Should we really predict the response of wild endotherms to climate change based on thermal responses measured in captivity?

Antoine Stier[1,2†]

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

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

†: corresponding author: antoine.stier@iphc.cnrs.fr

Keywords: Thermoregulation, Body temperature, Thermoneutral zone, Seabird, Heat load, Global warming

In their recent study, Beaman et al. [1] measured the metabolic response of the most abundant Arctic seabird, the dovekie (*Alle alle*), to experimental variation in air temperature. Based on their results on energy and water expenditure in captive conditions, Beaman et al. conclude that this Artic species should not suffer much from direct consequences of climate change. Indeed, their estimated upper critical temperature T_{UC} (*i.e.* temperature above which metabolic rate increases) was 22.4°C, which is *ca.* 15°C higher than the average air temperature, and *ca.* 2°C higher than the maximum temperature currently recorded at the breeding colony. While projecting their data under various climatic scenario, Beaman et al.[1] conclude that dovekies should even benefit of the ongoing climate warming from a thermoregulatory perspective.

While the data collection is quite standard in the field of thermal biology [2], I would like to offer my personal view on the potential perils of concluding about wild animal response to climate change based on data collected in 'a small dark box in the lab'. Classically, the thermal response of animals is evaluated using respirometry, which enables to quantify gas exchange (*i.e.* O_2, CO_2, H_2O) between an animal and its environment in response to variation in ambient temperature within a small metabolic chamber [2]. This is usually conducted in a post-absorptive state and in the dark to limit energy expenditure linked to digestion and physical activity. While such conditions are highly relevant to evaluate the minimum energy requirements of animals (*i.e.* basal metabolic rate), I question its relevance for evaluating the thermal responses of wild animals to the heat.

First, the risk for wild animals to suffer from warm environmental conditions are very unlikely to occur in a post-absorptive state during the night. The thermal physiology and the responses to warm conditions are thus likely to differ between an animal fasting and resting within a metabolic chamber and the same animal within its natural environment. For instance, the body temperatures of dovekies measured by Beaman et al. [1] during their respirometry assays differ markedly from the body temperature measured on the same species while resting at the breeding colony [3] as illustrated in Fig. 1. Dovekies resting at the breeding colony at an average air temperature (T_a) of 5.4°C had a body temperature 1.5°C higher than dovekies measured in respirometry chambers below the thermal inflexion point (average T_a = 14.5°C), and 1.1°C higher than those measured above the thermal inflexion point (average T_a = 28.4°C). Dovekies thus seem to be in a hypometabolic state while sitting in a dark respirometry chamber in a post-absorptive state. The results of Beaman et al. [1] for body temperature are relatively similar to those obtained in dovekies measured in respirometry chambers under full-light conditions (T_b = 40.1 ± 0.4°C) [4], which suggests that light exposure is unlikely the main driver of the hypometabolic state observed during respirometry. From my perspective, it thus seems that any conclusion on the thermal response of dovekies measured from respirometry studies should not be used, or used with extreme caution, to extrapolate the thermal response of free-living dovekies, especially to warm environmental conditions. While the precious data on body temperature collected by [3] and [1] on dovekies regarding this specific point is striking, it is likely that such assumption may apply to other wild endotherms.

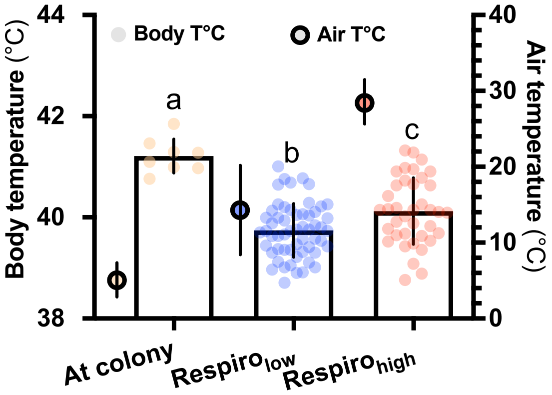

Fig. 1: Body temperature of wild dovekies measured at the corresponding air temperature *in situ* while resting at the breeding colony (yellow), and during respirometry assay both below (blue) and above (red) the thermal inflexion point. Data at the colony were retrieved and averaged for the N = 8 individuals (n = 4352 measures) from [3], while data for respirometry have been extracted from Fig. 2c in [1] using https://plotdigitizer.com/ but cannot be averaged for each individual (N = 36, n = 95 measures) considering the lack of information on individual identity. Mean ± SD are presented and have been analyzed for body temperature using non-parametric Kruskal-Wallis test (K-W χ^2 = 26.3, $p < 0.001$). Different letters represent significant differences in body temperature according to Dunn's post-hoc tests (all $p < 0.020$).

