Shrinking body size may not provide meaningful thermoregulatory benefits in a warmer world

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AUTHOR CONTRIBUTIONS

This commentary resulted from a lab meeting at the Department of Biology, Lund University, Sweden. AN, EP, JKRT and ET conceptualized the paper and drafted the outline. AN wrote the first complete draft, which was revised in equal measure by EP, JKRT, ET and AN. JKRT and AN constructed the heat balance model, JKRT performed the modelling, and JKRT and AN developed the graphic material. Author names are listed in alphabetical order to reflect equal contributions.

MAIN TEXT

In a recent and impressive analysis of avian morphological data (covering >250 000 male birds from 105 species), Youngflesh et al.[1] report that birds breeding in North America have become significantly lighter over the last three decades, coincident with rising breeding season temperatures. Because these observations recapitulate predictions under Bergmann's Rule (i.e., that the body size of congeners and conspecifics is usually larger near the cooler poles than near the warmer equator), the authors argue a thermoregulatory benefit to their occurrence under the assumption that smaller-bodied animals have lower cooling costs than larger-bodied animals in a warming world. We agree that warmer environments during reproduction may well explain avian body size declines. However, we question whether: (1) changes in heat balance attributed to these declines are sufficiently large to explain observed size reductions, and (2) increased thermoregulatory efficiency during the short windows where reproduction occurs is always relevant, particularly when tenancy in breeding ground temperatures is short (i.e., among migrants). Generalizability of these results may be limited further by sex-specific enquiry, which overlooks the possibility of divergent selection on body size in males and females under climate warming. In this commentary, we expand on these concerns hoping to instigate discussion on knowledge gaps that need closing if we wish to better understand the proximate and ultimate drivers of shapeshifting animals in a changing world.

Data presented by Youngflesh et al.[1] corroborate several recent reports detailing how animals are changing body size and shape in parallel with warming temperatures[2-4]. These collective observations are notable, and we share the view of Youngflesh et al.[1] that such temporal trends must be described and understood from both evolutionary and applied points of view[5,6]. We also agree that smaller animals are theoretically better equipped to withstand higher ambient temperatures in thermal environments characterised by net heat loss, since their higher surface area to volume ratios increase the proportion of integument usable for heat transfer. However, the reported mean body size shifts in this and other studies are small (here, -0.56%[1]; Fig. 1A) and so, according to currently available allometric relationships, yield near-negligible effects on mean body surface area (-0.38%) and surface area to volume ratios (+0.19%) across species (Fig. 1B). Such minor changes in morphology hold little thermoregulatory bearing, with conservative heat balance models (i.e., assuming both complete and static plumage cover) suggesting a mean increase in heat flux (W / cm^2) of around 0.14% Fig. 1B). The estimated effects on evaporative water loss (+0.10%), total heat loss rate (i.e., thermal conductance; +0.27%), basal heat production (i.e., basal metabolic rate; -0.39%), upper critical temperature (-0.05%), and the metabolic response to warmth (-0.48%) are similarly weak (Figs. 1B-C). Even for higher estimates of body mass change (e.g., -2.6% on average in ref.[4]), thermoregulatory benefits are still likely to be limited (e.g., +0.60% in heat flux, +0.42% in evaporative water loss, +1.10% in thermal conductance, and -1.56% in basal metabolic rate). By comparison, a typical physiological thermoregulatory response may lead to a 5- to 15-fold increase in evaporative water loss upon heat exposure[7]. In all, it seems doubtful that the observed shifts in body mass reported by Youngflesh et al.[1] and elsewhere will hold any significant bearing over the degree to which species can respond to thermoregulatory pressures caused by warming temperatures. In fact, available data suggest that, interspecifically, maximum tolerable air temperature in passerines has positive allometry[7], and reducing plumage depth by as little as 1% would over-double the heat dissipation effect ascribed to body shrinkage in ref.[1] (i.e., 0.39% reduction in heat flux relative to 0.14%). We therefore caution against such adaptationist conclusions in the absence of empirical evidence of thermoregulatory benefits.

