



Thermal imbalance drives avian performance and responses to climate warming

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Thermal performance curves are widely used to predict ectothermic responses to climate warming but are less effective for predicting endotherm performance across environmental conditions because thermoregulation often decouples body temperature from ambient temperature. We develop theory and provide empirical evidence for performance curves in endotherms structured by net sensible heat flux (Q), an integrative index of thermoregulatory imbalance. Using biophysical simulations in tree swallows, we show that performance varies predictably with Q (which we term “QPCs”), thereby explaining variation in nestling provisioning performance, reproductive fitness, and geographic limits, while also forecasting responses to climate change. We also demonstrate that thermal imbalance helps shape breeding ranges of birds across North America. Our findings introduce Q as a broadly relevant ecophysiological dimension that constrains performance in endotherms and provides a framework for predicting endotherm responses to climate warming.

ecophysiology | climate change | thermoregulation | biophysical ecology | tree swallow

Within an organism, life-sustaining physiological processes function optimally over a narrow range of body temperatures (1), resulting in reduced performance at temperatures above or below the optimum (2). Consequently, whole-organism performance (e.g., sprint speed, digestive efficiency) and population-level processes (e.g., population growth rate) of ectotherms typically exhibit a similar, nonlinear relationship with body temperature (2). The thermal performance curve (TPC) model, which describes this relationship, has long been the foundational framework for understanding the thermal sensitivity of fitness and predicting species' vulnerability to climate change (2–7). To date, efforts to develop TPC analogs for endothermic organisms have yet to achieve comparable predictive power or broad applicability (8). The central challenge is that endotherms have adaptations that can decouple body temperature from the thermal environment, complicating efforts to characterize the thermal dependence of performance (2, 8). This lack of a comparable framework not only limits insight into the basic environmental physiology of endotherms (8) but also hampers efforts to forecast their responses to climate change (9).

In the absence of TPCs, physiologically informed forecasts for endotherms have typically relied on identifying when environmental conditions exceed physiological thresholds [e.g., thermoneutral zone (TNZ)] or assumed critical limits, such as hyperthermic or dehydration limits (10, 11). However, threshold-based approaches do not capture the continuous nature of performance across thermal conditions. In response, recent efforts to develop TPC analogs for endotherms suggest using air temperature (T_{air}) (8) or core body temperature (T_b) to construct performance curves (12). Yet both T_{air} - and T_b -based models have important limitations. T_{air} -based models overlook key sources of heat flux (e.g., solar radiation, convection from wind, metabolic heat production, evaporative cooling), whereas T_b -based models can obscure substantial variation in the thermal environment because endotherms often behaviorally and physiologically regulate T_b . These omissions limit the ability of such models to describe the physiological and behavioral costs of thermoregulation faced by endotherms (13). A promising alternative is to model performance as a function of net sensible heat flux—the net rate of heat exchange between an animal and its environment that drives thermoregulatory demands. This metric integrates intrinsic variables, such as metabolic heat production and evaporative water loss, and extrinsic variables, such as radiation, convection, and conduction, which can be linked directly to the energetic and physiological costs of thermoregulation.

Endotherms are subject to the same thermodynamic laws as ectotherms but have evolved distinct strategies for managing heat flux (9). Rather than allowing body temperature to track environmental temperatures, homeothermic endotherms maintain relatively stable body temperatures by balancing heat gain and loss through multiple pathways, including

Significance

Climate change is reshaping species' performance, reproduction, and geographic distributions, yet predicting these responses is challenging for many organisms. For ectotherms, performance can often be predicted from environmental temperature, providing a powerful framework for understanding climate vulnerability. In endotherms, however, the maintenance of a relatively stable body temperature alters this relationship, limiting the application of similar approaches. Here, we develop a framework for thermal performance in endotherms based on thermal imbalance between organisms and their environment. We show that this framework accurately predicts relationships between environmental conditions, individual performance, reproductive success, and spatial distributions of songbirds. Our results establish a mechanistic foundation for endotherm thermal ecology and improve predictions of ecological responses to climate change.

The authors declare no competing interest.

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convection, conduction, radiation, and physiological mechanisms such as evaporative cooling and metabolic heat production (14). Among these, evaporative cooling is critical for offloading excess heat in hot environments, while increased metabolic heat production compensates for heat loss in cold environments. These physiological responses are accompanied by behavioral responses (e.g., ptiloerection), morphological adaptations such as an insulation

layer (i.e., plumage or pelage), and adjustments to body temperature – such as heterothermy or torpor – that reduce the need for sustained physiological effort to maintain homeothermy (14).

The combined effects of these environmental and physiological pathways can be collapsed into a single variable, net sensible heat flux (Q ; measured in watts (W); Fig. 1A) (15). This variable quantifies the fluxes primarily generated or regulated by the organism

