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Thermal imbalance drives avian performance and responses to climate warming

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Abstract

Thermal performance curves (TPCs) 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 new framework for predicting endotherm responses to climate warming.

Significance Statement

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.

Introduction

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, non-linear 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

77 endotherms have adaptations that can decouple body temperature from the thermal
78 environment, complicating efforts to characterize the thermal dependence of performance
79 (2, 8). This lack of a comparable framework not only limits insight into the basic
80 environmental physiology of endotherms (8) but also hampers efforts to forecast their
81 responses to climate change (9).

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

101 Endotherms are subject to the same thermodynamic laws as ectotherms but have
102 evolved distinct strategies for managing heat flux (9). Rather than allowing body
103 temperature to track environmental temperatures, homeothermic endotherms generally
104 defend a species-specific body temperature setpoint by balancing heat gain and loss
105 through multiple pathways, including convection, conduction, radiation, and
106 physiological mechanisms such as evaporative cooling and metabolic heat production
107 (14). Among these, evaporative cooling is critical for offloading excess heat in hot
108 environments, while increased metabolic heat production compensates for heat loss in
109 cold environments. These physiological responses are accompanied by behavioral
110 responses (e.g., ptiloerection), morphological adaptations such as an insulation layer (i.e.,
111 plumage or pelage), and adjustments to body temperature – such as heterothermy or
112 torpor – that reduce the need for sustained physiological effort to maintain homeothermy
113 (14).

114 The combined effects of these environmental and physiological pathways can be
115 collapsed into a single variable, net sensible heat flux (Q ; measured in watts (W); Fig.
116 1A)(15). This variable quantifies the fluxes primarily generated or regulated by the
117 organism (Fig. 1A; green box) and those driven by the organism–environment gradient
118 (Fig. 1A; blue box). We calculate Q by comparing internal heat flux with sensible heat
119 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 to quantify the magnitude and direction of the underlying thermal forcing acting on the organism (Fig. S1). 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 four-year 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 (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, *SI Appendix*, Fig. S2). In total, we obtained 3,011 one-hour 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 (see 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 = $-0.013 - 0.001$ 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,B). This asymmetry of the QPC (skewness = 0.65) is another feature shared with TPCs, likely due to asymmetric physiological stresses of warm versus cool conditions (2). We also found that provisioning rate peaked at an optimal air temperature ($T_{air} = 25.94^{\circ}\text{C}$, *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 ($\Delta\text{AIC} = 191.80$ [*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 ptiloerection) 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 (19). 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 (20) 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 (21), 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 ($Q_{\text{opt}} = -0.32$; 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*, Fig. S6B). These results suggest that, like TPCs, QPCs apply to multiple levels of biological organization (22) 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 – 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°, $Q = 53.4^\circ$, $T_{\text{air}} = 40.2^\circ$) and the upper and lower latitudinal limits (Fig. 2E-H). It also performed better at predicting the relative abundance (model sensitivity: $Q = 0.94$; $T_{\text{air}} = 0.37$) and overall breeding range (model sensitivity: $Q = 0.91$; $T_{\text{air}} = 0.35$). Both approaches showed similar specificity, predicting most absences (relative abundance: $Q = 0.70$; $T_{\text{air}} = 0.79$; breeding range: $Q = 0.80$; $T_{\text{air}} = 0.74$). Overall model performance was substantially higher for Q than for T_{air} (relative abundance: $Q = 0.82$; $T_{\text{air}} = 0.58$; breeding range: $Q = 0.86$; $T_{\text{air}} = 0.55$).

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 non-breeding 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° - 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 one month 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.

Unlike many bird species, tree swallows have expanded their southern range in recent decades, especially in the southeastern U.S. (23). 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 (24), some of which have been implicated in the southern breeding range expansion of tree swallows (25). At the same time, tree swallows are declining in parts of North America (26), with cold snaps underlying declines in some populations by lowering chick survival due to thermal stress and reductions in prey availability (27). 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, 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 (see SI). 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”)(28). Regardless, variable importance metrics showed that Q was the top predictor, based on percent contribution and permutation importance (Fig. 3C,D, 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 (29), 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. Non-linear 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 (30–33). Thus, QPCs might open new 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 (34–36).

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 37) 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 (*Tachycineta bicolor*) breeding in nest boxes at the Iowa State University Horticulture Research Farm (Iowa, USA) from 2021–2024. 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 (38), 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 artificial intelligence 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*) (36, 39). 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:

$$Q = M - E - C \frac{dT_b}{dt} = K_e (T_b - T_e) \quad (\text{eq. 1})$$

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 (20, 36).

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 (40; 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 (41, 42). Indeed, tree

swallows are so morphologically uniform across their range that no subspecies are recognized (43). Thus, our organismal trait data are likely representative of the species across its range.

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 thermal performance curve 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 standard deviation 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 (44); *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 hours per day (typical duration of daily provisioning required to fledge young (43)) 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 (45) 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_{air} 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 U.S. Geological Survey Bird Banding Laboratory (Permit 07014), U.S. 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 - 2024.

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Figures and Tables

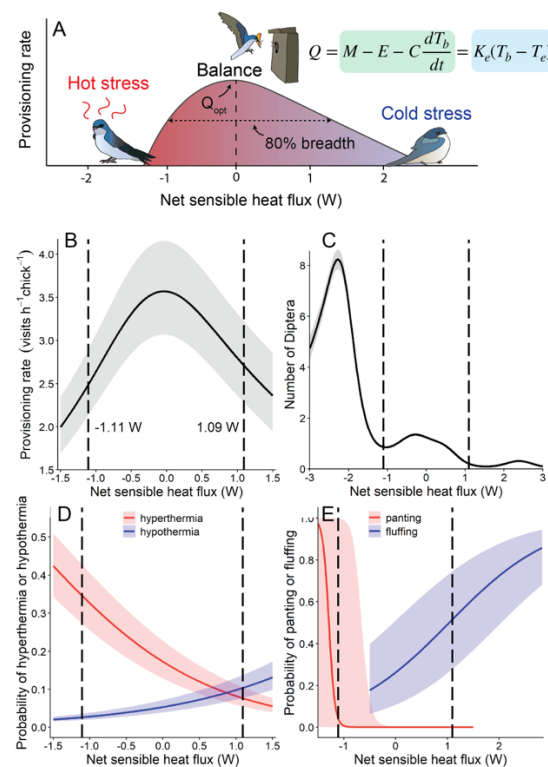


Fig. 1. Evidence for physiologically driven heat flux performance curves in tree swallows. (A) A conceptual figure illustrating how provisioning rate is related to net sensible heat flux, indicating performance was predicted to be highest during heat balance ($Q_{opt} = 0$, vertical dashed line; 80% 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) (see SI). Note that decreasing Q corresponds to increasingly warm environmental conditions, whereas increasing Q corresponds to increasingly cool conditions. Thus, unlike a traditional thermal performance curve 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 -0.006 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 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, E) or camera identification (C) (see SI for additional details). The shaded bands represent the model 95% confidence intervals. Illustrations by E.A.R.

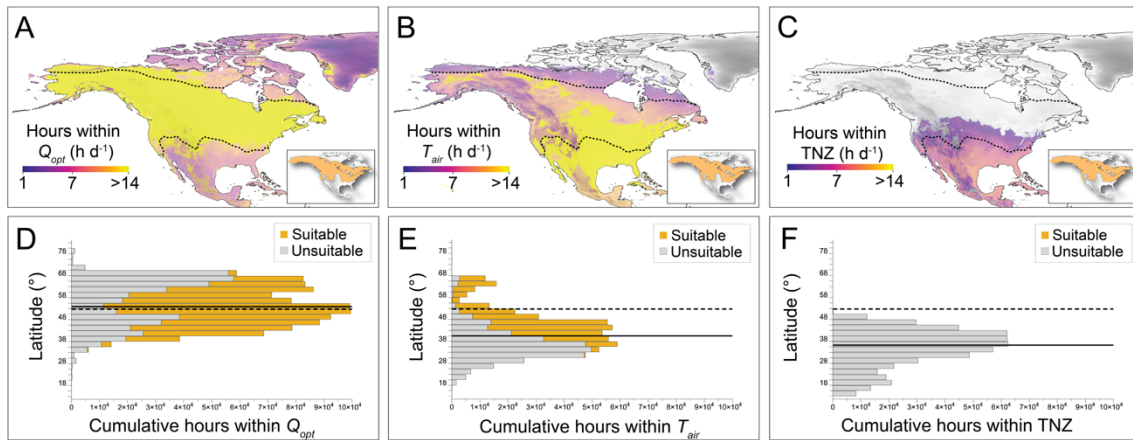


Fig. 2. Heat flux accurately predicts the spatial distribution of the tree swallow breeding range. (A) Suitable habitat for tree swallow breeding as determined by average hours within the 80% performance breadth for Q_{opt} . The bright yellow regions reflect areas that meet the minimal requirements 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 (see SI). (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 – 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.

