**). While initially surprising, this result is consistent with the fact that, in  
341 dovekeys at least, the energetic cost of heat production is greater than the energetic cost of  
342 heat dissipation. In other words, it is more energetically costly to maintain a high and stable  
343 body temperature at cold air temperatures than it is to dissipate excess body heat at  
344 warmer temperatures. Rather than being constrained by energy expenditure, the challenge  
345 faced at air temperatures above  $T_{UC}$  is water conservation: active mechanisms of  
346 evaporative water loss become increasingly important for maintaining core body  
347 temperature and preventing lethal hyperthermia. Indeed, our modelling predicts that the  
348 water cost of thermoregulation will increase under all future climate scenarios. Across a  
349 wide range of plausible values of  $T_{UC}$  (current estimate of  $22.4 \pm 7 \text{ }^\circ\text{C}$ ), our modelling  
350 predicts that water costs of thermoregulation will increase by a factor between 1.1 and 2 by  
351 2100.

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

362 Our results and their implications primarily concern the resting phase of dovekies,  
363 which represents 54% of their time budget during the summer breeding season [12], and  
364 64% during the inter-breeding winter period [34]. During the remaining time, birds engage  
365 in energetically demanding activities such as flying and diving (flying:  $7.24 \times$  basal metabolic  
366 rate; diving:  $9.37 \times$  basal metabolic rate [35]), which may lead to overheating. Yet, recent  
367 field measurements [36] demonstrated that dovekies efficiently alternate periods spent  
368 flying and diving, with resting at sea or at the colony enabling the rapid dissipation of  
369 muscular heat and body temperature decline.

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

376 foraging areas [37]. Dovekies buffered this indirect consequence of Arctic warming by  
377 increasing their foraging effort, and their breeding performance remained unchanged [38].  
378 Yet, they reached an energetic ceiling [39] and are more sensitive to contaminant exposure  
379 [40]. As a consequence, dovekie adult survival declined in Arctic areas most affected by  
380 climate warming [41], but overall population consequences of these changes remain  
381 unclear.

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

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

402

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

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437

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

447

448

449 **Figure 3.** Modelling the energetic and water costs of thermoregulation in dovekeys 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  
453 calculated air temperature data for an historical baseline decade (1996 - 2005) as well as  
454 mid-century (2036 - 2045) and late-century (2090 - 2099) decades, each under low (RCP2.6)  
455 and high (RCP 8.5) global greenhouse gas emissions scenarios (B). Using our physiological  
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  
458 whole summer for a range of  $T_{UC}$  values ranging from 1 to 36 to capture possible effects of  
459 variation in  $T_{UC}$  (caused by plasticity or adaptation). Lines in plots C and D show the mean  
460 total energy cost and mean total water cost for each of the five climate scenarios (see inset  
461 legend for colour and line type). To show how energy and water costs are predicted to  
462 change into the future, plots E and F show the factorial change in total energy and water  
463 costs relative to the baseline estimations. Arrows in plots C – E indicate the  $T_{UC}$  of dovekeys  
464 (22.4°C).