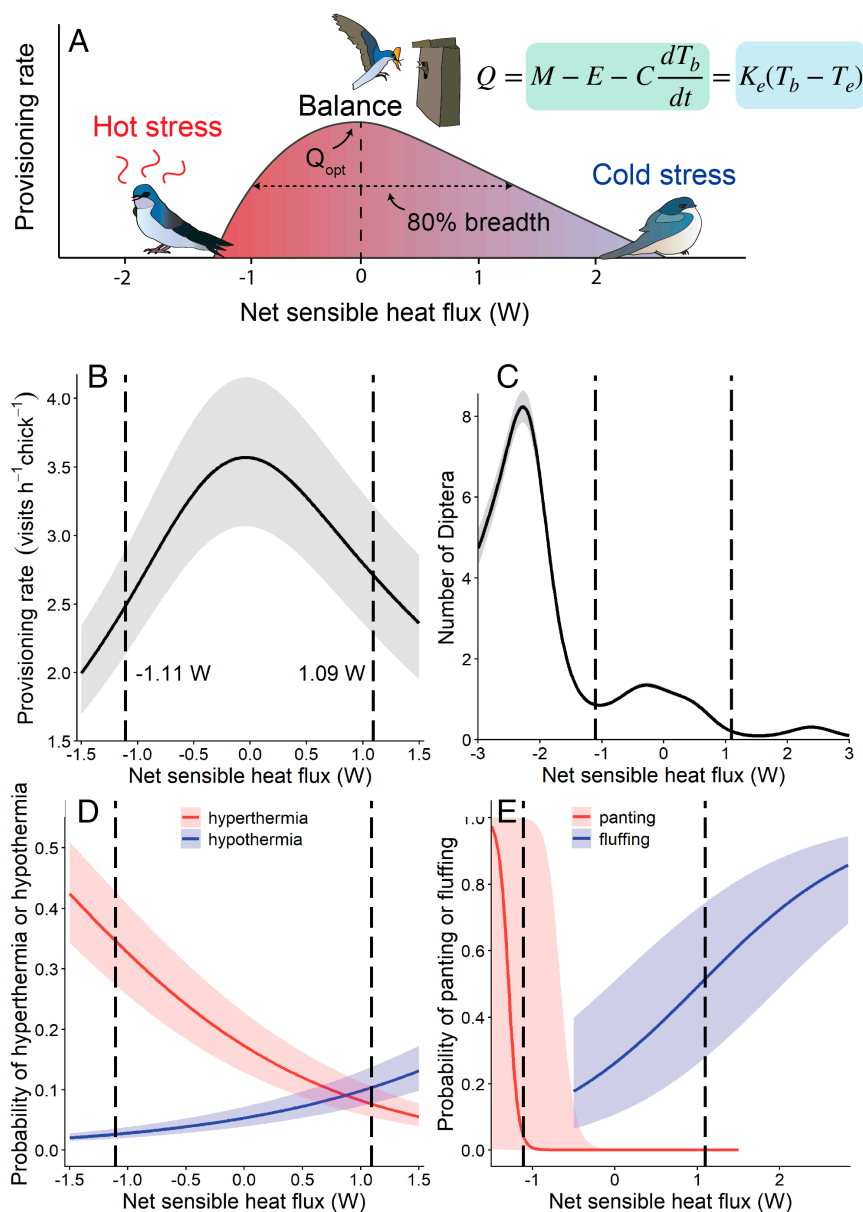


Fig. 1. Evidence for physiologically driven heat flux performance curves in tree swallows. (A) A conceptual figure illustrating how provisioning rate is related to net sensible heat flux, indicating performance was predicted to be highest during heat balance ($Q_{opt} = 0$, vertical dashed line; 80% performance breadth, horizontal dashed line). The equation for net sensible heat flux (Q) highlights the components shaped by the internal physiology of the organism (in green; M = metabolic heat production, E = evaporative heat loss, C = capacitance of isothermal core, dT_b/dt = the rate of change in body temperature) and heat flux experienced with the environment (in blue; K_e = effective conductance, T_b = body temperature, T_e = operative temperature) (SI Appendix). Note that decreasing Q corresponds to increasingly warm environmental conditions, whereas increasing Q corresponds to increasingly cool conditions. Thus, unlike a traditional TPC in which temperature increases from left to right, warmer conditions occur toward the left side of the x-axis ($Q < 0$ W), where organisms must dissipate heat, whereas cooler conditions occur toward the right ($Q > 0$ W), where organisms must generate or conserve heat. (B) Hourly, per chick provisioning rates by tree swallows were highest at -0.066 W [optimal Q (Q_{opt})] and declined above and below this point. The dashed vertical lines indicate the 80% performance breadth, which also appear in B–D. See SI Appendix, Fig. S2 for partial effects plot. (C) Variation in prey abundance was unlikely to drive the shape of the QPC because Diptera abundance increased dramatically as Q decreased below 0, despite concurrent declines in provisioning rates. Moreover, the highest provisioning rates occurred under conditions where insect abundance was comparatively lower. (D) The probability of hyperthermia (red) increased as Q decreased, and the probability of hypothermia (blue) increased as Q increased ($P < 0.001$ for both comparisons). (E) The probability of panting (red) increased as Q decreased ($P = 0.020$) and the probability of ptiloerection (blue) increased as Q increased ($P < 0.001$). The solid curves in all panels represent the predicted marginal effects of the predictor variable on the response variable from generalized additive mixed models that included random intercepts associated with individual bird identification (panels B, D, and E) or camera identification (C) (see SI Appendix for additional details). The shaded bands represent the model 95% CI. Illustrations by E.A.R.