Second, the authors base inference on data obtained during Northern Hemisphere springs and summers (May 1st to July 31st). While this in itself is perfectly reasonable, the overwhelming majority of the species studied were migrants (66%, or 69 of 105 species) or partial migrants (22%, 23 of 105)[8], suggesting short tenancy in at least some study regions, or even measurement during migratory stop-over. In these contexts, regressing morphology against local ambient temperature appears problematic. Specifically, conceptualization and hypothesis testing become difficult when the precise temperatures to which the birds are responding to morphologically are unknown, even if migrants may track their thermal environment across the annual cycle[9]. The problem of spatial asynchrony arguably lessens if shrinking body sizes reflect plastic effects of developmental temperature on final morphometry (as suggested by Youngflesh et al. and others[1,10]), but recent theory still contends that broad generalizations of warming environments during development and decreasing size are likely naïve[11]. In any case, spatial asynchrony between sites of measurement and sites of operation remains a concern if size declines reflect selection, for example via temperature-mediated, size-dependent mortality[1]. For this reason, we suggest life history parameters be carefully considered in future modelling efforts to shed light on the issues outlined above.

Last, inference in the study by Youngflesh et al.[1] is based only on male birds with the rationale that reproductive status (i.e., gravidity) renders true female mass uncertain (e.g., ref.[12]). Removing females from the dataset might well be appropriate statistically but raises concerns about the generality of conclusions if any selection for size is sex-specific. For example, larger females can lay larger eggs that produce larger chicks[13], and so, may sire offspring with higher survival[13,14]. It could therefore be expected that changes in body size in response to warming may be constrained in females relative to males. In line with this, a recent mammalian study found that while males and females responded qualitatively similarly to developmental temperature manipulations, the effect of body size was markedly larger when males were modelled alone compared to when measurements of both sexes were combined[15]. Other studies report that male and female birds show differential thermal sensitivity of reproductive investment[16]. While we understand that exclusion of females from the current data set may have been a necessity for modelling, we suggest that future studies consider the possibility that natural selection for body size differs between the sexes, instead of considering only the less variable sex or collapsing the data (e.g., refs.[3,4]).

By now, several ambitious studies have demonstrated that wild animals show concerted changes in body mass, size, and shape in conjunction with warming temperatures. Evidence suggests such shapeshifting probably stems from plasticity more than it reflects any adaptive evolutionary responses to changing thermal environments[17-19]. Whether such plasticity is adaptive, non-adaptive, or neutral remains unclear. However, predictions based on currently available allometries suggests that even if a reduction in body mass mediates changes to heat production and dissipation, the predicted shifts in mean trait levels are often too small to provide meaningful thermoregulatory value (see Fig. 1), especially when compared against those accrued by plastic, physiological responses to cold and warmth. For this reason, the precise role of declining size toward thermal balance under climate warming in birds – or any endotherms – is speculative and should remain acknowledged as such until further evaluated. We suggest future research focus be placed on *how* size declinations occur in the warmth (e.g., via selection, or plasticity) and *why* it matters by evaluating empirically the energetic and fitness benefits of reducing body size under climate warming by observed degrees.