Additionally, it is worth noting that the shape of the classical metabolism-ambient temperature curve measured for dovekies differ markedly between [1] and a previous study on the same species [4]. Here I put together these two studies in perspective in Figure 2 by restricting [4] to $T_a > 5$°C (its range was *ca.* -20°C to 23°C) and mean-centring all metabolic data. While the breakpoints do not differ drastically (*i.e.* 20.11, 95% C.I. [18.80-20.68] vs. 22.53 [19.63-25.00]°C), there is way less variation in the data of [4] (see spreading across the y axis), and the markedly steeper slope after the inflection point of this study suggests a cost of thermoregulation at high temperatures incommensurably higher than the data obtained by [1]. While Beaman et al. [1] mention that "in dovekies at least, the energetic cost of heat production is greater than the energetic cost of heat dissipation", this statement does not seem supported by their data, with the 95% confidence intervals of the slopes below [-0.153; -0.078] and above [0.040; 0.156] T_{UC} largely overlapping when converted to absolute value. The 3-fold variation in metabolic rate seen at a given temperature in [1] and not observed in [4] combined with the acknowledged inclusion of biologically unrealistic metabolic rate data (respiratory exchange ratio [0.45-0.65] and [1.00-1.20]) question the accuracy of Beaman et al. [1] respirometry data from my perspective.

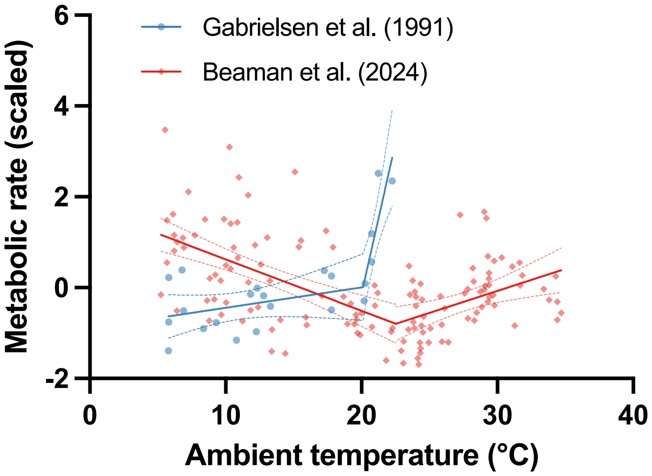

Fig. 2: Metabolic responses of captive dovekies to experimental variation in ambient temperature measured by Beaman et al. [1] (blue) and Gabrielsen et al. [4] (red). Metabolic data on mass-corrected VO_2 ([1] Fig 2a) and VCO_2 ([4] Fig. 1) have been extracted using https://plotdigitizer.com/ and mean-centred (*i.e.* scaled) to enable comparison of patterns between the two studies. Segmented regression analyses defining breakpoints, slopes and their confidence intervals have been performed using GraphPad Prism v10.3.0.