(Fig. 1A; green box) and those driven by the organism–environment gradient (Fig. 1A; blue box). We calculate Q by comparing internal heat flux with sensible heat exchange with the environment to estimate the residual imbalance in the heat budget. When $Q = 0$ W, an organism is in thermal balance and requires no additional thermoregulatory effort. Values that deviate from zero require the organism to engage in behavioral and physiological responses to restore balance—responses that typically come at an energetic or functional cost (16, 17), potentially compromising other aspects of performance. Specifically, positive Q values ($Q > 0$ W) indicate a need to generate more heat or reduce losses, while negative values ($Q < 0$ W) imply a need to shed heat or minimize further gain. Because endotherms can compensate for thermal imbalance through diverse responses with often unknown energetic and functional consequences, we estimate Q in the absence of compensatory thermoregulatory responses and a stable T_b to quantify the magnitude and direction of the underlying thermal forcing acting on the organism exhibiting perfect homeothermy (SI Appendix, Fig. S1). Though clearly a simplifying assumption, this approach provides a standardized measure of thermoregulatory demand in a common energetic currency (watts) integrating across both internal and external sources of heat. We propose that net sensible heat flux provides an appealing ecophysiological axis that could influence endotherm performance analogous to the effect of temperature on ectotherm performance.

Here we show that net sensible heat flux influences fitness-related performance and accurately predicts the geographic distribution of the breeding range in a widely distributed migratory passerine (tree swallow; *Tachycineta bicolor*). We used a 4-y field study on tree swallows to understand the relationship between Q and hourly rates of per chick nestling provisioning, an important metric of reproductive performance (18). We first evaluated whether performance curves developed from net sensible heat flux Q Performance Curve (QPCs) predicted provisioning rates in tree swallows assuming constant metabolic heat production, evaporative water loss, and T_b representative of provisioning adults. We also assessed whether this variation in performance was driven by intrinsic, thermoregulatory processes as opposed to extrinsic factors, like prey abundance. We then determined whether provisioning rates were related to fitness, a key assumption of TPCs (4). Further, we evaluated whether QPCs predicted the observed breeding range of tree swallows across North America and predicted future responses to climate change based on the forecasted changes in heat flux. To explore the generality of the approach, we also assessed whether net sensible heat flux could predict the geographic distribution of additional bird species widely distributed across North America. Together, these approaches reveal how heat flux constrains performance and shapes the fundamental niche of birds.

Results

Evidence of QPCs for Provisioning Rate. Here we show that net sensible heat flux provides an integrative framework to describe the sensitivity of endotherm performance to thermoregulatory demands across a range of environmental conditions. We found evidence of QPCs in tree swallows by combining temperature-sensitive PIT tags, nest monitoring, and biophysical estimates of Q derived from on-site measurements of air temperature, wind speed, and humidity, together with modeled solar radiation (Fig. 1A and SI Appendix, Fig. S2) (19). In total, we obtained 3,011 1-h observations of provisioning rate, calculated as the number of provisioning trips per chick to the nest box during each hourly observation period, from 56 adult tree swallows across four breeding seasons. For these and all other analyses,

we used mixed effect models to account for nonindependence among observations (*Materials and Methods*). Similar to the peak performance observed in ectothermic TPCs (that is, T_{opt}), tree swallows exhibited a clear optimum (Q_{opt}) for provisioning nestlings (Fig. 1B, $Q_{opt} = -0.006$ W; 95% CI = -0.013 to 0.001 W). The 80% performance breadth—a commonly used metric for performance breadth in the TPC literature—spanned zero, indicating optimal performance coincided with heat balance (Fig. 1B, -1.11 , 1.09 W). Provisioning rates declined both above and below Q_{opt} , and reductions in performance were steeper at the warm end (low Q values) than at the cool end (high Q values; Fig. 1A and B). This asymmetry of the QPC (skewness = 0.65) is another feature shared with TPCs, likely due to asymmetric physiological stresses of warm vs. cool conditions (2). We also found that provisioning rate peaked at an optimal air temperature ($T_{air} = 25.94$ °C, SI Appendix, Fig. S3) and exhibited a classic asymmetrical TPC shape. However, the model with heat flux performed substantially better than the air temperature model [$\Delta AIC = 191.80$ (SI Appendix, Provisioning rate and Q)].

Analysis of hourly provisioning rates from two additional tree swallow populations (Ontario and Colorado; SI Appendix, Testing for QPCs in Other Tree Swallow Populations) found evidence of QPCs that resemble that of the focal Iowa population (Ontario: $Q_{opt} = -0.65$ W, 80% performance breadth = -2.15 , 0.85 W; Colorado: $Q_{opt} = -0.45$ W, 80% performance breadth = -1.57 , 0.68 W; SI Appendix, Fig. S4), suggesting that the QPC from the focal population is representative of other populations. Moreover, the 80% performance breadth around Q_{opt} in all populations overlapped the expected optimal conditions for sustaining homeothermy (i.e., $Q \approx 0$ W; that is, heat production balances heat loss to the environment). In other words, provisioning rates are highest when thermoregulatory stress is lowest, consistent with thermoregulatory constraints on performance.

Indeed, multiple lines of evidence suggest that provisioning rates are limited by thermoregulatory constraints, rather than alternative factors like prey abundance. Variation in provisioning rate was unlikely to be fully explained by prey abundance, as numbers of their primary prey (Diptera; SI Appendix, Artificial Intelligence Detection Model) increased in warmer conditions outside of Q_{opt} based on analysis of 335,649 insect camera trap images (Fig. 1C). Nonetheless, lower prey abundance may partially influence lower rates of provisioning in colder conditions and prey availability in this system may be more complex than prey abundance alone (SI Appendix, Food Abundance: Flying Insect Activity). However, we also found evidence that variation in provisioning rate reflects intrinsic thermoregulatory constraints. Under conditions away from Q_{opt} , birds became increasingly likely to deviate from their typical (i.e., modal) body temperature, exhibiting both hyperthermic and hypothermic responses (504,181 measurements from 56 adults; Fig. 1D). Similarly, tree swallows were more likely to exhibit behavioral thermoregulation (that is, panting and piloerection) at conditions outside of Q_{opt} , with predicted probabilities increasing under these conditions (Fig. 1E). Panting, in particular, is a clear sign of heat stress (17) and increases rapidly as Q exceeds the lower threshold of the performance breadth (Fig. 1E). Furthermore, previous experimental work on tree swallows found evidence for thermoregulatory constraints on provisioning rates under both cold and hot conditions (20). Finally, higher provisioning rates in the early stages of nestling development (when nestling growth rates are highest) were associated with a higher probability of nestling-to-fledgling survival (SI Appendix, Fig. S5). Thus, our measure of performance (provisioning rates) was related to reproductive fitness in tree swallows, a key assumption of TPCs that is often untested (9).