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CONFLICT OF INTEREST

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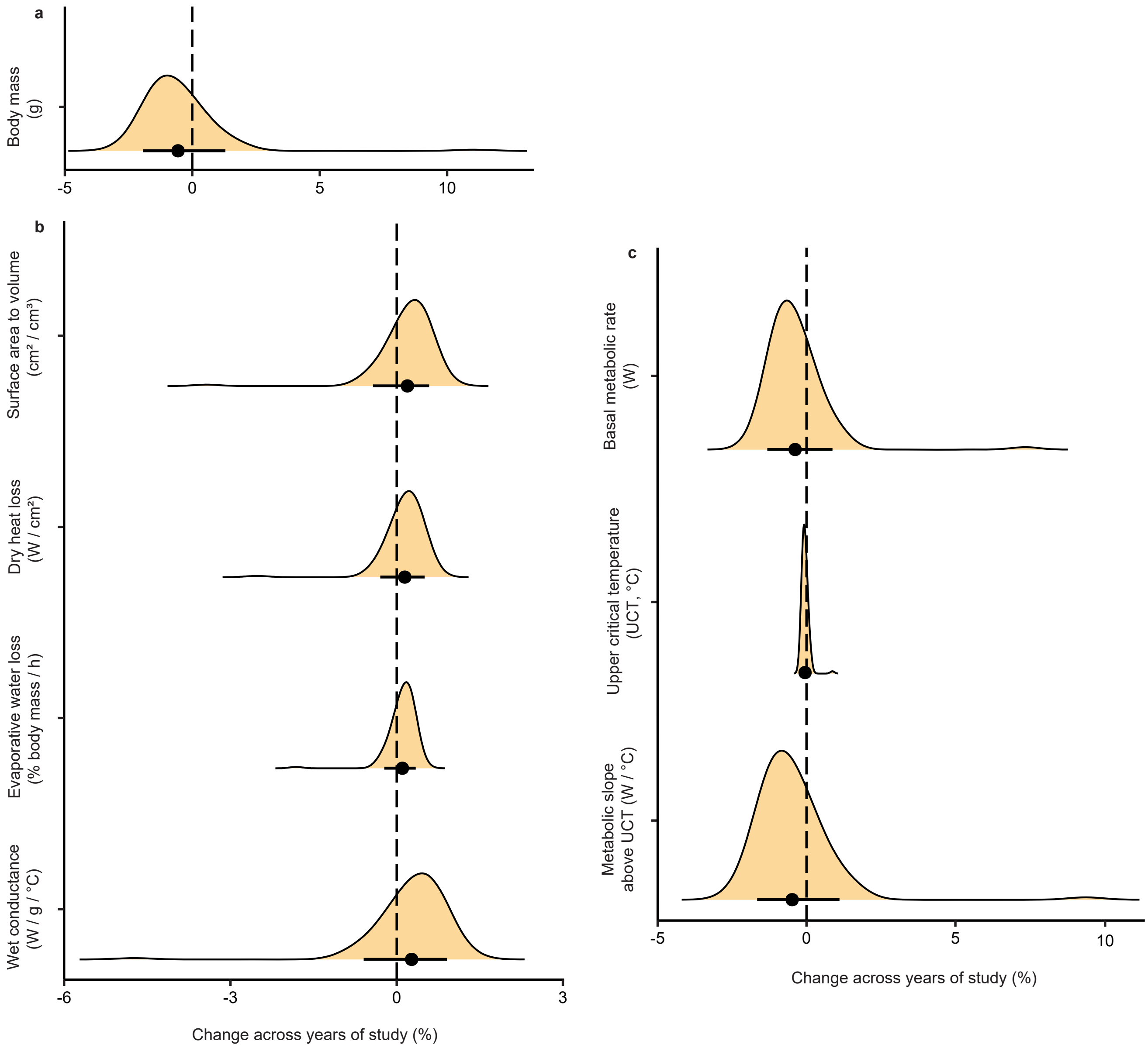
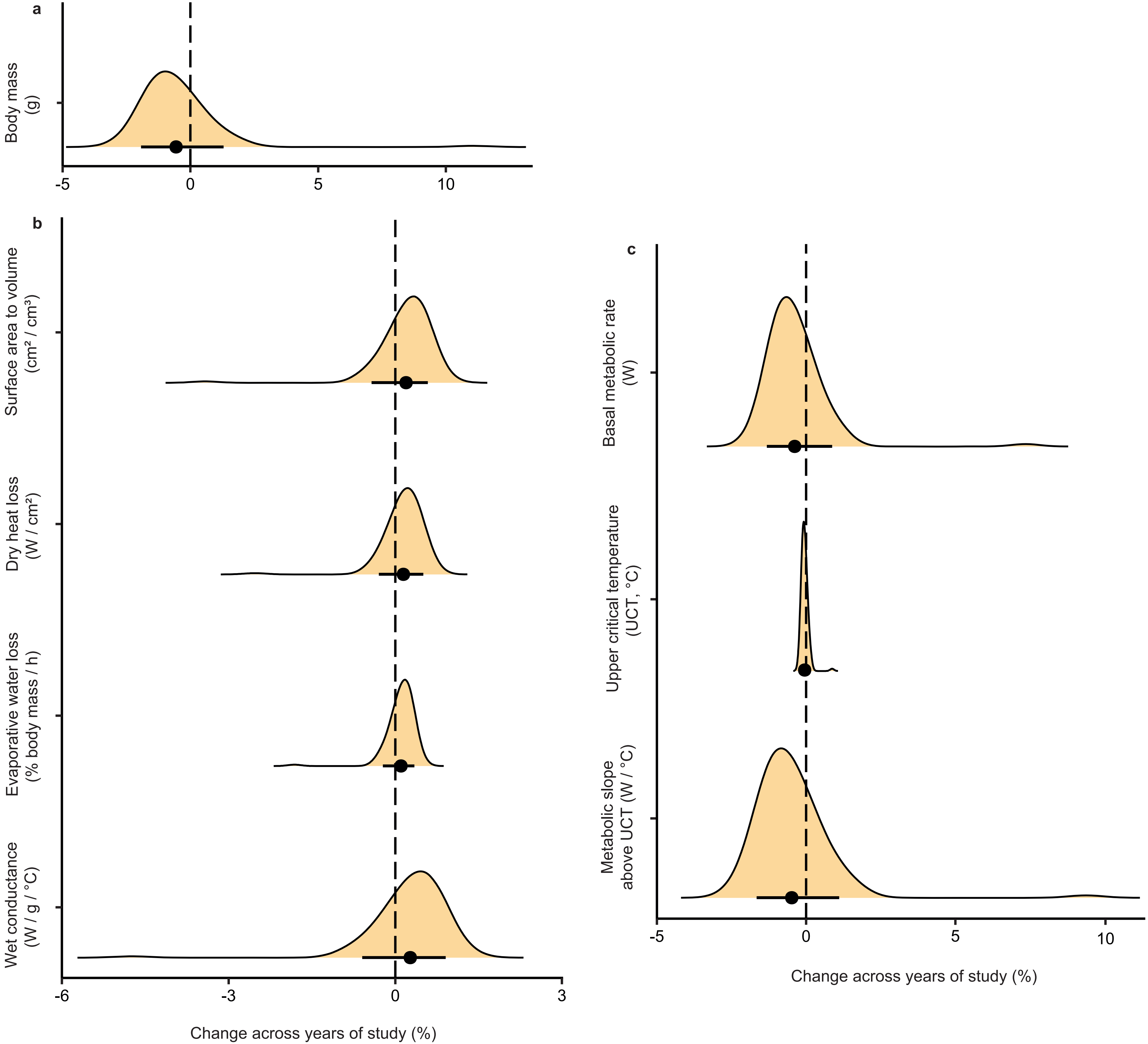
FIGURE LEGENDS

