

Comment



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Comment on an analysis of endotherm thermal tolerances: systematic errors in data compilation undermine its credibility

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1. Introduction

Understanding the vulnerability of animal populations and communities to rapid climate warming is a critically important endeavour and has recently been informed by a variety of meta-analyses (e.g. [1]). One current area of interest is the synthesis of thermoregulatory data from mammals and birds to examine geographical variation in thermal limits, by comparing thermoregulatory parameters such as thermoneutral zone (TNZ) breadth and variation in the upper and lower critical temperatures that bound the TNZ [2–5]. Here, we report wide-ranging errors in the dataset that is the foundation of Khaliq *et al.*'s [2] analysis.

Khaliq *et al.* [2] presented a large meta-analysis that extracted data on thermoregulation in birds (161 species) and mammals (297 species) from the physiological literature, with the goal of examining the relationships between physiological capacities and geographical variation in climate. From these individual studies, they compiled data on the lower (LCT) and upper (UCT) critical temperatures, which represent the upper and lower boundaries of the TNZ, the range of environmental temperatures over which resting metabolic rate is constant in endothermic homeotherms.

Our discovery that many unsuitable or non-existent data had been included in the dataset compiled by Khaliq *et al.* [2] was initially triggered by our surprise at the large number of mammal UCT data ($N = 297$). At the time, we were conducting a comprehensive review of mammalian thermoregulation in the heat and had found far fewer studies (approx. 100) that contained data permitting the determination of a UCT. We then examined the methods section in the electronic supplementary material, figure S1 and accompanying text, which indicated that Khaliq *et al.* had indeed used the appropriate definitions of LCT and UCT. Given this disparity, we reviewed the source data from a subset of the studies cited by Khaliq *et al.* [2] and found that many of these studies did not involve measurements of metabolic rate at air temperatures high enough to allow a determination of the UCT. Without valid UCT data, the breadth of the TNZ could also not be determined—invalidating many of TNZ breadth data as well. After this limited initial survey, we then examined every available source study cited by Khaliq *et al.* [2] and conducted a comprehensive survey of the data and methods. The review of the source data, which we present here, differs from that of Khaliq *et al.* [2] in total numbers of species and studies because of a few instances of cited references not matching reported data, or unpublished/unavailable references (birds: 4/161 species; mammals: 13/297 species; data for only 295 species listed in supporting information accompanying [2]).

We examined the original papers cited as the sources of 157 of 161 avian data and 284 of 295 mammalian data provided in Appendix S1 of Khaliq

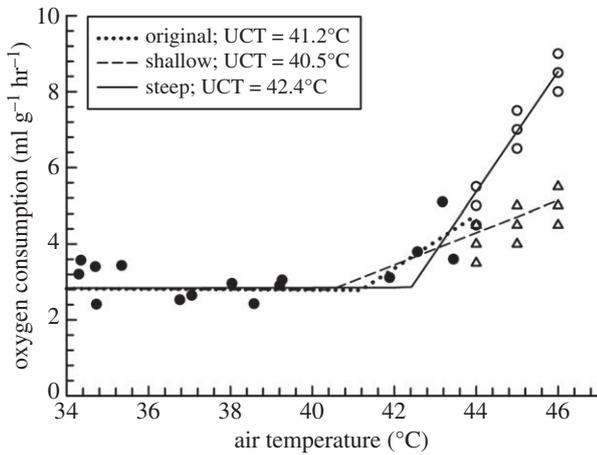


Figure 1. Estimates of upper critical temperature (UCT) are strongly dependent on the air temperature (T_a) range over which resting metabolic rate is measured. Ambrose *et al.* [6] measured oxygen consumption in spinifexbirds (*Eremiornis carteri*) over a T_a range extending up to approximately 43°C (actual data shown as filled circles); this is an example of a dataset that we classified as Category 2 (Insufficient data). The dotted line is a regression model fitted to the original data using the R package *segmented*, and yields a UCT of 41.2°C. However, in this dataset resting metabolic rate (RMR) has not, in our opinion, been measured at over a wide enough range T_a for this UCT estimate to be reliable. To illustrate, we have added hypothetical data (open symbols) to show how the actual RMR versus T_a relationship could vary at high T_a . The estimated UCT varies by nearly 2°C between these two scenarios: the steeper increase in RMR (circles) results in an estimated UCT of 42.4°C, whereas the shallower line yields a value of 40.5°C. For some species that use cutaneous evaporation or gular flutter a UCT may not even exist. Data for *E. carteri* were extracted from the original figure using Digitizeit software (<http://www.digitizeit.de>).

et al. [2]; electronic supplementary material. Each datum was allocated to one of the following categories:

- (i) *Good data.* The source study empirically demonstrated an increase in metabolic rate above the TNZ, with a clear inflection point defining the UCT based on data for at least two individuals per species and over a sufficiently wide range of air temperatures above the TNZ to reliably estimate the UCT.
- (ii) *Insufficient data.* The original study provided some empirical evidence of an increase in metabolic rate above the TNZ, but was based on only a single individual and/or measurements at too few air temperatures to reliably estimate a UCT. Estimating a credible UCT requires that there be sufficient data above the UCT to produce a line that would intersect the thermoneutral line and thus define the UCT (figure 1).
- (iii) *No UCT.* In the original source study, metabolic rate was not measured at air temperatures high enough to elicit an increase above thermoneutral levels. For these datasets, the UCT is unknown, but if one exists it would presumably be above the highest measured temperature.