QPCs at Higher Levels of Biological Organization. We incorporated the QPC from our focal population into validated biophysical models (21) to test if reproductive fitness varied with Q across the North American breeding range of tree swallows. Across 83,484 nests in the NestWatch database (22), fledging success was higher in regions where tree swallows experienced more hours per day within the optimal heat flux range for provisioning, as defined by the 80% performance breadth (SI Appendix, Fig. S6A). Fledging success was also highest in regions where average hourly Q during daylight was close to zero ($Q_{opt} = -0.32$; 80% performance breadth = $-1.18, 0.53$ W) and declined above and below Q_{opt} (SI Appendix, Testing for QPCs at Higher Levels of Biological Organization and Fig. S6B). These results suggest that, like TPCs, QPCs apply to multiple levels of biological organization (23) and can be used to model both individual- and population-level dynamics.

QPCs Predict the Breeding Range of Tree Swallows. We also integrated the QPC from our focal population into biophysical models to test whether Q could predict the tree swallow breeding range across North America (Fig. 2A). We assessed the overlap between relative abundance of tree swallows during the breeding season and regions predicted to be suitable for nestling provisioning by meeting the minimum number of hours for provisioning within the 80% performance breadth of Q (SI Appendix, Predicting Habitat Suitability Using Heat Flux Across Space and Time). We also compared the ability of Q to predict the breeding distribution against T_{air} -based curves and operative temperatures within the TNZ for tree swallows (29 to 39 °C) using the same approach (SI Appendix, Comparing the Performance of Heat Flux Relative to Other Mechanistic Approaches).

Heat flux substantially outperformed T_{air} -based curves in predicting the breeding range (Fig. 2A–C). Specifically, Q performed better than T_{air} at predicting the median latitude of the breeding range (abundance = 52.3°, $Q = 53.4^\circ$, $T_{air} = 40.2^\circ$) and the upper and lower latitudinal limits (Fig. 2E–H). It also performed better at predicting the relative abundance (model sensitivity: $Q = 0.94$;

$T_{air} = 0.37$) and overall breeding range (model sensitivity: $Q = 0.91$; $T_{air} = 0.35$). Both approaches showed similar specificity, predicting most absences (relative abundance: $Q = 0.70$; $T_{air} = 0.79$; breeding range: $Q = 0.80$; $T_{air} = 0.74$). Overall model performance was substantially higher for Q than for T_{air} (relative abundance: $Q = 0.82$; $T_{air} = 0.58$; breeding range: $Q = 0.86$; $T_{air} = 0.55$).

The TNZ failed to predict any suitable environmental conditions for tree swallows (Fig. 2C), as the thermal conditions required for provisioning young fall well below the limits of the TNZ. We also found that tree swallows appear to track thermal balance (Q) during winter, with the most thermally suitable regions located in the nonbreeding range (SI Appendix, Fig. S7). Moreover, the QPC approach outperformed correlative species distribution models in predicting the breeding range of tree swallows (SI Appendix, Fig. S8; maximum performance for correlative models = 0.74). Therefore, net sensible heat flux performs well at predicting the geographic range of tree swallows, especially relative to widely used mechanistic and correlative approaches.

Our biophysical model predicted substantial spatial and/or temporal shifts in the tree swallow breeding range under future warming scenarios. Our simulations forecasted the lower latitudinal limit to shift northward by 6.3° to 9.8° (SI Appendix, Fig. S9A), depending on the climate warming scenario. Tree swallows might also advance breeding phenology to maintain the same lower latitudinal limit, and under the worst-case warming scenario (SSP5-8.5), tree swallows may need to shift peak breeding 1 mo earlier to maintain the current lower latitudinal limit (SI Appendix, Fig. S9B). Importantly, these projections assume no plastic or evolutionary changes in thermal physiology in response to climate change and that tree swallow range shifts are not limited by prey availability. Furthermore, tree swallows at higher latitudes might not need to shift spatially or temporally because most (77.9%) of the contemporary breeding range remains in suitable conditions for provisioning during the same time of year under the most severe warming scenario. Regardless, our simulations forecast dramatic shifts in the southern range limit of tree swallows.