Secondly, Beaman et al. [1] seem to assume that wild dovekies are only submitted to variation in air temperature. The heat load faced by wild animals depends on more than T_a alone. T_a has even been suggested to play a relatively minor role in the actual heat load faced by many wild animals [5]. While it seems obvious that our human thermal comfort depends on the combination of air temperature, solar radiations, wind speed and humidity, many studies related to the thermal biology of wild animals continue to ignore the last 3 factors in their analyses, including [1]. To illustrate the importance of solar radiations for seabirds, it has for example been shown that while panting behaviour occurs at a T_a of *ca.* 24°C in the shade, it occurs at *ca.* 15°C when common guillemots (*Uria aalge*) are exposed to solar radiations [6]. It has recently been suggested that a field-friendly and informative way of measuring the heat load faced by wild animals is to use the black globe temperature (T_g) instead of $\mathrm{T_a}$ [5], considering that this metrics is influenced by T_a, solar radiations and humidity [7]. Scientists working with farmed animals have also developed and validated several indexes to quantify heat load, including the widely used Heat Load Index (HLI) that incorporates $\mathrm{T_a}$, relative humidity, wind speed and solar radiations [8]. While measured in a respirometry chamber, animals are not exposed to wind nor to solar radiations, and are often provided with dried air that facilitates analytical calculations but also facilitates passive evaporative cooling [9]. The humidity at which Beaman et al. [1] measured dovekies does not seem to be reported, and I thus assumed three scenarios for the following calculations, namely dry air ($RH = 0\%$), moderate humidity ($RH = 50\%$) and saturated air ($RH = 100\%$). Based on the climatic conditions (T_a, wind speed, RH) experienced by wild dovekies from [3] and the solar radiations estimated at their study site during the study period (https://open-meteo.com/en/docs/historical-weather-api), I calculated both the T_g (based on equation from [7]) and HLI (based on equation for $T_g < 25°C$ from [8]) experienced by wild dovekies and putted them in perspective of the T_g and HLI experienced within the respirometry chamber at the upper critical temperature determined by [1] (Fig. 3). While Beaman et al. [1] seem to conclude that wild dovekies should not really suffer from heat stress based on T_a alone, the data presented in Fig. 3 suggest that wild dovekies are most likely experiencing environmental conditions above their upper critical temperature quite frequently when solar radiations are high. It is also worth noting here that the maximum local T_a reported by [3] and used for Fig. 3 calculations is *ca.* 13.5°C, while local T_a can reach more than 20°C according to both [1] and (https://open-meteo.com/en/docs/historical-weather-api). This suggests that the projection of Fig. 3 is likely underestimating the actual risk of heat stress for wild dovekies.

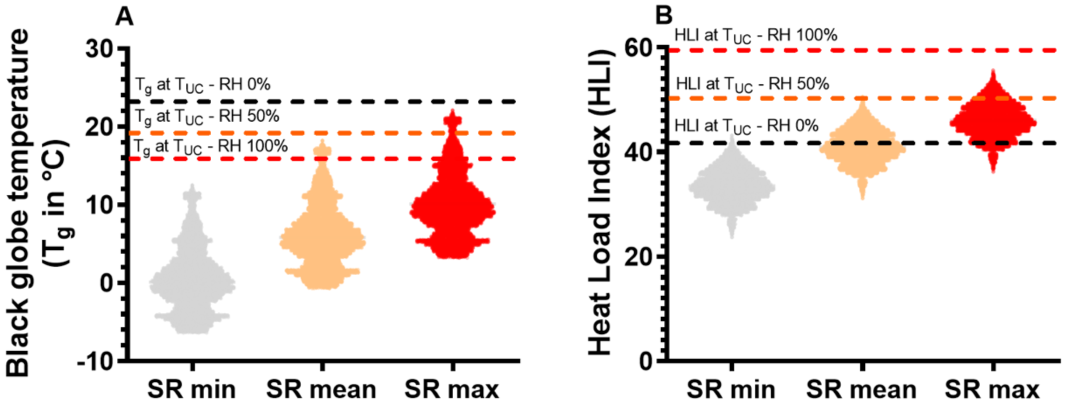

Fig. 3: Heat load indexes (A: black globe temperature T_g; B: heat load index *HLI*) calculated for wild dovekies from [3] **under three solar radiation (SR) conditions (*i.e.* minimum, mean, maximum) according to the heat load experienced by dovekies in a respirometry chamber at their upper critical temperature (T_{UC})** [1] **under three relative humidity conditions (*i.e.* RH = 0%, 50% or 100%)**.

Thirdly, while Beaman et al. (2024) acknowledge that their data is restricted to inactive birds, they do not seem to consider much further in their predictions the fact that wild dovekies are spending approximately half of their time engaged in energy expensive and heat-producing activities that are likely to increase the risks of heat stress. The *heat dissipation limit theory* posits that the capacity to dissipate metabolic heat limits the maximum rates of energy expenditure in endotherms, and that managing hyperthermia risk constrains the biology and ecology of wild endotherms [10,11]. Therefore, I believe that caution should be taken when extrapolating the effect of warm environmental conditions on wild animals if measurements are limited to individuals at rest. If dovekies have to rest at sea or in the colony to cool down as suggested by Beaman et al. [1], they are likely to suffer from warm environmental conditions in terms of foraging performance, which should be costly for reproductive success and/or body maintenance.