2. Results

Of the 284 UCT data we checked for mammals, Category 1 (Good data) included only 33.1% of the original data (94 species), Category 2 (Insufficient data) accounted for 25.4% of the data (72 species) and Category 3 (No UCT) accounted for 41.5% of the data (118 species) included in the original dataset (electronic supplementary information). Consequently, UCT

and TNZ breadth data are available for only 33.1% of the mammal species included in Khaliq *et al.*'s [2] analysis.

Of the 157 UCT data we checked for birds, Category 1 (Good data) accounted for only 22% of the original data (34 species), Category 2 (Insufficient data) accounted for 21% of the data (33 species) and Category 3 (No UCT) accounted for 57% of the data (90 species) included in the original dataset. Consequently, UCT and TNZ breadth data are available for only 22% of the bird species included in Khaliq *et al.*'s [2] analysis (electronic supplementary information).

We found serious errors in the data compilation methods of Khaliq *et al.* [2]. Although the authors clearly stated and graphically defined the UCT in the methods section in their electronic supplementary material, figure S1, they failed to follow these criteria during actual data collection, which led to the inclusion of UCT data that did not exist (47% of all data). In almost all cases, the authors simply took the highest air temperature at which metabolic rate was measured and designated it the UCT—even though there was no increase in resting metabolism above thermoneutral levels. A few of the original source studies contain statements such as ‘thermoneutrality extended from XX to YY °C’ (e.g. [7–9]). Statements such as these could be interpreted as implying that the higher of the two air temperatures represented the UCT, but even cursory examination of the figures in these papers reveals that data collection had ended at a temperature below the UCT.

We also found a substantial portion of the data that were based on sample sizes too small to produce a line above the UCT that could be used to define this point. We suggest that reasonable data inclusion criteria (e.g. $N > 2$ individuals, $N > 2$ data points above UCT needed to reliably fit a line) would have resulted in a more credible dataset. Based on the above observations, we found that only 29% of the bird and mammal data presented in Khaliq *et al.* [2] provide meaningful estimates of the UCT and TNZ breadth. We believe that the loss of approximately 71% of the data used in this study creates significant uncertainty as to validity of the conclusions reached by the authors.

We suggest that explicitly stated, expertly informed data inclusion criteria and a more than cursory knowledge of the source data/discipline are often critical for robust meta-analyses [10]. To illustrate our view, we provide two examples of how expert knowledge could have been used inform data selection for this particular analysis.

- (i) The measurement conditions (e.g. chamber humidity, time of day, feeding state) used in physiological studies are likely to directly impact the comparability of the source data and their suitability for inclusion in any meta-analysis. Most animals, for example, have circadian cycles of activity and rest and metabolic measurements taken during the active phase of the daily cycle are on average 20–25% and 28% higher than rest phase values in birds [11] and small mammals [12], respectively. These differences argue for not mixing active and rest phase measurements because the higher heat loads associated with active phase metabolic values are very likely to produce different critical temperature values compared with rest phase measurements. Our analysis of the source data from Khaliq *et al.* [2] found that within the Category 1, ‘Good’ data, where circadian phase could be determined, 29% of the bird data (9/31) and 8% (5/60) of mammal data were collected in active phase animals. For mammal data, in an additional 29 of the ‘Good’ cases the measurement phase was unclear.

These observations could affect both the estimated LCT and UCT values (and TNZ breadth) and should have been acknowledged and considered.

- (ii) Expert knowledge of the differences in functional traits among species may also help identify the source studies and species that are suitable for inclusion in a given meta-analysis. One might argue that in this study, the metabolic values obtained at the highest air temperatures measured provide insight into minimum values for the UCT and these data thus would provide insight into the minimum TNZ breadth. This assumption, however, has problems if the sample includes species that do not exhibit a UCT. Increases in metabolism associated with active heat dissipation above the UCT may only be found in species that actively pant to increase evaporative heat loss. For species that have pathways of evaporative heat dissipation that do not require panting and movement of the entire respiratory tract, increasing heat stress may not be manifested by a sharply defined increase in metabolic rate and a definable UCT. This phenomenon is exemplified in avian orders where increases in evaporative heat

dissipation through cutaneous pathways (Columbiformes) or by means of gular flutter (Caprimulgiformes and others) involve negligible metabolic costs (e.g. [13,14]). Among mammals, including humans, in which sweating is the primary mode of evaporative heat dissipation, we would also not expect a pronounced metabolic response to increasing heat stress [15]. Here, we have just provided two of a number of possible examples and suggest that selecting source data for inclusion in meta-analyses may not be a simple task and that expert knowledge may be of significant benefit.

We sincerely hope that our observations lead to an increased awareness of the need for highly informed approaches to data mining in meta-analyses and the critical need for expert participation and/or review. We suggest, as a minimum, that the authors undertake a full reanalysis of the more constrained dataset and report their new findings.

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