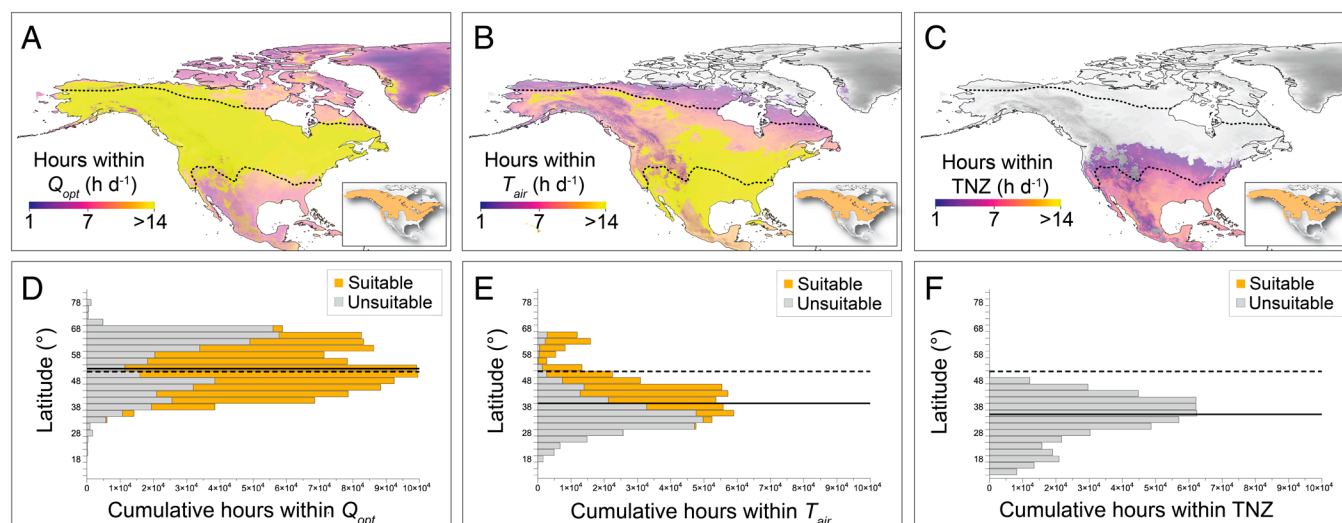


Fig. 2. Heat flux accurately predicts the spatial distribution of the tree swallow breeding range. (A) Suitable habitat for tree swallow breeding as determined by average hours within the 80% performance breadth for Q. The bright yellow regions reflect areas that meet the minimal requirements for fledging young. Dashed lines correspond to the upper and lower latitudinal limits of tree swallow relative abundance. The inset is the breeding range of tree swallows, which closely corresponds to relative abundance (SI Appendix). (B) Suitable habitat for tree swallows as determined by average hours within the 80% performance breadth for T_{air} . (C) Suitable habitat for tree swallows as determined by hours within operative temperatures that define the TNZ (29 to 39 °C). (D–F) Cumulative values for hours within Q_{opt} (D), hours within optimal T_{air} (E), and hours within the TNZ (F) within 2.5° latitude bins. The solid horizontal line indicates the median latitude for suitability of each method, and the dashed line represents the median observed abundance for tree swallows. Suitable (yellow) and unsuitable (gray) hours are stacked as bar plots.

Unlike many bird species, tree swallows have expanded their southern range in recent decades, especially in the southeastern United States (24). Our QPCs indicate these areas are currently suitable for nestling provisioning (Fig. 2B), suggesting tree swallows have reached their fundamental niche limit at lower latitudes. Therefore, other ecological or environmental barriers might have previously prevented tree swallows from inhabiting these areas. Although QPCs reveal areas that are physiologically suitable, realized distributions may lag behind physiological suitability due to factors such as sampling effort, historical constraints, or biotic interactions (25), some of which have been implicated in the southern breeding range expansion of tree swallows (26). At the same time, tree swallows are declining in parts of North America (27), with cold snaps underlying declines in some populations by lowering chick survival due to thermal stress and reductions in prey availability (28). These findings suggest that heat flux shapes the physiological conditions necessary for successful reproduction and thus plays a central role in defining the fundamental niche of endotherms. However, the realized distribution and population trends are further influenced by a complex interplay of abiotic conditions, biotic interactions, evolutionary responses, and historical constraints.

Heat Flux as a General Predictor of Avian Distributions. We used correlative species distribution models built on a combination of uncorrelated bioclimatic variables and species-specific maps of net sensible heat flux to evaluate whether Q predicts geographic

distributions of nine additional bird species during the breeding season (*SI Appendix, Correlative Species Distribution Model: Evaluating Generality*). We chose species that provision young at their nest, have widespread breeding ranges, and for which field metabolic rate data were available. On average, peak suitability occurred at a slightly positive Q value (Fig. 3A, mean ≈ 0.3 W), and the curve overlapped zero, indicating conditions that encompassed thermal balance. Although some species exhibited peak suitability near thermal balance ($Q = 0$ W), occurrence rates for most species peaked at positive Q values when assuming average wind speed (Fig. 3B), indicating that birds were generally distributed in regions that would require efforts to minimize heat loss or generate heat. However, when assuming low wind speeds, most species were distributed in regions associated with thermal balance (Fig. 3B and *SI Appendix, Fig. S10*). This pattern suggests that birds may preferentially breed in environments that remain near thermal balance during periods of low or near-zero wind speed, which are common due to natural variation in wind as well as the effects of vegetation, terrain, and nest-site microhabitats (*SI Appendix*). Under these conditions, convective cooling is reduced and the risk of overheating is greatest. Thus, selecting environments that promote heat loss may prevent birds from rapidly overheating and experiencing steep declines in performance during hot, low-wind conditions, similar to the idea that cooler suboptimal temperatures can maximize performance due to thermal variation (i.e., “suboptimal is optimal”) (29). Regardless, variable importance