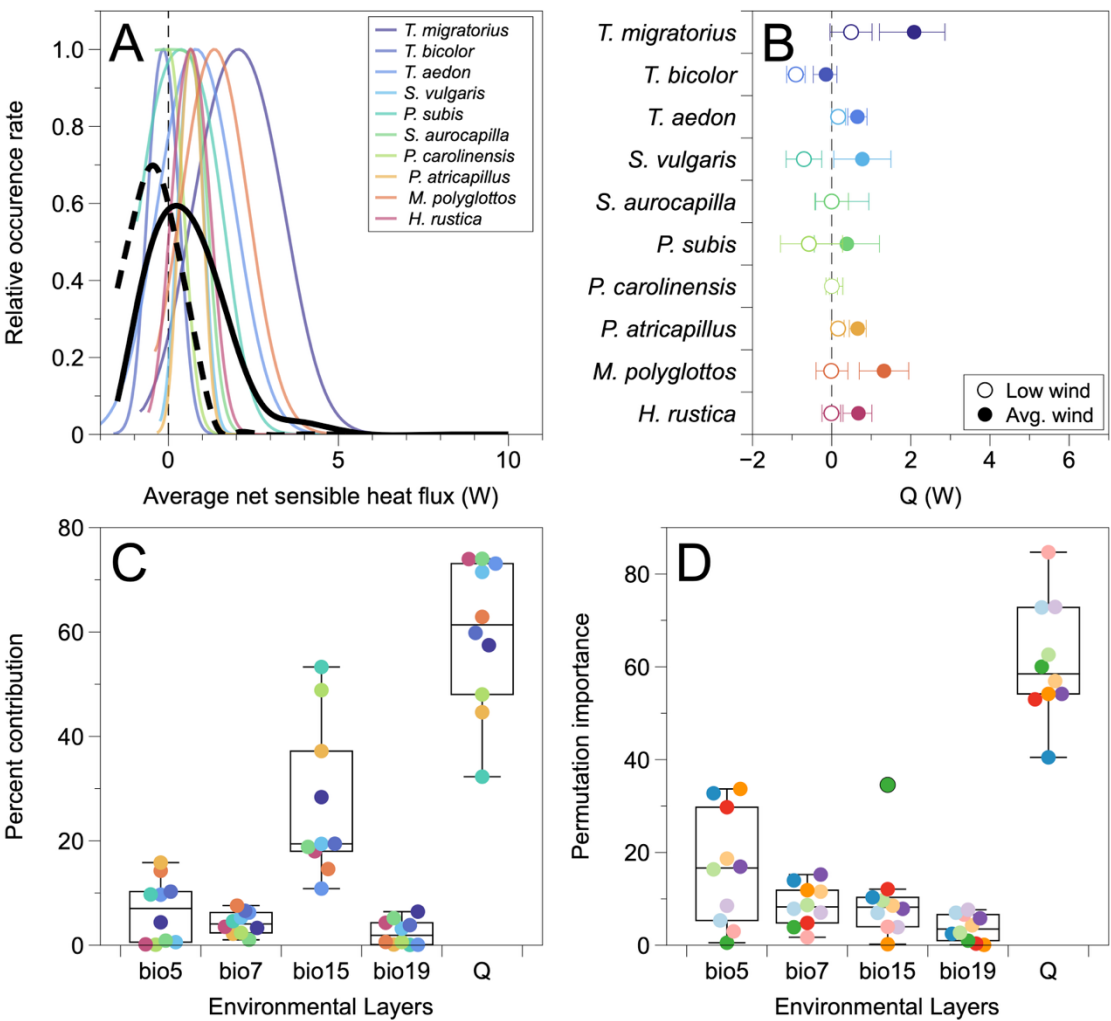


Fig. 3. Evidence for heat flux shaping breeding distributions in nine additional bird species. (A) Response curves for net sensible heat flux predicting relative occurrence rate in tree swallows and nine additional species. The solid black line represents the average response curve across all species 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).

Supplementary Materials for

Thermal imbalance drives avian performance and responses to
climate warming

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Materials and Methods

Supplementary Text

Figs. S1 to S21

Table S1

References

Materials and Methods

Tree swallow provisioning performance

Study area and PIT tags

We conducted fieldwork between April and July over four years (2021 - 2024) at the Iowa State University Horticulture Research Farm (latitude: 42.106328, longitude: -93.589807). Tree swallow nest boxes are spaced 10-20 m apart throughout the farm, with a total of 138 available nest boxes.

Shortly after tree swallows returned from migration, we began checking nests every three days for signs of nest construction, eggs, and young. Tree swallows lay one egg daily, so we back-calculated lay dates if eggs were laid on days when we did not check nests (46). After eight days of egg incubation, we used hinged traps to capture adults. We banded, measured, weighed, and injected adults with a unique temperature-sensitive PIT tag (Bio-Therm13, Biomark, Boise, ID, USA). We injected PIT tags subcutaneously over the abdomen by gently pulling loose skin away from the bird and inserting the syringe near, but to the side of, the cloaca. Subcutaneously injected PIT tags in small birds (<25 g, like tree swallows) provide similar body temperature measurements to tags inserted in the body core and reduce the risk of injury to the animal (47). However, subcutaneously injected PIT tags may migrate under the skin to different parts of the body, which could increase the variance in body temperature readings. We did not independently calibrate PIT tag temperature measurements and instead relied on the manufacturer's stated accuracy (± 0.5 °C). Previous evaluations of PIT tags indicate relatively small deviations from true temperature (e.g., ~ 0.3 °C)(48), and our mean body temperature estimates closely matched those reported in independent studies of tree swallows (49). In our analyses, PIT tag data were used either as a fixed representative body temperature for model parameterization or to quantify within-individual deviations (heterothermy), such that small systematic measurement offsets are unlikely to influence our results.

We conducted this work with proper permits and protocols from the Bird Banding Lab (Permit #: 07014), United States Fish and Wildlife Service (Permit #: MBPER0003052), Iowa Department of Natural Resources (License #: SC1428), and the Institute for Animal Use and Care Committee at Iowa State University (Reference #: IACUC-20-169). All permits were valid from 2021-2024.

Nestling provisioning rates and body temperature

We used an automated system commonly used for tracking provisioning rates and body temperatures in cavity nesting birds, including tree swallows (19). We collected data on hourly nestling provisioning rates and body temperature (T_b) with a BiomarkTM SSM8 multiplexing radio frequency identification (RFID) antenna system attached near the entry point of nest boxes. This allowed us to simultaneously record provisioning visits to the nest and T_b of adults. RFID antennas recorded continuous PIT tag readings but included a 10 s lag between data logging events for a given individual. When possible, we deployed up to three antennas to nearby nest boxes to increase the number of nests that could be simultaneously monitored. Every 1-4 days we moved the multiplexing system to different nests such that we were able to collect data at each nest 1-3 times (for typically 1-4 days) during the breeding season. These measurements served as the basis for generating performance curves built upon heat flux.

Thermoregulatory behaviors: Panting and ptiloerection

We also aimed to understand whether tree swallows exhibited changes in thermoregulatory behaviors with respect to heat flux in natural environments. These behavioral changes would provide evidence that variation in provisioning performance with respect to heat flux is associated with thermoregulatory (that is, endogenous) processes, similar to thermal performance curves (50). After hatching began, we used four Browning™ BTC-5PXD motion-activated trail cameras mounted on tripods (approximately 0.75 m from the nest box entrance) to record the behavior of adults visiting nest boxes. We positioned trail cameras to focus on the entry point of nest boxes. When activated, trail cameras recorded a 10-second video (1920 × 1080 pixel). We moved trail cameras to different nests every 1-4 days, allowing us to collect data on each nest for 1-3 periods. Based on hourly air temperature data, we inspected videos from the five hourly periods with the coldest temperatures that were visible (see details below), the five hourly periods with the hottest temperatures, and five hourly periods at ~26°C (close to the optimal air temperature for tree swallow provisioning, see below) in 2021 and 2023. For each nest during each hourly period, we recorded whether adults were observed panting (i.e., gaping when breathing; Fig. S11); a thermoregulatory response to avoid overheating by facilitating evaporative cooling (51). We only collected data if we could score at least 10 video clips for a given nest box in a given hourly period and if birds were not observed interacting with other individuals, that is not engaged in threat displays that involve opening the bill (43).

We also studied the relationship between estimated heat flux and feather ptiloerection, a thermoregulatory response associated with cold exposure that increases insulation. Immediately after tree swallows returned from migration in early April of 2024, we began collecting data on ptiloerection through behavioral observations of adults in the field. Early in the breeding season, adults spend much of the early morning hours perched on nest boxes. We observed birds on nest boxes from inside a vehicle with 10 × 42 binoculars at a minimum distance of 40 m from 0630 to 1030 on 14 days. We only conducted behavioral observations if it was not raining or snowing and if wind speed was less than 4 m/s to avoid feathers appearing “fluffed” due to mechanical influence from high winds. If we were able to observe a bird perched for at least 10 seconds (and it was not engaged in behavioral interactions with other individuals), we recorded whether its feathers were puffed (i.e., full ptiloerection). We considered full ptiloerection to be present if the contour feathers of the body were clearly raised such that most of the tarsometatarsus was covered by feathers and there was a visible “hump” of raised feathers on the nape (Fig. S12; see (52) for a similar approach to defining full ptiloerection).

Food abundance: Flying insect activity

We also sought to understand whether variation in provisioning rate was related to external factors, specifically prey abundance. Tree swallows are aerial insectivores and catch their prey during flight (53). If provisioning rates are related to prey abundance, then our measure of performance may be less related to the effects of the thermal environment on avian physiology and more related to activity of their prey. In 2021, 2023, and 2024 we used two Wingscapes™ WCT-00126 time-lapse cameras to record insect activity (i.e., food abundance for tree swallows) throughout the breeding season. We placed the cameras in two habitats that tree swallows regularly forage in: a large meadow and the edge of an experimental pond. We attached cameras to stakes ~0.5 meters above the ground and ~1.5 meters in front of a 120 x 90 cm white plastic board staked into the ground. We also placed an array of six wooden dowels in front of the boards to encourage perching by flying insects (Fig. S13). We programmed cameras to take a 6080 × 3420 pixel photograph of the board (and any insects on the dowels or board) every 60 seconds,

beginning at 0500 and ending at 2100 every day. In 2021, we deployed cameras from 16 June to 13 July, in 2023 we deployed cameras from 7 April to 31 July, and in 2024 we deployed cameras from 19 April to 5 May. These images were then analyzed using artificial intelligence to detect one of their primary sources of food.