Fourthly, based on the relatively modest increase in water requirement projected for dovekies under climate warming (1.1 to 2.0 the actual needs), Beaman et al. [1] suggest that water availability should not be much of an issue for wild dovekies, especially since they have easy access to seawater and possess salt glands. While the water requirements are likely under-estimated since T_a only (and not heat load) has been used in their projections, there are two other likely constraints for dovekies in terms of water availability. First, drinking seawater is not cost-free since the metabolic cost of drinking seawater has for instance been estimated to *ca.* 15-20% of basal metabolic rate in wild shorebirds [12]. Second, leaving the nest for reaching seawater is not cost-free since it implies letting the egg or chick unattended, and thus exposed to adverse environmental conditions and predators. It has for instance been shown that it increases the risk of reproductive failure in wild guillemots [6]. At *ca.* 5°C, the dovekies measured by Beaman et al. [1] evaporate approximately 5.8g of H_2O/day (while resting and not digesting), which represents ca. 6% of their total body water [4], while at their T_{UC} (*i.e.* way before the inflexion point for evaporative water loss), it represents 15.6g of H_2O/day or 16% of their total body water. Those data are likely underestimating massively the water loss of wild dovekies, since water influx in free-living individuals has been estimated to *ca.* 137 g/day [4]. Therefore, I believe that more work is needed on the water balance of wild dovekies (and seabirds in general) in the context of climate change, and that the easy access to seawater mentioned by Beaman et al. [1] is likely too simplistic and far from being cost-free.

While measurements under experimental conditions at various T_a are undoubtedly extremely valuable to evaluate the thermal physiology at the species or individual level, my opinion is that extreme caution should be taken when using such data to predict the response of wild animals to climate change or extreme climatic events such as heat waves. I suggest that to really grasp the perils faced by wild animal in response to climate change and extreme climatic events, *in-situ* measurement of the biological responses to variations in heat load (encompassing not only T_a but also solar radiations, wind speed and humidity measured at the micro-climatic level [5]) should be assessed, using behavioural signs of heat stress (*e.g.* panting as in [6]), time-activity budgets (*e.g.* to gather information on reduced foraging activity or parental care under warm conditions [13]) and physiological measurements (*e.g.* body temperature, activity and energetics through heart rate (*e.g.* as in [14]), as well as dehydration status (*e.g.* as in [15])). Such approach should ideally be complemented by studying the impact of warm environmental conditions on reproductive success (see for instance the impact of warm conditions on reproductive failure in [6]) and on the potential delayed effects for survival prospects (see for instance the negative effects of warm/dry environmental conditions on telomere length [16], a biomarker of ageing and survival prospects).

Wild animals live in a complex environment and demonstrate complex responses to environmental variations. While one necessarily needs to simplify the biological complexity to model its future trends, an over-simplification of the complexity of thermal biology might lead to misleading conclusions when forecasting the effects of climate change on wild animal populations.

Data availability

The datasets used in this manuscript are available on *FigShare*: 10.6084/m9.figshare.26509378

Author's contribution

Study design: AS. Funding acquisition: AS. Data collection and analysis: AS. Writing: AS.

Ethical note

Only data previously collected by [4], [3] and [1] were used for this commentary

Acknowledgments

AS is grateful to [3] for providing raw data in their original publication, to A. Noiret for helpful discussions on theoretical concepts, and to an IdEx grant from the Université de Strasbourg on a related topic (*HotPenguin*).