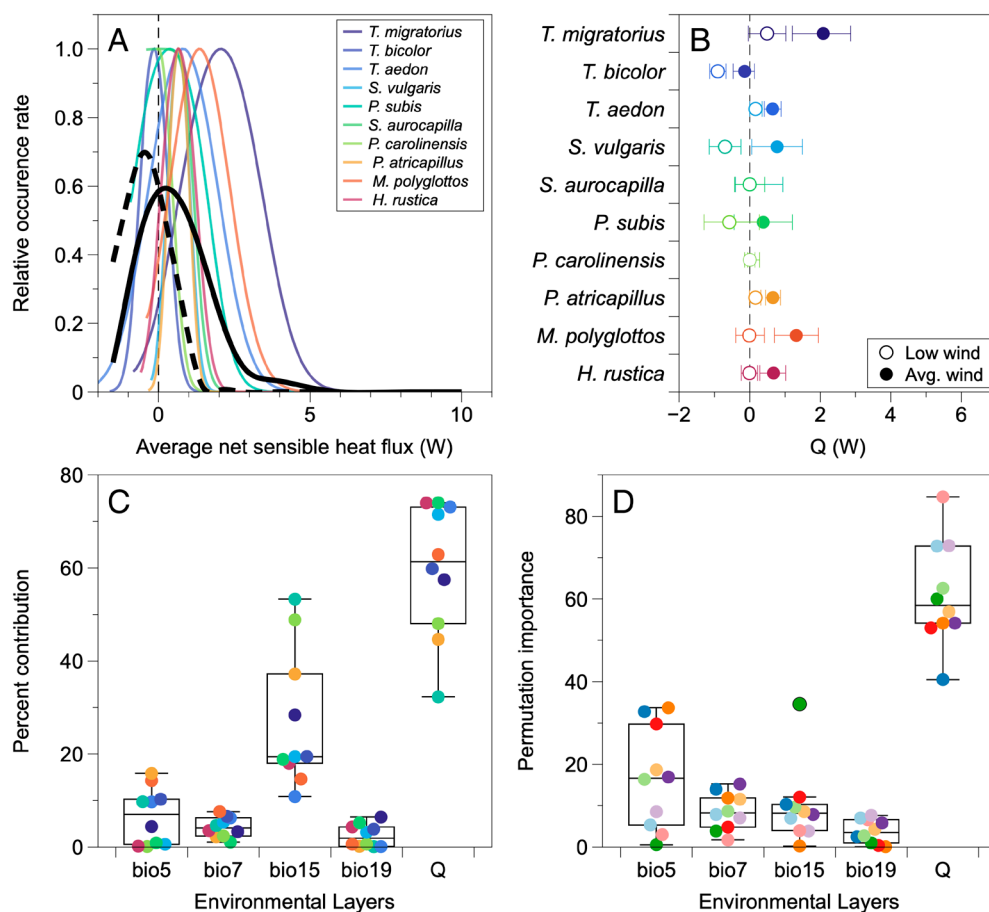


Fig. 3. Evidence for heat flux shaping breeding distributions in nine additional bird species. (A) Response curves for net sensible heat flux predicting relative occurrence rate in tree swallows and nine additional species. The solid black line represents the average response curve across all species at average wind speeds. The dashed line represents the average response curve at low wind speeds. The vertical dash represents thermal balance ($Q = 0$). (B) The heat flux value at average wind speed (solid points) and low wind speed (open points; 0.1 m/s) associated with maximum occurrence rate with error bars indicating the bounds for 80% occurrence rates for each species. (C) Percent contribution for the uncorrelated bioclimatic variables and net sensible heat flux. (D) Permutation importance for the uncorrelated bioclimatic variables and net sensible heat flux. The uncorrelated bioclimatic variables here are maximum temperature of the warmest month (bio5), annual range in air temperature (bio7), precipitation seasonality (bio15), and precipitation of the coldest quarter (bio19).

metrics showed that Q was the top predictor, based on percent contribution and permutation importance (Fig. 3 C and D and SI Appendix, Fig. S10). These results support the hypothesis that net sensible heat flux is a broadly relevant component of species' niches influencing the geographic distribution of breeding birds.

Discussion

Human-driven climate change is altering biodiversity and species distributions worldwide (30), highlighting the urgent need to predict the extent, pace, and mechanisms of ecological responses. In this study, we introduced the QPC, a performance curve in which net sensible heat flux is the independent variable, as a tool for evaluating the thermal dependence of performance in endotherms (see SI Appendix, General Theory on QPCs and Comparisons with TPCs for more conceptual theory). We demonstrated that QPCs can be used to predict the geographic distribution of bird species and their responses to climate warming. Although this study focused on insectivorous, altricial birds, emerging evidence suggests QPCs could be applied more broadly. Nonlinear relationships between air temperature and physiologically demanding metrics of performance (e.g., maximal flight performance, endurance running, lactation) have recently been documented in an ecologically and phylogenetically diverse sample of endotherms (31–34). Thus, QPCs might open insight into the environmental limits of endotherm performance, which would have critical consequences for climate change given their high capacity for work and energetic demands. QPCs might also help to generate high-resolution, predictive models to prevent population declines and mass mortality events in endotherms already observed under climate change (35–37).