Our measure of prey abundance focused on the activity of Diptera, but there could be other factors that affect the availability of insects to tree swallows not captured by our methods. For example, flight performance of insects often shows a classic thermal performance curve with a well-defined optimal air temperature (T_{opt}) (54). If insect activity is highest at T_{opt} , this may not correspond with maximal prey availability for tree swallows if insects are most difficult to capture under these conditions. However, previous work has shown that invertebrate activity, invertebrate availability to foraging birds, and the profitability of birds foraging on invertebrates all increase with air temperature (55, 56) especially for aerial insectivores like tree swallows (57). Furthermore, we found clear evidence of costly thermoregulatory responses by tree swallows outside the range of optimal heat flux conditions for provisioning young (see Main Text, Fig. 1D,E). Thus, although we acknowledge that complex interactions between the performance curves of predators and prey can affect prey availability (58), the combined evidence for thermoregulatory constraints on provisioning performance in tree swallows (i.e., thermoregulatory behavioral data, body temperature data, food abundance data, and previous experimental work [19]) is robust.

Artificial intelligence detection model

To understand whether variation in provisioning rate was related to prey abundance (as opposed to thermal imbalance), we investigated the sensitivity of insect activity to the thermal environment using photos from camera traps and artificial intelligence. We focused on Dipterans for this analysis because they are a major constituent of nestling diets, with 40% to 57% of nestling diets consisting of insects from the Order Diptera (53, 59, 60). We note that we were unable to classify insects beyond Order, and thus we included insects in suborders such as Nematocera (e.g., black flies) and Brachycera (e.g., the house fly). Regardless, both have been shown to be important constituents of the nestling diet (53, 59).

We collected over 335,649 images during our camera-trap survey. To efficiently analyze this large dataset, we trained an artificial intelligence framework to scan all the images and count the number of flies (Dipterans) in each image. Specifically, we developed an object detection model to identify flies, count them, and log the results for each image. To train the model, we created a training, validation, and test dataset by manually annotating 1,330 images containing flies. Additionally, we included 2,550 empty images to teach the model to ignore background objects such as leaves and dirt on the whiteboards. To enhance model robustness, we applied rotation augmentation to the bounding boxes, varying between -10° and $+10^\circ$. Other augmentations, such as brightness and contrast adjustments, were tested but found unnecessary due to the consistency of the lighting conditions. The annotation, augmentation, and training were conducted using the Roboflow platform (61). We trained the YOLOv8 detection model, a widely used object detection framework known for its speed and accuracy, via the Roboflow Python package (62). The dataset was split into 84% for training, 10% for validation, and 6% for testing, following standard practices for robust model evaluation (61).

Our fly-detection model performed well, achieving an accuracy of 98% in predicting the number of flies per image based on counts from an observer. These results indicate that our

approach can effectively automate the labor-intensive task of analyzing camera-trap data, providing reliable counts that can be used for ecological studies and pest population management.

Modeling net sensible heat flux of tree swallows at our field site

Estimating net sensible heat flux – General approach

We used an established method for predicting heat flux across landscapes using biophysical simulations for endotherms (*Endoscape*) (36, 39). 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:

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

where M is the rate at which heat is generated through metabolic processes, E is the rate at which heat is lost through evaporative cooling, C is the capacitance of the isothermal core, T_b is the core body temperature, K_e is the effective conductance, and T_e is the operative temperature (13, 15). *Endoscape* estimates heat exchange separately for the dorsal and ventral surfaces, including differences in absorbed radiation, longwave exchange, and surface area, and then integrates these components to estimate operative temperature and net sensible heat flux for the whole animal. Net sensible heat flux is the combination of the microclimate experienced by the organism and the physiology, behavior, and morphology of the organism. When the intermediate quantity is equal to the final value, the organism is in heat balance ($Q = 0$). We estimate imbalance by comparing the internal heat flux expected for a normothermic provisioning tree swallow (based on FMR, EHL, and T_b while provisioning) with the sensible heat exchange experienced by that same idealized bird in a given environment. The difference between these quantities is Q : positive or negative values indicate the magnitude and direction of thermoregulatory compensation required to maintain heat balance. Predictions of net sensible heat flux from this model have been validated against physiological responses measured in laboratory experiments and independent estimates of operative temperatures in complex thermal environments across birds and mammals (20, 36). Here, we integrated empirical data to parameterize *Endoscape* to predict heat flux in tree swallows from downscaled macroclimatic data and weather stations.

We note that net sensible heat flux is similar conceptually to operative temperature (T_e), which also represents an appealing axis to describe performance for endotherms. Operative temperature is an integrative measure of temperature that represents the combined effects of multiple variables (e.g., air temperature, wind speed, solar radiation, thermal radiation, and insulation) to estimate the equivalent temperature that an organism would experience in a blackbody environment (63). It is the temperature of a theoretical, non-living object (often a model animal or a physical sensor with the same size, shape, and thermal properties as the animal) that achieves thermal equilibrium with its surroundings (63). However, there are several reasons why we elected to use net sensible heat flux instead. First and foremost, operative temperature ignores metabolic heat production and evaporative water loss from the animal and

thus does not address heat balance. Second, the units for T_e ($^{\circ}\text{C}$) are not ones that can be measured on a live animal and typically require the use of a replica of the animal (15). Conversely, measurements of metabolic rate, water loss rate, and body temperature are routinely taken by animal physiologists and thus easily integrated into or compared with estimates of net sensible heat flux.

To visualize the conceptual basis of our Q framework, in which Q represents the underlying thermal forcing acting on an endotherm prior to compensatory thermoregulatory responses, we developed a series of simulations illustrating how birds can behaviorally and physiologically modify heat exchange to maintain thermal balance across the diel cycle (Fig. S1). Starting from an unregulated baseline simulation in which skin conductivity, plumage depth, body shape, and T_b remained constant, we sequentially allowed birds to alter these traits within empirically realistic bounds to bring net sensible heat flux (Q) toward thermal balance ($-0.1 < Q < 0.1 \text{ W}$). Skin conductivity was allowed to vary from 0.204 to $2.8 \text{ W m}^{-1} ^{\circ}\text{C}^{-1}$, plumage depth was increased up to twofold, body length was reduced by up to 40% to simulate a more compact posture, and T_b was either held constant or allowed to fluctuate on a diel basis between 40 and 44°C . Within any given time point, regulatory responses were applied hierarchically such that each trait adjustment reached its allowable limit before additional thermoregulatory mechanisms were invoked. These simulations demonstrate that realistic changes in morphology and physiology can substantially reduce thermal imbalance and bring birds close to thermal balance across much of the diel cycle, with the remaining imbalance achievable through additional thermoregulatory mechanisms not explicitly modeled here, such as metabolic heat production, evaporative cooling, or microhabitat selection (69). Importantly, endotherms in our simulations do not actively thermoregulate to achieve thermal balance. Instead, we use an idealized animal with fixed morphology and physiology to quantify the magnitude and direction of environmental thermal forcing that would necessitate a wide array of behavioral and physiological thermoregulatory responses. In reality, we recognize that endotherms generally maintain approximate thermal equilibrium with their environment ($Q \approx 0$) through these compensatory responses.

Our approach is also fundamentally different from alternative endotherm models (64). The NicheMapR endotherm model, for instance, solves for a steady-state heat balance by iteratively adjusting metabolic heat production and a sequence of physiological and behavioral responses (e.g., posture, tissue conductivity, panting, sweating) until energy balance is achieved at a specified or flexible core temperature. In this framework, metabolic heat production is treated as a dynamic variable that is modulated to offset environmental heat fluxes, and evaporative pathways are invoked when sensible heat exchange is insufficient. In contrast, our approach specifies a fixed internal state (i.e., body temperature, metabolic rate during provisioning, and associated water loss) and evaluates the resulting heat budget without allowing compensatory adjustments. Thus, the model asks whether a bird performing the behaviors required for provisioning can maintain heat balance under given environmental conditions, and if not, the magnitude of the imbalance that must be offset. By not prescribing the sequence, magnitude, or type of thermoregulatory responses, our framework avoids assumptions that are likely to be highly species-specific and instead provides a more general measure of environmental heat load and its consequences. The NicheMapR approach is more mechanistically explicit, incorporating detailed physiological and physical processes (e.g., respiratory and cutaneous evaporation and panting dynamics) within a fully coupled heat and mass balance framework. This allows specific mechanisms, such as the efficiency and limits of evaporative cooling via panting, to be explicitly parameterized and evaluated, which is not possible in our simplified approach. Consequently,

NicheMapR is well suited for investigating species-specific thermoregulatory pathways and physiological limits, whereas our approach sacrifices mechanistic detail for generality.

Modeling microclimatic conditions in the field

We simulated the microclimatic conditions experienced by tree swallows at our field site by estimating the thermal, radiative, evaporative, and convective conditions of the environment. For the thermal environment, we simulated heat flux based on hourly or minute-by-minute air temperature data from a weather station located at our field site (station AEE14: <https://mesonet.agron.iastate.edu/agclimate/hist/hourly.php>). The maximum distance between the weather station and a tree swallow nest box was approximately 930 m. For the radiative environment, our simulations estimate direct, reflected, and diffuse solar radiation as well as longwave radiation from the ground and air (36).