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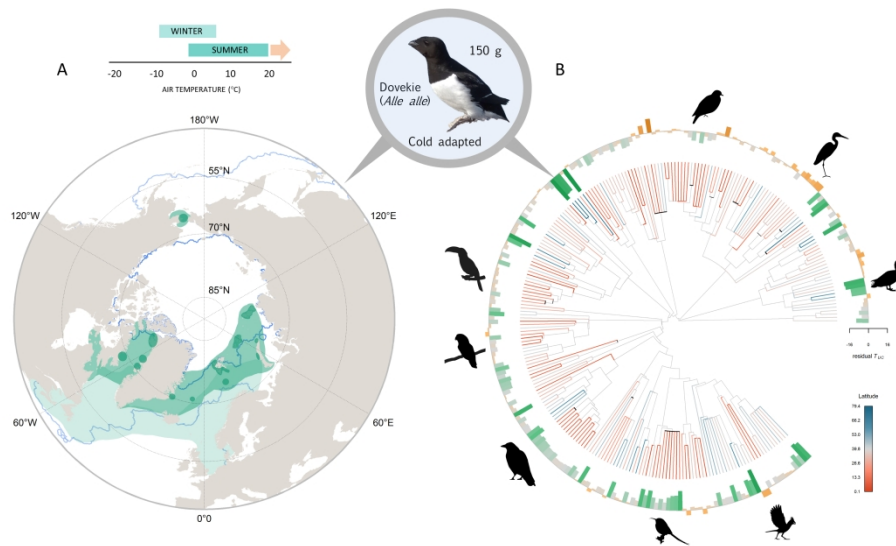
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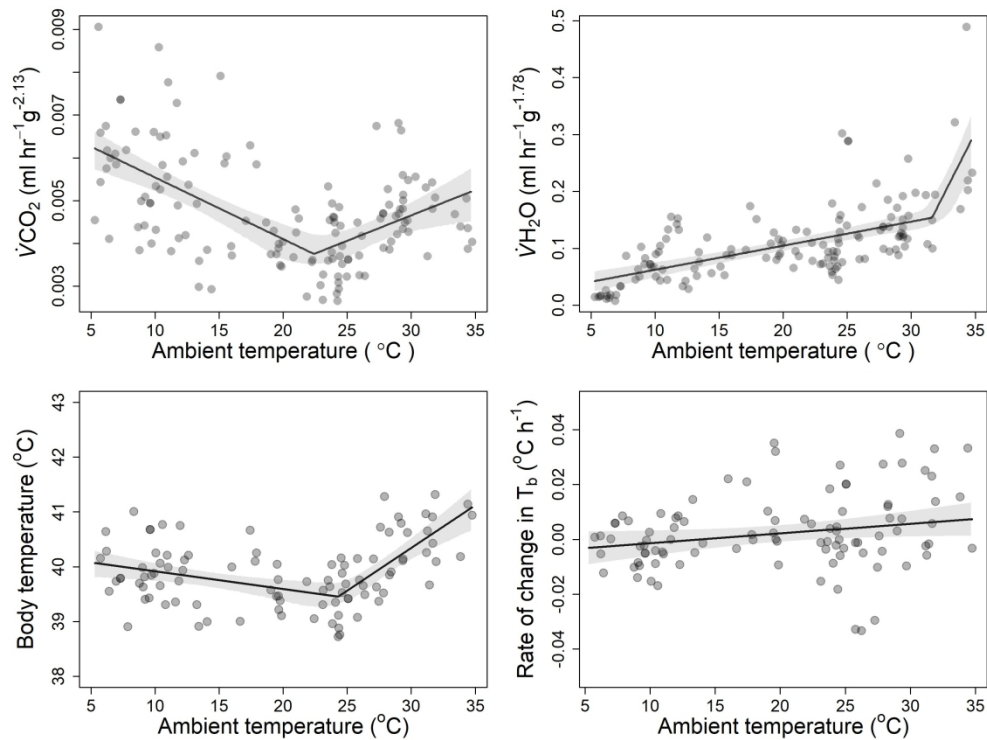
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**Figure 1. Dovekies exhibit lower  $T_{UC}$  than predicted for a bird of its body mass and habitat latitude.** (A, map inset) Dovekies (*Alle alle*) are the most abundant seabird in the Arctic. The geographic distribution of dovekies in winter, summer 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).