More broadly, QPCs offer the promise of a unified framework for understanding the thermal dependence of performance across ectotherms and endotherms. In both frameworks, operative temperature (T_e) integrates multiple pathways of heat exchange between an organism and its environment and provides the mechanistic basis for predicting performance. In ectotherms, body temperature closely tracks T_e , such that performance can be modeled directly as a function of temperature. In endotherms, thermoregulation decouples body temperature from T_e and performance is likely shaped by the demands of maintaining thermal balance, captured by net sensible heat flux (Q). Moreover, QPCs can accommodate a wide range of heterothermic strategies in endotherms, although highly heterothermic taxa ("protoendotherms" sensu ref. 38) may be better studied with T_e -based performance curves (SI Appendix, General Theory on QPCs and Comparisons with TPCs). QPCs likely suffer from the same issues as TPCs, including complex relationships between performance and fitness and variability across space and time (4). There will also be unique challenges associated with the use of QPCs, such as the body size dependence of heat flux and dynamic feedback loops between heat flux and performance (SI Appendix, General Theory on QPCs and Comparisons with TPCs). Nevertheless, we demonstrated here that Q performs better than several other approaches for explaining endotherm performance and predicting geographic distributions. Thus, QPCs could be applied across endotherms more broadly, thereby addressing a pressing need for physiological frameworks that forecast climate vulnerability in endotherms.

Materials and Methods

Tree Swallow Field Study and Provisioning Performance. We studied tree swallows (*T. bicolor*) breeding in nest boxes at the Iowa State University Horticulture Research Farm (Iowa, USA) from 2021 to 2024. Nests were checked throughout the breeding season to track breeding phenology and reproductive

fitness (i.e., nestling mass prior to fledging and fledgling success). Adults were captured during incubation and fitted with temperature-sensitive PIT tags. Nestling provisioning visits and adult body temperature were recorded continuously using temperature sensitive PIT tags and radio frequency identification (RFID) antennas mounted at nest-box entrances. This allowed us to measure hourly provisioning rates by adults (both males and females) and adult body temperatures across a range of heat flux conditions (SI Appendix, Nestling Provisioning Rates and Body Temperature). Hourly provisioning rates by adults served as our metric of performance in our performance curves built upon heat flux (QPCs). We also used these data to test whether individual variation in provisioning rates predicted variation in reproductive fitness.

Thermoregulatory Behaviors and Prey Abundance in Response to Heat Flux Variation. To evaluate whether variation in provisioning performance reflected variation in thermoregulatory processes, we quantified heat- and cold-associated thermoregulatory behaviors across a range of net sensible heat flux values (SI Appendix, Thermoregulatory Behaviors: Panting and Ptiloerection). Panting behavior, which facilitates evaporative cooling during heat stress (17) was scored from videos of adults recorded at nest box entrances using motion-activated cameras during hot, cold, and intermediate thermal conditions. Ptiloerection, which reduces heat loss during cold stress (39), was assessed during standardized field observations of adults perched on nest boxes early in the morning during the beginning of the breeding season. These behaviors not only serve as indicators of thermoregulatory stress which could compromise provisioning performance, but they also reflect time and energetic demands that directly trade off with provisioning activity. To evaluate whether variation in provisioning performance could instead be explained by extrinsic variation in prey abundance, we quantified diurnal flying insect abundance on a minute-by-minute basis during the breeding season. Specifically, we placed time-lapse cameras in foraging habitats of tree swallows and used an object-detection AI model to count insects in each image across a range of heat flux conditions (SI Appendix, Food Abundance: Flying Insect Activity).

Biophysical Modeling of Net Sensible Heat Flux. We used an established method for predicting heat flux across landscapes using biophysical simulations for endotherms (Endoscape) (37, 40). The simulation estimates the amount of heat that endotherms need to generate via metabolic heat production or lose via evaporative cooling to maintain a stable body temperature. Specifically, the model estimates net sensible heat flux (Q), which is defined as

$$Q = M - E - C \frac{dT_b}{dt} = K_e(T_b - T_e), \quad [1]$$

where M is the heat generated through metabolic processes, E is the heat lost through evaporative water loss, C is the capacitance of the isothermal core, T_b is core body temperature, K_e is the effective conductance, and T_e is the operative temperature (13, 15). Net sensible heat flux is the combination of the microclimate experienced by the organism and the physiology, behavior, and morphology of the organism. In the model, we assume M , E , and T_b are fixed based on empirical values from provisioning tree swallows to assess the heat imbalance that may occur while provisioning. This allowed us to estimate how heat imbalance changes across environmental conditions relative to the physiological state and energetic demands associated with provisioning young. When the intermediate quantity is equal to the final value, the organism is in heat balance ($Q = 0$ W). Nonzero Q should not be interpreted as realized heat storage or loss from storage. Instead, nonzero Q represents the residual thermal imbalance that would have to be corrected by thermoregulatory responses to maintain thermal steady state. Predictions of net sensible heat flux from this model have been validated against physiological responses measured in laboratory experiments and against independent estimates of operative temperatures in complex thermal environments across birds and mammals with a wide range of phenotypes (21, 37).

We built a tree swallow model in Endoscape based on several biophysical traits of adult tree swallows, including body mass, body size and shape, body temperature, feather density, full-spectrum feather reflectance, and more (SI Appendix, Biophysical Traits of Tree Swallows). The tree swallow model also incorporated previously published estimates of evaporative water loss and metabolic heat production based on field metabolic and water loss data from adult tree swallows that were provisioning young (41; See SI Appendix, Biophysical Traits of Tree Swallows,

for a discussion on the use of field metabolic rate and evaporative water loss data). Although our tree swallow model was parameterized with trait data from our focal population and other populations (in the case of physiological data), previous work has found little evidence for morphological and genetic variation across the geographic range of tree swallows (42, 43). Indeed, tree swallows are so morphologically uniform across their range that no subspecies are recognized (44). Thus, our organismal trait data are likely representative of the species across its range. We modeled heat flux for a representative exposed bird at approximately perch height above the ground, rather than attempting to reconstruct the instantaneous thermal environment associated with every behavioral state, perch location, or flight bout. This simplification was intentional because our goal was to estimate general environmental thermal load for provisioning birds, not to model the exact realized heat budget of each individual at every moment.