We also used an iterative analytical approach to estimate ground surface temperature, which was then used to estimate longwave radiation reaching the ventral side of the bird. This approach incorporates radiative heat flux, heat flux with the soil, and evaporative heat flux (65). In these simulations, we assumed the ground exhibited a similar albedo (0.25) and surface resistance (60 s m^{-1}) as grass (63). We also assumed that soil properties were similar to organic soils (thermal conductivity = $0.25 \text{ W m}^{-1} \text{ K}^{-1}$; bulk density = 900 kg m^{-3} ; specific heat capacity = $1.92 \text{ J g}^{-1} \text{ K}^{-1}$). The first iteration of the soil model (including equations, routines, and validation) can be found in Porter et al. (39). In this study, we also included evaporation from the soil, assuming 30% water content of soil, which approximates water potential of moderately moist soils (63). We estimated humidity for simulating evaporative heat flux from soil surfaces using minimum nightly temperature, which typically approximates the dew point at night (66). While the dew point in western North America is often lower than the nightly minimum air temperature (67), this approach provides a reasonable approximation for estimating soil surface temperatures, particularly since these surfaces have limited influence on the heat flux experienced by birds perching well above the ground. Previous validations of the soil model focused on dry soils (39). Here, we validated the model for moist soils across North America using the Soil Climate Analysis Network (<https://www.nrcs.usda.gov/resources/data-and-reports/soil-climate-analysis-network>), which included 11 sites spanning 11° of latitude in North America and consisted of 1,852,640 soil temperature measurements across four different soil depths. We found a correspondence near unity between observed and predicted soil temperatures at multiple depths (Fig. S14, $R^2 = 0.85 - 0.92$ depending on depth).

For convective conditions, we used hourly or minute-by-minute wind speed data from the local weather station referenced above. We assumed that tree swallows experienced wind speeds associated with 1.5 m above the ground surface (the typical height of a tree swallow nest box) using a logarithmic wind profile correction (68). Tree swallows commonly perch at this height and are exposed to wind speeds at this height (Fig. S12).

Biophysical traits of tree swallows

The simulation also incorporates several morphological traits measured on tree swallows that influence heat flux. We also verified our conclusions were robust to these assumptions using a sensitivity analysis (see below). We assumed a body mass of 20 g based on approximate values for adults in our population (69) (average mass $\pm$ standard deviation: males = $20.8 \pm 1.1 \text{ g}$, $n = 34$; females = $21.2 \pm 1.6 \text{ g}$, $n = 265$). We also assumed a feather conductivity value of $0.145 \text{ W m}^{-1} \text{ }^\circ\text{C}^{-1}$ based on the range of values published in the literature (70, 71). We assumed an average

body shape, feather length, and plumage depth based upon allometric relationships between each of these traits and body mass developed from similar studies (36). We simulated tree swallows to maintain a stable body temperature of 42°C during the day, which was based on measurements of T_b from the PIT tags (Fig. S15, S17B) that measured 504,181 T_b readings from 56 adults. Although we assumed body temperatures are constant, birds are unlikely to match thermoregulatory responses to Q to maintain a perfectly stable core body temperature. Rather, Q represents the thermal load that must be offset through a combination of anticipatory responses and feedback-mediated adjustments that necessarily come with some degree of error. Skin conductivity is an important component of endotherm morphology that strongly influences rates of heat exchange and can be dynamically adjusted through changes in peripheral blood flow. Thus, we simulated the conductivity of the skin to change dynamically with the operative temperature of the environment based on critical thermal limits to reduce and maximize heat exchange in cool and hot environments, respectively (36, 72). For a subset of measurements in the field observations that occurred before sunrise, we assumed body temperature changed to 39°C and body length reduced by 20% to more accurately reflect their state during this time of day. That said, these changes had minimal effects on overall heat flux and no effect on our conclusions (also see sensitivity analysis below).

We measured the solar absorptance of feathers from 29 live adult tree swallows ($n = 27$ females and 2 males) to estimate the amount of solar radiation absorbed across the dorsum and ventrum. There is no known sexual dichromatism between male and female tree swallows (73). We measured dorsal and ventral feather reflectance in the ultraviolet and visible light spectrum using the Ocean-HDX-XR (Ocean Insight, Ocean Optics Inc., Cincinnati, OH 45263) and the near-infrared light spectrum (up to 2000 nm) using the NIRQUEST + 2.5 (Ocean Insight). We excluded measurements between 2000 and 2500 nm because we found them to be unreliable. Nevertheless, our absorptance measurements (280 - 2000 nm) encompass approximately 90% of the wavelengths from direct solar radiation on Earth's surface. We also evaluated the relative importance of this trait in our models using a sensitivity analysis (see below).

Prior to each measurement, we used a Spectralon™ white standard to standardize spectroradiometer readings. We measured feather reflectance using a balanced deuterium tungsten light source (DH-2000-BAL, Ocean Insight) a standardized distance (~2 cm) from the feather surface with a 45° angle between the light source and fiber optic cable (QR200-12-MIXED, Ocean Insight). The angle, distance, and area of measurement were standardized using the RPH-1 reflection probe holder (Ocean Insight). For each individual, we recorded three dorsal feather patches (crown, mantle, rump) and one ventral feather patch (breast), which were averaged to calculate an average solar absorptance (dorsal and ventral) for each individual. We then corrected reflectance curves for solar radiation using the ASTM G-172 standard irradiance spectrum for dry air provided by SMARTs version 2.9.2. We calculated the solar-corrected reflectance value of the dorsum and ventrum by multiplying the intensity of solar radiation by the empirical reflectance, integrating across all wavelengths, and dividing by the total intensity of solar radiation (74). We averaged solar absorptance (1–reflectance) of the dorsum and ventrum across all individuals and incorporated the averaged value into our biophysical model for the species.

The simulations also included metabolic heat production (M) and evaporative cooling (E) based on field metabolic and water loss data collected while tree swallows were provisioning young. These measurements were collected using the doubly labeled water technique from a population of tree swallows on Kent Island in New Brunswick, Canada (40). To estimate M and E , we used 2.60 W for M and 0.52 W for E based on the average metabolic heat production and

evaporative water loss for a provisioning adult in the study. Specifically, a tree swallow provisioning a brood of five nestlings (average number of nestlings provisioned in our dataset) typically generates between 2.31 and 2.89 W (average = 2.6 W). This combined with an average water efflux of 19.9 mL per day (40) and the latent heat of vaporization of water ($2.5 \times 10^6 \text{ J kg}^{-1}$) indicates that provisioning tree swallows typically lose around 0.52 W from evaporative cooling. We note that the estimate of M is based on field metabolic rates estimated over a 24-hour period, which integrates provisioning activity (our focus) and periods of inactivity, namely at night (63). Long periods of inactivity could generate lower estimates of MHP that do not reflect levels produced during intense provisioning activity. However, incubating/brooding females expend nearly the same hourly energy ($\sim 201 \text{ mL CO}_2 \text{ h}^{-1}$) as actively provisioning adults ($\sim 211\text{--}231 \text{ mL CO}_2 \text{ h}^{-1}$; 63). Thus, our approach of dividing daily MHP evenly across the 24-hour cycle is reasonable, as hourly field metabolic rate during provisioning is well-approximated by the daily average. Therefore, our simulations incorporate the major components of heat generated and lost from tree swallows during provisioning activity in the field.

We did not explicitly include humidity in our model of avian net sensible heat flux (Q) for several reasons. First, humidity would primarily influence net sensible heat flux by limiting evaporative cooling (E). While high humidity can impede evaporative cooling under extreme heat (75–77), tree swallows operate well below such thresholds. Their optimal thermal conditions ($T_e \sim 19^\circ\text{C}$) fall below the range where humidity meaningfully limits heat dissipation (this study), and provisioning rates already decline steeply at slightly warmer temperatures. Moreover, empirical work shows that thermoregulatory responses in many birds are minimally influenced by humidity under mild to moderate temperatures (78–80), including tree swallows (69). Approximately 93% of our provisioning rates were measured at air temperatures between 15–32°C, which is the range of temperatures over which thermoregulatory responses by tree swallows are minimally affected by humidity (69). Second, if the effects of humidity were to be included, the model would also require species-specific information on the sensitivity of evaporative cooling to humidity at high temperatures. However, Q quantifies the degree to which heat gain or loss exceeds balance, regardless of how that imbalance is physiologically addressed. This makes the model broadly generalizable across species with diverse thermoregulatory mechanisms. Finally, although our model does not include humidity as an input, the fixed evaporative heat loss value was derived from field measurements collected across naturally variable environmental conditions, including variation in humidity (40). Thus, this value should be interpreted as an ecologically relevant average for provisioning tree swallows, not as a model of humidity-specific variation in evaporative heat loss. If needed, future implementations of Q could incorporate humidity where relevant, but in this system, the effects would be negligible.

Data processing and statistical analysis of field data

Modeling hourly variation in provisioning rate

All analyses were conducted in R (version 4.4.2; R Development Core Team 2024). We used the *feedr* package (81) to convert raw RFID visits to hourly provisioning rates per nestling based on code from a recent study on tree swallows (19). We then used generalized additive mixed models (GAMMs) from the *mgcv* package (82) to test the effect of Q on provisioning rate while accounting for the effects of wind speed, year (as a factor), nestling age, and sex. We also included individual bird as a random effect and a first-order autocorrelation structure with hour of day and day of year to control for temporal autocorrelation (83). Thus, our model accounts for potential variation in hourly provisioning rates due to interference from wind, year-to-year

variation, nestling age (and thus demands on parents as nestlings grow), male-female differences in provisioning rates, time of the day, and time of the year. Because wind speed, year, and sex had effective degrees of freedom (EDF) near one, we modeled these as unsmoothed terms (82), but we modeled all other predictors as smoothed terms. Our model used a Tweedie error distribution to account for increases in variance with the mean. We modeled the effect of Q on provisioning rate by setting the smoothing parameter (k) to 3. We did this to reduce issues related to model overfitting at high and low values of Q , where we had fewer provisioning data. Overfitting is especially problematic for analyses that generate predictions from generalized additive models (82, 84), which was partly our goal for this analysis (i.e., for predicting suitable habitat using the biophysical model). Adjusting the smoothing parameter had indiscernible effects on the model residuals, suggesting that we were not underfitting this model.