References

1. Beaman JE, White CR, Clairbaux M, Perret S, Fort J, Grémillet D. 2024 Cold adaptation does not handicap warm tolerance in the most abundant Arctic seabird. *Proc. R. Soc. B* **291**, 20231887. (doi:10.1098/rspb.2023.1887)

2. Short JC, Freeman MT, McKechnie AE. 2022 Respirometry protocols for avian thermoregulation at high air temperatures: stepped and steady-state profiles yield similar results. *J. Exp. Biol.* **225**. (doi:10.1242/jeb.244166)

3. Grunst ML, Grunst AS, Grémillet D, Kato A, Gentès S, Fort J. 2023 Keystone seabird may face thermoregulatory challenges in a warming Arctic. *Sci. Rep.* **13**, 16733. (doi:10.1038/s41598-023-43650-5)

4. Gabrielsen GW, Taylor JRE, Konarzewski M, Mehlum F. 1991 Field and Laboratory Metabolism and Thermoregulation in Dovekies (Alle alle). *Auk* **108**, 71–78. (doi:10.1093/auk/108.1.71)

5. Mitchell D, Maloney SK, Snelling EP, Fonsêca V de FC, Fuller A. 2024 Measurement of microclimates in a warming world: problems and solutions. *J. Exp. Biol.* **227**. (doi:10.1242/jeb.246481)

6. Olin A, Dück L, Berglund P, Karlsson E, Bohm M, Olsson O, Hentati-Sundberg J. 2023 Breeding failures and reduced nest attendance in response to heat stress in a high-latitude seabird. *Mar Ecol Prog Ser* (doi:10.3354/meps14244)

7. Hajizadeh R, Dehghan SF, Golbabaei F, Jafari SM, Karajizadeh M. 2017 Offering a model for estimating black globe temperature according to meteorological measurements. *Meteorol. Appl.* **24**, 303–307. (doi:10.1002/met.1631)

8. Gaughan JB, Mader TL, Gebremedhin KG. 2011 Environmental Physiology of Livestock. , 243–265. (doi:10.1002/9781119949091.ch14)

9. Dyk M van, Noakes MJ, McKechnie AE. 2019 Interactions between humidity and evaporative heat dissipation in a passerine bird. *J. Comp. Physiol. B* **189**, 299–308. (doi:10.1007/s00360-019-01210-2)

10. Speakman JR, Król E. 2010 Maximal heat dissipation capacity and hyperthermia risk: neglected key factors in the ecology of endotherms. *Journal of Animal Ecology* **183**, no-no. (doi:10.1111/j.1365-2656.2010.01689.x)

11. Grémillet D, Meslin L, Lescroël A. 2012 Heat dissipation limit theory and the evolution of avian functional traits in a warming world. *Funct. Ecol.* **26**, 1001–1006. (doi:10.1111/j.1365-2435.2012.02048.x)

12. Gutiérrez JS, Masero JA, Abad-Gómez JM, Villegas A, Sánchez-Guzmán JM. 2011 Understanding the energetic costs of living in saline environments: effects of salinity on basal metabolic rate, body mass and daily energy consumption of a long-distance migratory shorebird. *J. Exp. Biol.* **214**, 829–835. (doi:10.1242/jeb.048223)

13. Ven TMFN van de, McKechnie AE, Cunningham SJ. 2019 The costs of keeping cool: behavioural trade-offs between foraging and thermoregulation are associated with significant mass losses in an arid-zone bird. *Oecologia* **191**, 205–215. (doi:10.1007/s00442-019-04486-x)

14. Menzies AK, Studd EK, Majchrzak YN, Peers MJL, Boutin S, Dantzer B, Lane JE, McAdam AG, Humphries MM. 2020 Body temperature, heart rate, and activity patterns of two boreal homeotherms in winter: Homeostasis, allostasis, and ecological coexistence. *Funct. Ecol.* **34**, 2292–2301. (doi:10.1111/1365-2435.13640)

15. Salaberria C, Celis P, Rull IL, Gil D. 2014 Effects of temperature and nest heat exposure on nestling growth, dehydration and survival in a Mediterranean hole-nesting passerine. *Ibis* **156**, 265–275. (doi:10.1111/ibi.12121)

16. Eastwood JR, Connallon T, Delhey K, Hall ML, Teunissen N, Kingma SA, Porte AML, Verhulst S, Peters A. 2022 Hot and dry conditions predict shorter nestling telomeres in an endangered songbird: Implications for population persistence. *Proc National Acad Sci* **119**, e2122944119. (doi:10.1073/pnas.2122944119)