We combined these organismal features with air temperature and wind speed data from a weather station located at our Iowa field site (we used either hourly or minute-by-minute averages depending on the analysis; *SI Appendix, Modeling Microclimatic Conditions in the Field*). We used the same biophysical modeling approach for analyses of QPCs in Ontario and Colorado tree swallow populations (*SI Appendix, Testing for QPCs in Other Tree Swallow Populations*). Based on these organismal and climatic inputs, Endoscape estimates Q for an adult tree swallow for each hour or minute, depending on the analysis. We also ran a variety of sensitivity analyses incorporating variation in biophysical traits and found that estimates of Q were generally robust to realistic phenotypic variation (*SI Appendix, Sensitivity Analyses*).

Statistical Modeling of Performance, Thermoregulatory Responses, and Insects Relative to Q. We tested for QPCs by modeling hourly provisioning rate as a function of Q using generalized additive mixed models while accounting for year, wind speed, nestling age, sex, adult identity, and temporal autocorrelation (*SI Appendix, Modeling Hourly Variation in Provisioning Rates*). We then extracted the predicted relationship between provisioning rate and Q and fit standard TPC functions to estimate QPC parameters, including the optimal Q for provisioning (Q_{opt}) and the 80% performance breadth around Q_{opt} (*SI Appendix, Estimating QPC Parameters*). We also tested whether thermoregulatory state varied with Q by modeling deviations from normothermic body temperature (hourly T_b readings within ± 1 SD of an individual's modal T_b were considered normothermic) using PIT tag body temperature data and by modeling panting and ptiloerection occurrence as functions of Q (*SI Appendix, Modeling Thermoregulatory Responses to Q*). We used a similar approach to model flying insect abundance as a function of Q to assess whether provisioning patterns could be explained by prey activity alone (*SI Appendix, Modeling Insect Prey Abundance*).

Mechanistic Species Distribution Models and Response to Climate Change. To test if QPCs can be used to predict the geographic range of tree swallows, we used Endoscape to estimate Q across North America during the breeding season based on downscaled climate surfaces from WorldClim [v. 2.1 (45); *SI Appendix, Modeling Microclimatic Conditions Across North America*]. For each location, we estimated Q for each hour of the day during the breeding season and determined whether the estimated Q fell within the optimal heat flux conditions for provisioning based on the 80% performance breadth. We then determined whether a tree swallow could provision in optimal heat flux conditions for at least 14 h per day [typical duration of daily provisioning required to fledged young (44)] for each month of the breeding season. We considered locations that met these requirements to be suitable for reproduction (*SI Appendix, Predicting Habitat Suitability Using Heat Flux Across Space and Time*). To determine model sensitivity, we downloaded eBird observations (46) of tree swallows during the breeding season and determined the proportion of 1,000 randomly sampled

observations that fell within suitable breeding habitat. We also determined the proportion of 1,000 randomly sampled locations outside of the breeding range that fell outside of suitable breeding habitat to assess model specificity. We compared sensitivity, specificity, and overall performance of this Q-based approach to alternative metrics that have been proposed as indices of endotherm performance (T_{ai} and the TNZ; *SI Appendix, Comparing the Performance of Heat Flux Relative to Other Mechanistic Approaches*). Finally, we modeled spatial variation in suitable heat flux as above under three future warming scenarios to forecast tree swallow range shifts and phenological responses to climate change.

Correlative Species Distribution Models in Tree Swallows and Other Birds.

We used an ensemble modeling approach (generalized linear models, random forest, and maximum entropy) to evaluate the performance of our mechanistic model relative to commonly used correlative species distribution models. These models were developed based on eBird observations of tree swallows during the breeding season and four uncorrelated WorldClim bioclimatic variables (Maximum Temperature of Warmest Month, Temperature Annual Range, Precipitation Seasonality, and Precipitation of the Coldest Quarter). We then converted the continuous suitability outputs from these models into binary maps (suitable vs. unsuitable) using a range of quantile-based thresholding approaches (*SI Appendix, Correlative Species Distribution Model: Evaluating Performance*). These binary maps were then used to calculate model sensitivity, specificity, and overall performance, enabling direct comparison with our mechanistic species distribution model. We also built a hybrid species distribution model that incorporated bioclimatic variables and Q to evaluate the relative importance of each layer in shaping the distribution of tree swallows. To evaluate whether net sensible heat flux serves as a general predictor of avian geographic distributions, we compiled occurrence records for nine additional bird species that breed widely across North America, provision young at the nest, and for which field metabolic rate data were available. We then used a similar hybrid modeling approach with these additional species to assess the importance of Q in shaping each species' breeding distribution (*SI Appendix, Correlative Species Distribution Model: Evaluating Generality*).

Ethics and Permits. All field procedures were conducted under approvals and permits from the US Geological Survey Bird Banding Laboratory (Permit 07014), US Fish and Wildlife Service (MBPER0003052), Iowa Department of Natural Resources (SC1428), and the Iowa State University IACUC (IACUC-20-169). All permits were valid from 2021 to 2024.

Data, Materials, and Software Availability. All data and code associated with this manuscript are available at Zenodo (19).

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