To test whether variation in Q or T_{air} better explained variation in provisioning rate, we compared model performance based on ΔAIC values using the $\text{AIC}()$ function in R. We also ran a separate analysis with average hourly body temperature (T_b) as the measure of thermal conditions experienced by tree swallows (Fig. S16), but otherwise this model was identical to the Q and T_{air} models. To explore the effect of interspecific-level differences in body size on the range of Q values experienced by birds, we ran the previously described Q model for hypothetical tree swallows of body masses between 10-640 g (as previously described; Fig. S17A). We then fit the relationship between body mass and the 80% performance breadth (see below) using a power function (Fig. S17C). Finally, we also fit these same body mass models using operative temperature (T_e) as the measure of thermal conditions experienced by birds to demonstrate the utility of this approach for comparative analyses involving species that differ in body size (Fig. S17B).

Estimating QPC parameters

Next, we extracted the predicted marginal effects of Q on provisioning rate using the $\text{ggpredict}()$ function from the ggeffects package (85). Finally, we used the rTPC package to fit 17 thermal performance curve models to the marginal effects of Q on provisioning rate from our GAMMs. We then used the best-fit thermal performance curve model to estimate the optimal Q for provisioning rate (Q_{opt}), the 80% performance breadth around Q_{opt} , and the degree of skewness in the performance curve. We incorporated the 80% performance breadth around Q_{opt} into downstream analyses (i.e., modeling tree swallow distribution and relative abundance) as this is a commonly used measure of performance breadth in the TPC literature (86).

Modeling insect prey abundance

We also used GAMMs to test whether Dipteran abundance varied with respect to the heat flux conditions experienced by tree swallows. This analysis was designed to assess whether variation in provisioning rates was associated with an extrinsic factor that can influence feeding rates (that is, prey abundance), rather than intrinsic factors (that is, maintaining heat balance). We used Dipteran abundance recorded from camera traps (modeled as counts of Diptera with a negative binomial error distribution) while controlling for the effects of wind speed, year, relative humidity, and habitat type of camera (prairie or pond). We also included a first-order autocorrelation structure to control for temporal autocorrelation (as above). We modeled year and habitat type as unsmoothed terms, but we modeled all other predictors as smoothed terms. We

note that our camera traps were programmed to take photographs every minute, so the temporal resolution of Diptera counts and weather variables were minute-by-minute.

Modeling deviations from normothermic body temperature

To understand whether variation in provisioning rate was related to intrinsic, thermoregulatory factors, we used body temperature (T_b) data from temperature-sensitive PIT tags to calculate the heterothermy index (HI; [27]) for each bird to characterize the extent of heterothermy exhibited by individuals. HI is mathematically equivalent to standard deviation of T_b , with modal T_b substituted for average T_b (87). We compiled all T_b readings for each adult and calculated each bird's modal T_b and HI during daylight hours (0500 to 0900) and under relatively mild T_{air} conditions ($10^{\circ}\text{C} < T_{air} < 30^{\circ}\text{C}$). Unlike a recent study on heterothermy in tree swallows (19), we did not restrict our estimate of modal T_b to T_b readings from birds at rest for at least 5 minutes because we did not find a consistent relationship between rest duration and T_b across individuals (Fig. S15).

Next, we compiled individual T_b readings. If a bird's T_b in a given minute exceeded their modal T_b plus their HI, the measurement was scored as hyperthermic (19). If T_b was less than a bird's modal T_b minus their HI in a given minute, the measurement was scored as hypothermic. In other words, we treated hyperthermia and hypothermia as deviations above or below modal T_b , respectively, that exceed an individual's typical T_b variation. We used GAMMs to test the effect of Q on the probability of hyperthermia and hypothermia (separate models for each, both modeled as a binary outcome with a binomial error distribution) while controlling for the effects of provisioning rate, nestling age, hour of the day, year, and individual variation in HI. We also included individual bird as a random effect and a first-order autocorrelation structure to control for temporal autocorrelation. Because provisioning rate, Q, sex, and HI had EDFs near one, we modeled these as unsmoothed terms, but we modeled all other predictors as smoothed terms.

Modeling thermoregulatory behaviors

We also modeled the occurrence of panting and ptiloerection as binary outcomes using binomial error distributions with GAMMs. Our models included Q as a fixed effect and nest box identification as a random effect (note that we could not distinguish individual tree swallows in either analysis). Nonetheless, the relationships between thermal conditions and thermoregulatory behaviors like panting and ptiloerection are well-described in birds (52, 88–90) and our findings closely match those of others (see Supplemental Text). Like the Diptera activity and T_b analyses, the temporal resolution of the panting and ptiloerection analyses were minute-by-minute.

Linking performance to fitness

Ideally, thermal performance curves measure a component of performance that affects individual fitness (91). To test if provisioning rate was associated with reproductive fitness, we modeled fledging success as the number of fledglings out of the total number of nestlings per nest using a generalized linear model with a quasi-binomial error distribution and logit link function to account for overdispersion. We included provisioning rate (provisioning visits per chick per hour)

as a predictor, and analyses were conducted in R using the *glm* function (92). Specifically, we measured provisioning rate as the average visits per chick per hour at each nest during 1-7 days post-hatching, which is when tree swallow nestling growth rates are highest (93) and thus most likely to be sensitive to variation in provisioning rates. We also note that previous work in tree swallows has found that higher provisioning rates are associated with greater fledgling condition and body mass (19, 94), which is often predictive of post-fledgling survival in altricial songbirds (95).

Evaluating the generality of the QPC in our focal tree swallow population

Testing for QPCs in other tree swallow populations

We searched for additional studies of hourly tree swallow provisioning rates and local weather station data from other geographic locations. We found two such studies, both involving RFID tags: one in Ontario (19) and one in Colorado (96). To model heat flux in these populations, we combined local hourly weather data with the average biophysical traits of tree swallows from our Iowa population in *Endoscape* as described above. We note that there are no described subspecies of tree swallows and phenotypic divergence among populations is minimal (97), justifying the use of biophysical trait data from our Iowa population. For the Ontario population, we only analyzed data from unmanipulated control individuals (excluding experimental birds with trimmed feather patches), but the statistical model was identical to the one we used for our Iowa population. The statistical model was similar for the Colorado population, except we did not incorporate sex in the model, as all provisioning data came from females. We also did not have information on the age of nestlings from the Colorado population. We estimated QPC parameters for both populations as described above for our Iowa population using the *rTPC* package.

Testing for QPCs at higher levels of biological organization

TPCs have been documented across levels of biological organization, from subcellular function to population dynamics (22). To test if QPCs are also present at multiple levels of biological organization, we tested if geographic variation in heat flux (see next section for details) can explain variation in reproductive fitness across the breeding range of tree swallows. We downloaded 152,019 tree swallow nesting records from across North America in the NestWatch database (98) in February 2025. After removing records with erroneous data (e.g., number of young fledged > number of eggs laid) and records with zero young fledged (to minimize the impact of catastrophic sources of nest failure, such as depredation), we retained 83,484 nest records for analysis. We first tested if geographic variation in average number of hours per day (during June and July) within optimal heat flux conditions (as defined by the 80% performance breadth of our Iowa population) was correlated with geographic variation in fledging success (as defined in our individual-level analyses). We modeled this using a big additive model with a quasibinomial distribution that included a smoothed fixed effect of average hours per day within the 80% performance breadth as well as smoothed fixed effects of latitude and longitude. Next, we tested if geographic variation in average hourly Q during daylight hours (also during June and July) was associated with geographic variation in fledging success. We modeled this using a big additive model with a quasibinomial distribution that included smoothed fixed effects of average hourly Q, latitude, and longitude.

Modeling net sensible heat flux of tree swallows across the breeding range

Modeling microclimatic conditions across North America

To model net sensible heat flux of tree swallows across their breeding range, we used the same general biophysical modeling approach previously described for our focal tree swallow population. The methods for incorporating the radiative environment, ground surface temperature, and biophysical traits were identical to the previously described approach. For estimating the thermal environment, we simulated heat flux for an average day of each month in the breeding season (June and July) using minimum and maximum monthly temperature from *WorldClim* (v. 2.1) (44). These minimum and maximum values were converted into hourly air temperatures using standard analytical approaches (36, 63). The approach for estimating the radiative environment and ground surface temperatures were the same as previously described.

For convective conditions, we transformed monthly average wind speeds from *WorldClim* into hourly wind speed across North America. Wind speed is difficult to model because it varies markedly over time and often exhibits non-normal distributions. On average, wind speed fluctuates between day and night in a sinusoidal pattern (similar to air temperature), with peak wind speeds occurring during midday (Fig. S18). However, because wind speeds are often skewed, the median and mode better capture temporal variation. For example, although the median nighttime wind speed is $\sim 1 \text{ m s}^{-1}$ (Fig. S18), the most frequent (modal) value at night is often much closer to 0.