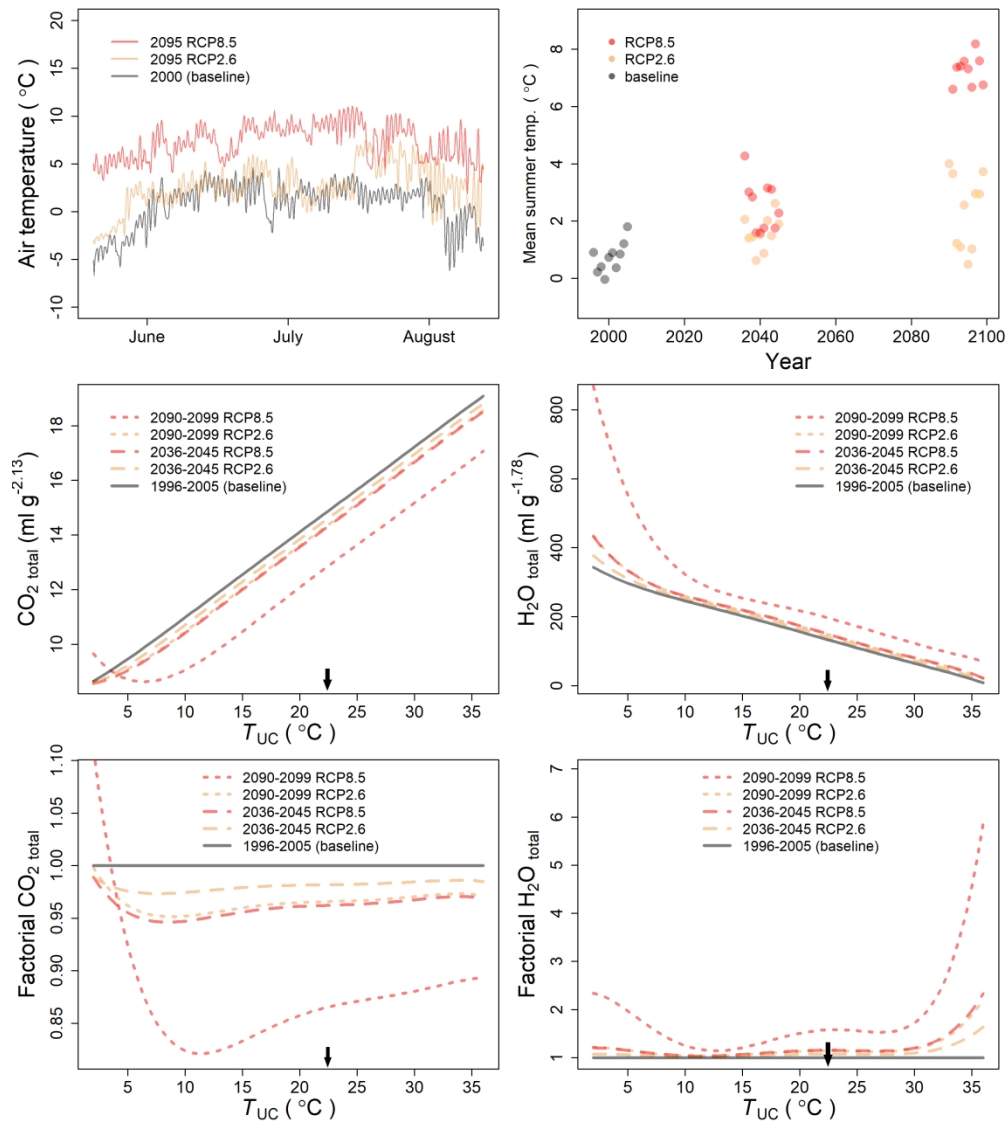
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**Figure 2. Thermoregulatory physiology of dovekeys (*Alle alle*).** Basal metabolic rate in our study population coincided with an air temperature of 22.38 °C, and energy expenditure increased less with increasing air temperature than it did with 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). Dovekeys 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  $T_b$  ( $\Delta T_b$ ) during high temperature exposure was insensitive to ambient temperature (D).

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**Figure 3. Modelling the energetic and water costs of thermoregulation in dovekeys under warming Arctic climates.** 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 (A). We calculated air temperature data for an historical baseline decade (1996 - 2005) as well as mid-century (2036 - 2045) and late-century (2090 - 2099) decades, each under low (RCP2.6) and high (RCP 8.5) global greenhouse gas emissions scenarios (B). Using our physiological data, we modelled total energy expenditure and water loss for the whole of summer in each year of our climate scenarios (C and D). Energy and water costs were calculated for the whole summer for a range of  $T_{UC}$  values ranging from 1 to 36 to capture possible effects of variation in  $T_{UC}$  (caused by plasticity or adaptation). Lines in plots C and D show the mean total energy cost and mean total water cost for each of the five climate scenarios (see inset legend for colour and line type). To show how energy and water costs are predicted to change into the future, plots E and F show the factorial change in total energy and water costs relative to the baseline estimations. Arrows in plots C - E indicate the  $T_{UC}$  of dovekeys (22.4°C).

793x898mm (96 x 96 DPI)