Fig. 1. For most bird species, temporal changes in body masses are too small to contribute biologically meaningful shifts in heat production and dissipation, suggesting thermoregulatory benefit is an unlikely outcome of shapeshift under climate warming. A) Data on mean shifts in body masses from Youngflesh et al.[1]. B) These data were used to predict changes in body proportions, heat flux and several thermo-physiological variables of relevance for how a bird exchanges heat with its environment. We predicted body surface area from body mass[20] and then assumed body densities of 1.1 g / cm^2 (ref.[21]) to estimate effects on surface area to volume ratios. Shifts in surface area were then used to estimate the change in sensible ("dry") heat loss using biophysical equations from Porter and Kearney[22] and assuming still air conditions, no conductive heat loss (i.e., contact heat loss between the integument and the environment), static skin surface temperature of 41°C (i.e., a representative small bird body temperature[23]), a soft tissue thermal conductivity of 0.5 W / m / °C[22], a plumage conductivity of 0.0272 W / m / °C[22], and a plumage depth equalling 1/3 × log10 of body mass in cm. Latent ("wet") heat loss (i.e., evaporative water loss) was estimated based on data in McKechnie et al.[7], and total mass-specific heat dissipation rate (i.e., thermal conductance) was predicted based on Aschoff's allometry for daytime conditions[24]. C) Body size data were also used to estimate changes in basal heat production (i.e., basal metabolic rate), upper critical temperature (UCT, i.e., the temperature above which heat dissipation mechanisms must be engaged to prevent increasing body temperature), and the slope of the relationship between resting metabolic rate and air temperature above UCT, using allometric relationships in refs.[7,25]. Solid plotting symbols show mean trait levels and bars denote the 89% quantile intervals.


a
Body mass
(g)
-5
0
5
10
b
Surface area to volume
(cm² / cm³)
Dry heat loss
(W / cm²)
Evaporative water loss
(% body mass / h)
Wet conductance
(W / g / °C)
-6
-3
0
3
Change across years of study (%)
c
Basal metabolic rate
(W)
Upper critical temperature
(UCT, °C)
Metabolic slope
above UCT (W / °C)
-5
0
5
10
Change across years of study (%)


a
Body mass
(g)
-5
0
5
10
b
Surface area to volume
(cm² / cm³)
Dry heat loss
(W / cm²)
Evaporative water loss
(% body mass / h)
Wet conductance
(W / g / °C)
-6
-3
0
3
Change across years of study (%)
c
Basal metabolic rate
(W)
Upper critical temperature
(UCT, °C)
Metabolic slope
above UCT (W / °C)
-5
0
5
10
Change across years of study (%)