To estimate daily fluctuations in wind speed for each hour of the day, we used the same sinusoidal functions to predict daily variation in air temperature using minimum and maximum wind speed (63). We assumed minimum wind speeds were similar to wind speeds occurring approximately near the ground surface using a logarithmic wind profile correction (68). These wind speeds essentially reached 0 m s^{-1} at night, reflecting the modal wind speed during this time (Fig. S18). For wind speeds during the day, we used the values reported from *WorldClim*, but then calibrated those wind speeds based on empirical data collected from weather stations. We first identified 20 long-term USCRN stations (<https://www.ncei.noaa.gov/pub/data/uscrn/products/subhourly01>) with subhourly data over the last 18 years across a set of target states selected to achieve an even geographic distribution across North America. We then chose one representative station per region based on data availability and completeness. These weather stations record wind speed in open, often grassland habitats at 1.5 m from the ground surface, reflecting conditions that tree swallows often experience in nature (99). We therefore calibrated our *WorldClim* maximum wind speeds to match those experienced at these sites over the last two decades. Specifically, we adjusted the logarithmic correction until the predicted median wind speed matched the observed median wind speed (Fig. S18). In doing so, the predicted wind speeds closely matched the observed wind speeds from North American weather stations (Fig. S18). In total, we used 4,448,596 observations of wind speeds in June and July to calibrate our modeled wind speeds, with approximately 90,000 observations per hour. We also explored the effects of variation in wind speed in our sensitivity analysis (see below). In addition, we ensured that our predicted air temperatures were similar to those recorded at weather stations, and we found close associations between observed and predicted air temperatures (Fig. S18). We note that ambient wind speed does not capture the full convective environment experienced by birds during flight, and future work could improve estimates of Q by incorporating flight-induced convection, flight duration, posture, and activity-specific metabolic heat production.

Predicting habitat suitability using heat flux across space and time

We used *Endoscape* to predict suitable conditions for nest provisioning in four climate scenarios: a contemporary climate scenario and three future warming scenarios (Shared Socio-economic Pathway [SSP] 245, 370, and 585). All climate data were downloaded from *WorldClim* (www.worldclim.org, 2.5 arcmin), and for the future warming scenarios, we averaged across all available global circulation models (GCMs) on *WorldClim* (13 GCMs for SSP2-4.5, 12 GCMs for SSP3-7.0, and 13 for SSP5-8.5) to produce an average warming scenario that accounted for variability among forecasting models. The SSP2-4.5 represents a moderate warming scenario in which the world continues to use a mix of energy sources, including fossil fuels (100). The SSP3-7.0 represents a more pronounced warming scenario as a result of limited technological advances and greater reliance on fossil fuels (100). The SSP5-8.5 represents the upper bound of climate warming expectations and assumes minimal efforts to limit reliance on fossil fuels (100). We ran these simulations from January through July to provide data for our spatial and temporal analyses.

To estimate suitable habitat for provisioning, we determined whether predicted net sensible heat flux (Q) for June and July was within 80% performance breadth of the optimal heat flux (Q_{opt}) for nestling provisioning (Fig. 1B, -1.11 W to 1.09 W) for each hour of the day. Although Q explained substantial variation in the average provisioning response (Fig. 1), hourly provisioning rates remained highly variable around the fitted relationship (Fig. S2). Therefore, the QPC should be interpreted as describing the mean response of provisioning performance to thermal imbalance, rather than as precisely predicting the provisioning rate of any single future observation. We averaged maps from June and July because 91.6% of tree swallow hatchings occur during these two months (as determined by the NestWatch database [74]), thus representing the predominant period in which tree swallows provision nestlings. The 80% performance breadth was determined using *rTPC* package in *R* (see *Data processing and statistical analysis* above), similar to analyses conducted on ectotherms. We then determined whether a tree swallow could provision for at least 14 hours per day for each month, which reflects typical durations required to fledge nestlings (43). Sites that met these requirements were considered suitable for reproduction. We considered using the correlation between provisioning rate and fledging success to estimate habitat suitability. However, peak average provisioning rate coincided with a ~75% probability of fledging young, thus requiring an arbitrary threshold value to delineate suitable and unsuitable habitat. Therefore, we opted to use the hours within the 80% performance breadth to avoid the arbitrary threshold and ground the model in an empirically based mechanism (i.e., in the amount of time needed to provision young each day during the nestling stage).

Sensitivity analyses

We conducted sensitivity analyses on *Endoscape* in previous studies (30), but to ensure our results were robust to variables that could influence heat flux estimates, we conducted additional sensitivity analyses to assess whether model parameterization influenced model sensitivity and specificity. We ran simulations in which field active body temperature was 40°C or 44°C based on the variation in empirical data (Fig. S15). We also ran simulations in which feather absorptance was 20% lower or higher (low = 0.78; high = 1.0) and evaluated whether 20% reductions or increases in body mass (and shape) affected our results. We also ran simulations in which we adjusted feather conductivity and wind speed by 20%. We found that our estimates of model sensitivity and specificity (and thus model performance) were robust to changes in most values (Table S1). Body mass (and thus shape), however, had a more pronounced effect on model sensitivity (Table S1). This likely occurred because the range of heat flux values increased rapidly with body size and surface area, while the assumed range of optimal heat flux values

remained unchanged across body masses. In reality, larger birds likely tolerate and provision across a broader range of heat flux conditions, which would reduce the decline in sensitivity observed in our simulations. In a separate analysis, we also explored the consequences of body size to understand how heat flux may scale differently between species. To explore this, we ran simulations assuming body masses of 10, 20, 40, 80, 160, 320, and 640 g, accounting for allometric relationships with all relevant biophysical traits (Fig. S17A, C). Nevertheless, these parameters may be particularly important for understanding heat balance in endotherms and, if not accounted for, could contribute to inconsistent relationships between heat flux and performance.

Comparing the performance of heat flux relative to other mechanistic approaches

To assess model performance, we downloaded the breeding range vector shape file and relative abundance of tree swallows as estimated by eBird (<https://science.ebird.org/en/status-and-trends/download-data>, accessed November 14th, 2024). We then used a custom script in Python to import the relative abundance raster as an array to assess model sensitivity (the proportion of correctly identified presences) and model specificity (the proportion of correctly identified absences) (101, 102). For model sensitivity, we specifically determined whether sites predicted to have a relative abundance greater than zero fell within the sites predicted to be suitable for provisioning. For the breeding range, we generated 1000 random points using QGIS (v. 3.34) within the breeding range to determine the proportion of sites that fell within the sites predicted to be suitable for provisioning. For model specificity of the breeding range, we generated 1000 random points in North America outside of the breeding range to determine the proportion of sites that fell outside the region predicted to be suitable. For the non-breeding range, we downloaded occurrence locations from eBird as above during January to compare the spatial distribution of heat flux estimates with the non-breeding range and occurrence locations.

To test alternative metrics that have been proposed as indices of endotherm performance, we then determined whether air temperature (based on the T_{air} -based curve; Fig. S3) or operative temperatures within the thermoneutral zone (TNZ) could predict the spatial distribution of the tree swallow breeding region. For air temperature, we assessed model sensitivity based on the 80% performance breadth of the optimal air temperature for provisioning based on the TPC we constructed in our Iowa population (12.61 – 39.28 °C; Fig. S3). We used the same criteria as net sensible heat flux to determine suitable habitat (that is, at least 14 hours per day within the optimal range) and the same criteria for estimating model sensitivity and specificity. In addition, we assessed model sensitivity using the thermoneutral zone by determining whether eBird relative abundance was associated with operative temperatures within the thermoneutral zone (TNZ, defined as the range of temperatures in which an endotherm exhibits a minimal metabolic heat production for thermoregulation assuming conditions for basal metabolic rate are met) using the same criteria as above. For the TNZ, we used a lower critical temperature of 29°C, which we measured directly in laboratory experiments (69). We estimated the upper critical temperature (39°C) based on values commonly observed in temperate passerines (103). We note that selecting a higher or lower upper critical temperature did not change our results qualitatively. For these analyses, we exported ASCII files generated by *Endoscope* into QGIS to generate the maps of suitable conditions, and we used DataGraph® to generate the bar plots and histograms of suitable conditions under current and future warming scenarios. We then integrated these figures into a single figure using Adobe Illustrator®.

Although some studies have suggested that there is little overlap between the TNZ and the conditions experienced by endotherms in nature (104–107), such conclusions are often based

on air temperature. This is problematic because the TNZ is measured in a metabolic chamber in a controlled setting and thus does not necessarily correspond to the thermal conditions at the same air temperature in natural, complex thermal environments due to radiative, convective, and conductive heat exchange (63). Therefore, we elected to assess the overlap between the TNZ and operative temperatures, as estimated by the biophysical model. We note that similar approaches using operative temperature have found that endotherms spend significant time within their TNZ in natural field settings (108–110). Even more concerning, however, is the practice of using air temperature to determine whether endotherms experience conditions outside of the TNZ as indices of climate vulnerability (10, 111–115). Consequently, relying on air temperature or simplistic thermal indices to assess climate vulnerability in endotherms is not only inadequate but may also lead to fundamentally misleading conclusions about species' physiological limits and exposure.

Predicting future range and phenological shifts

We predicted the shift in suitable habitat for tree swallows under the three climate warming scenarios described above, with a specific focus on the shift in the lower latitude limit, representing the warm edge of the range. For each climate scenario, we estimated the lower latitudinal limit using the vector line tool in QGIS (v. 3.34) to trace the continuous delineation of suitable habitat at low latitudes. For these analyses, we ignored isolated regions (such as areas at high elevations) and focused on describing the continuous delineation of suitable habitat across latitude (Fig. S19). We also conducted the same procedure for the eBird relative abundance data to illustrate the spatial shift in lower latitudinal limit of breeding habitat between current and future warming scenarios. Similar to above, we averaged the hours within 80% performance breadth of Q_{opt} for June and July in the future to determine the spatial distribution of future breeding behavior at the same time of year. To quantify the latitudinal shift in each scenario, we generated 1,000 random points along the latitudinal limit (in QGIS) to extract the average latitude for each linear latitudinal limit.

We also predicted the temporal shift in breeding phenology that would allow tree swallows to maintain their current breeding range. For this analysis, we determined the sites that were within the same threshold (at least 14 hours within the 80% performance breadth) for each month of the year. We then generated the lower latitudinal limit of the suitable breeding habitat for each month and compared it to the current lower latitudinal limit from eBird. We could then identify the month at which tree swallows would need to shift breeding phenology to maintain the same lower latitudinal limit of their current breeding range. Similar to above, we used 1,000 random points to extract the average latitude for each latitudinal limit.

For both analyses, we also included the upper latitudinal limit of the eBird breeding range as well as the latitudinal limit of the treeline (116). The purpose was to understand whether the current upper latitudinal limit appears to be constrained by the treeline (because tree cavities are required for breeding in tree swallows, at least in areas without artificial nest boxes from humans) and assess the extent to which the treeline will constrain range shifts to higher latitudes under future warming scenarios.

Array-based approach and implementation

We used new routines for estimating heat flux across North America using the NumPy library in Python. Instead of conducting calculations for each site individually, we adjusted the simulation to perform the calculations across the entire continent simultaneously using arrays. Doing so

greatly reduced the computation time and resources required to run the simulations by several orders of magnitude. We were thus able to run simulations on our personal computers, with a climate scenario taking approximately 32 min on a single CPU (Mac OS, 32 GB RAM, Apple M2). To run the simulations across more CPUs, we conducted the final simulations on the Longleaf High Performance Computing Cluster at the University of North Carolina at Chapel Hill.

Evaluating the performance and generality of net sensible heat flux

Correlative species distribution model: Evaluating performance

We used an ensemble modeling approach to evaluate the performance of our mechanistic model relative to commonly used correlative species distribution models. We implemented this using the *SSDM R* package (117), combining three widely used algorithms: generalized linear models (GLM), random forest (RF), and MaxEnt. Each algorithm was trained independently using presence-only occurrence data and a consistent set of environmental predictors (see below). The resulting models were then integrated into a single probabilistic projection, allowing us to account for differences in how each algorithm interprets the species–environment relationship. Ensemble approaches are particularly valuable because they can improve robustness and predictive accuracy by leveraging the strengths of individual models (118).

We began by downloading all available observations of tree swallows from the eBird database (N = 4,092,058). To focus on breeding-season distributions, we filtered these records to include only observations from June and July, resulting in 987,842 records. We removed several records located well outside of the species' known range in North America. To reduce spatial bias and overrepresentation of clustered observations, we thinned the data, a common technique used to build correlative SDMs (119). Specifically, we randomly sampled 10,000 points from the filtered dataset, calculated pairwise distances using the *geodist()* package, and excluded any points located within 20 km of one another. This procedure resulted in a final set of unique presence locations for model development. We note that thinning improved model performance by approximately 7-8% relative to models that used the full 10,000 randomly selected points. To account for variation introduced by random subsampling, we repeated the entire thinning and modeling workflow 10 times, generating replicate models to assess how sensitive model outputs were to the initial selection of occurrence points.

Before running the models, we reduced multicollinearity among predictor variables by excluding highly correlated bioclimatic variables (Pearson's correlation > 0.7) (120). The final set of predictors included four *WorldClim* bioclimatic layers: BIO5 (Maximum Temperature of Warmest Month), BIO7 (Temperature Annual Range), BIO15 (Precipitation Seasonality), and BIO19 (Precipitation of Coldest Quarter). We found that this uncorrelated subset yielded increased model performance by 2.5% compared to using all 19 bioclim variables.

We converted the continuous suitability outputs from the ensemble models into binary maps (suitable vs. unsuitable) using a range of quantile-based thresholding approaches. Specifically, we applied thresholds corresponding to the 10th through 90th percentiles (in 10% increments) of predicted suitability values at known presence locations. This allowed us to systematically explore how varying the threshold affected the balance between sensitivity and specificity. These binary maps were then used to calculate model sensitivity, specificity, and overall performance using the same independent point sets from the species range map, enabling direct comparison with our biophysical model. This range of thresholds also helped capture the

observed tendency for some values to overpredict or underpredict species occurrences, providing a practical framework for interpreting the predictive behavior of correlative SDMs across a spectrum of conservative to liberal suitability thresholds.

We also developed a more targeted correlative species distribution model using MaxEnt to allow for greater customization (121). MaxEnt estimates the probability distribution of maximum entropy for species occurrences, subject to constraints imposed by environmental conditions at known presence locations. We ran the model under two scenarios: first, using MaxEnt's default settings, which allow complex feature types and interactions; and second, using a simplified configuration that included only linear and quadratic features to reduce the risk of overfitting and improve interpretability (122). Model performance was comparable between the two approaches (see results below), suggesting that the simpler model retained predictive strength while offering greater transparency.

We also used the same MaxEnt framework to build a hybrid species distribution model that incorporated both bioclimatic variables and mechanistic predictors. This allowed us to explicitly compare climate and biophysical layers in a statistical, species distribution modeling framework. For the mechanistic predictor, we used the average Q values across North America during June and July, matching the breeding-season observations. We used two standard MaxEnt output metrics to assess the importance of bioclimatic and mechanistic layers: percent contribution and permutation importance. Percent contribution reflects how much each variable influenced the model during training, though it can be sensitive to the model-fitting path (121). Permutation importance measures how much shuffling the values of a variable reduces model performance, providing a more stable estimate of each variable's influence (121). We also tested whether MaxEnt could reproduce the QPC by examining whether predicted suitability peaked near $Q = 0$, the physiologically optimal value. Together, this modeling framework offers a robust and interpretable comparison between traditional correlative models and mechanistic models based on physiological constraints.

Correlative species distribution model: Evaluating generality

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 (Fig. S20), provision young at the nest, and for which field metabolic rate (FMR) data were available: barn swallow (*Hirundo rustica*), American robin (*Turdus migratorius*), black-capped chickadee (*Poecile atricapillus*), European starling (*Sturnella vulgaris*), house wren (*Troglodytes aedon*), Carolina chickadee (*Poecile carolinensis*), purple martin (*Progne subis*), ovenbird (*Seiurus aurocapilla*), and northern mockingbird (*Mimus polyglottos*) (123, 124). Measurements of FMR for most species occurred while provisioning young (*P. subis*, *H. rustica*, *T. bicolor*, *T. aedon*, *S. vulgaris*, *S. aurocapilla*, *P. carolinensis*). Other rates were measured on individuals during the breeding season, but we could not corroborate whether each individual was provisioning nestlings (*T. migratorius* and *M. polyglottos*). FMR for *P. atricapillus* was estimated during the winter, and we assumed FMR during the breeding season was 10% higher than these rates (125). This assumption did not alter our conclusions. The FMR values for *M. polyglottos* were based on Nagy et al. (123) and confirmed by studies using activity-based methods (126). For *S. vulgaris*, we used the FMR associated with females because these rates were significantly higher, likely due to higher rates of provisioning by females in this species. For all other species, we used average rates because male

and female rates were generally not significantly different (123, 124). We reduced FMR values by 20% to account for evaporative heat loss—based on empirical estimates from tree swallows as above—and used the adjusted values as the net internal heat flux in calculations of net sensible heat flux. We emphasize that this 20% adjustment is an approximation intended for broad comparative modeling of breeding-season thermal load, not a claim that evaporative heat loss is constant across all environmental conditions, species, or behavioral states. This general framework allowed us to assess whether habitat suitability peaks near thermal balance (i.e., when net sensible heat flux ≈ 0). Morphological parameters, including body length, width, height, insulation depth, and feather length, were scaled based on body mass using empirically derived allometric relationships (36). We assumed an active body temperature of 42°C (a typical field active body temperature for a small songbird in North America (127)) and assigned feather absorptance values representative of typical avian plumage, with a darker dorsum (0.75) and lighter ventrum (0.40) (74). While these input values are estimated or generalized, they enable a standardized modeling framework for assessing the broader role of heat flux in shaping avian distributions.

After downloading eBird presence data for each species, we filtered observations to the peak provisioning months of June and July for most North American songbirds and thinned presence records using a 20 km minimum distance filter to reduce spatial autocorrelation (and ensure each pixel was not included more than once). We then used MaxEnt to generate species distribution models, incorporating a set of uncorrelated bioclimatic predictors along with a species-specific Q map representing average thermal exposure during June and July. For each species, we extracted response curves for Q and calculated variable importance metrics, including percent contribution and permutation importance. Predicted response curves were normalized to a 0–1 scale to compare the heat flux niche profiles across species and assess whether peaks in habitat suitability were near heat balance ($Q \approx 0$). We also conducted the same analyses assuming low wind speeds (0.1 m/s) to understand how suitability changes with convective conditions.

Supplementary Text

General theory on QPCs and comparisons with TPCs

Here, we introduced the concept of a QPC for endotherms as a complementary framework to TPCs in ectotherms. We found many similarities between the two concepts, but we also wanted to highlight some important differences. In terms of similarities, TPCs and QPCs are simply a statistical way to explain variation in performance relative to an independent variable. In both cases, the independent variables are related to the effects of temperature (TPCs) or heat flux (QPCs). In addition, both curves have an optimum (T_{opt} vs. Q_{opt}), a breadth, and (potentially) curve asymmetry which reflects asymmetric physiological stresses of hot versus cold conditions (2). These components of the curve are generally synonymous across TPCs and QPCs with respect to the conclusions that can be drawn. Specifically, they indicate the environmental value at which performance is maximized, the change in performance above and below the optimum, and the sensitivity of performance to the independent variable. As performed in analyses on ectotherms (3, 9), we also used the 80% performance breadth to model suitable conditions for performance. Nonetheless, there are also important differences between QPCs and TPCs

TPCs are bounded by critical temperatures (i.e., CT_{min} , CT_{max}), at which performance (i.e., population growth, sprint speed, etc.) typically drops to zero. In our study, we did not observe analogous critical limits, at which tree swallows stopped provisioning, for instance.

Instead, provisioning rate declined as birds experienced thermal conditions further from Q_{opt} (Fig. 1). Importantly, small reductions in provisioning rate can have large effects on reproductive fitness (Fig. S5), such that fitness may approach zero before provisioning itself ceases. Thus, QPCs may not yield discrete thermal limits in the same way as TPCs, but instead capture continuous, sub-lethal declines in performance. Future work could identify the extreme values of Q at which survival or reproduction approaches zero, extending beyond traditional thermal limits to link continuous performance declines with ultimate fitness consequences (128).

There are also differences in the interpretation of the independent variable. In TPCs, the axis is either the body temperature of the organism or ambient temperature in a controlled setting, where ectotherms can be assumed to be in thermal equilibrium. However, as discussed above, body temperature is generally much less variable in endotherms when maintaining normothermy. Additionally, endotherms generate high levels of metabolic heat during activity (2), which can lead to a positive correlation between measures of performance and body temperature (e.g., Fig. S16A). In our data, this observed pattern suggests that most variation in T_b is associated with heat production during provisioning activity itself, with T_b varying by approximately 4°C across provisioning rates, whereas T_b varies by only approximately 0.4°C across the environmental gradient (Fig. S16B). This illustrates why T_b alone is difficult to use as the independent axis of a performance curve in endotherms. T_b is partly a consequence of performance and thermoregulatory state, rather than an external thermal load that independently predicts performance. This also occurs in at least some ectotherms (129), but the magnitude of the effect is likely to be much lower than in endotherms. Thus, while body temperature variation may affect performance in endotherms (130), there may also be direct effects of performance on body temperature, complicating interpretations of T_b -based TPCs. While this bidirectional causality is also an issue with QPCs (given that the change in body temperature is one component of net sensible heat flux), the feedback loop is partially decoupled because several environmental and organismal sources of heat flux are integrated together. Moreover, the organismal sources of heat flux can be held constant (as in our approach here), which provides a measure of the extent of organismal responses (through changes in behavior and/or physiology) required to achieve heat balance in the face of varying environmental conditions. Thus, net sensible heat flux more reflects an index of thermal imbalance (or thermal stress), rather than the direct physiological state of the endotherm. Therefore, QPCs are more complex and dynamic than TPCs in ectotherms, but they offer important advantages relative to body temperature-based TPCs in endotherms.

Another key difference between QPCs and TPCs is the body size-dependence of net sensible heat flux. Because larger organisms experience heat exchange across a larger surface area, they will experience a wider range of heat flux values than smaller organisms (Fig. S17A; 12). Across endotherms, there is no consistent relationship between body size and body temperature (131). As such, comparing QPCs across species will require that the size-dependence of heat flux be taken into account. We envision two solutions. The first is to use operative temperature rather than net sensible heat flux. The equation for net sensible heat flux is quantitatively identical to operative temperature if metabolic heat production, evaporative water loss, and changes in body temperature are held constant (13). Operative temperature could be used to at least compare the performance breadth with respect to the external thermal environment (Fig. S17B). Curves developed from operative temperature also represent an effective way to compare thermal optima between species. However, we still argue that net sensible heat flux is preferable to operative temperature because physiological responses are incorporated into the former and not the latter, which also provides a clear expectation for the optimum ($Q_{opt} = 0$ W). That said, we also acknowledge that T_e has the advantage of being easily compared across species, including those that differ dramatically in body size (Fig. S17B). The

second solution is statistical and corrects for the size-dependence of net sensible heat flux. Analogous to the use of mass-specific metabolic rates (132), size-corrected metrics of net sensible heat flux and the performance breadth around Q_{opt} could be used to facilitate comparisons across species (Fig. S17C,D). A related approach may be to standardize Q relative to basal metabolic rate instead of body mass.

In ectotherms, TPCs are used widely to explain variation in population-level and individual-level traits, such as growth rate, sprint speed, endurance, and metabolic rate (4). QPCs are not likely to be used as widely, simply because traits like sprint speed may not be immediately sensitive to net sensible heat flux as they are more dependent on the body temperature of the animal (which is likely relatively stable during activity). Rather, traits related to endurance (such as provisioning rate or endurance on a treadmill) are more likely to be related to net sensible heat flux because the trait is more likely to decline over time as animals begin to lose heat, overheat, or use thermoregulatory strategies for maintaining heat balance that lower performance. Such responses have been observed in the endurance of running in mice, for instance (31). However, there are a wide range of traits that appear to be sensitive to the thermal environment in endotherms, including lactation, digestion, and ovary development (133, 134). Although there are likely limitations on the traits that would demonstrate a QPC, traits like endurance, lactation, or provisioning rate are likely related to survival or reproductive fitness, either directly or indirectly (as observed here). Therefore, QPCs provide a useful axis to explore variation in endotherm performance, especially in traits closely related to reproductive fitness and survival.

Finally, there is growing recognition that endotherms vary substantially in the extent to which stable body temperatures are regulated (12). Most birds and mammals exhibit relatively minor fluctuations in active body temperature, while more pronounced fluctuations occur primarily in a handful of phylogenetically older taxa inhabiting tropical regions (135, 136). From the QPC perspective, the latter animals would be near $Q \sim 0$ W in cases where body temperature closely tracks air temperature (37), assuming the organism is in thermal equilibrium with its environment. We suggest that these species (which, in some cases, have been described as “protoendotherms”; 36) would be better studied using TPCs built on operative temperature (which our biophysical approach is already capable of estimating; Fig. S17B). It is also worth noting that many of these species primarily engage in “deep heterothermia” during inactive rest phases (e.g., torpor; 126), when common measures of performance like sprint speed are not relevant. Most birds and mammals exhibit relatively minor fluctuations in body temperature while active (often termed “active-phase shallow heterothermia”), similar to tree swallows. Although, in extreme cases, such as intense exercise, metabolic heat production can dominate this balance and drive rapid increases in body temperature (e.g., exercise-induced heat stroke) (138). Regardless, our biophysical approach accommodates this because net sensible heat flux incorporates variation in body temperature in addition to metabolic heat production and evaporative cooling. In this specific case, we did not incorporate heterothermia into our simulations. The main reason for this was to hold all organismal sources of heat flux (including body temperature) constant at values typical for the species. The advantage of this approach is that our estimates of Q describe the magnitude of organismal responses that would be needed to achieve heat balance, given current environmental conditions. Modifications to body temperature (heterothermia) are simply one of many ways that endotherms can achieve heat balance (12), which may come at a functional cost (16, 17) as with other thermoregulatory strategies. Thus, the QPC approach described here could be expanded to cover the vast majority of endotherm thermoregulatory strategies.

Provisioning rate and Q

We obtained 3,011 hourly provisioning rates for 56 adult tree swallows (6 males and 50 females). On average, we obtained 50 hourly provisioning rate measurements per individual (range: 10 – 167 hours). After accounting for wind speed, hour of day, nestling age, sex, individual identification, and temporal autocorrelation, we found a significant, non-linear effect of Q on provisioning rate ($\text{EDF} = 1.99$, $F = 105.45$, $p < 0.001$) that has characteristics of a classic thermal performance curve (Fig. 1A). Specifically, provisioning rate peaked at Q of -0.006 ± 0.007 W (estimated optimal Q $\pm$ 95% CI) but decreased both above and below this. Moreover, the positive (right) skew of the curve (0.65) indicates that provisioning rates declined most steeply as Q decreased. In other words, provisioning rates decreased most dramatically as birds experienced increased heat stress, similar to patterns observed in TPCs. We also found evidence for a significant, non-linear effect of T_{air} on provisioning rate in the same model with T_{air} substituted for Q ($\text{EDF} = 1.94$, $F = 9.86$, $p < 0.001$), with provisioning rates peaking at T_{air} of 25.94 ± 0.04 °C. However, the Q model performed substantially better than the T_{air} model ($\Delta\text{AIC} = 191.80$).

Provisioning rates as a measure of performance

We found that provisioning rates early in nestling development were positively correlated with fledging success ($\beta = 0.97 \pm 0.47$ SE; $P = 0.048$), with predicted fledging probability increasing from ~0.49 at 1 visit per chick per hour to ~0.98 at 5 visits per chick per hour (Fig. S5). Thus, provisioning rate is a meaningful measure of reproductive performance in our tree swallow population, and likely in the species generally, given our results combined with prior work (18, 94).

Hyperthermia, hypothermia, and thermoregulatory behaviors

To further test for thermoregulatory constraints on performance, we tested whether deviations above and below modal T_b (hyperthermia and hypothermia, respectively) varied with Q during nestling provisioning. Overall, we obtained 504,181 T_b readings from 56 individuals (6 males and 50 females). After accounting for wind speed, hour of day, nestling age, provisioning rate, individual variation in HI, sex, individual identification, and temporal autocorrelation, we found that the probability of hypothermia increased as Q increased ($\beta = 0.66$, $z = 52.07$, $p < 0.001$; Fig. 1C) and the probability of hyperthermia increased as Q decreased ($\beta = -0.84$, $z = -61.17$, $p < 0.001$; Fig. 1C).

Hyperthermia and hypothermia could constrain performance because they represent deviations from modal T_b , which is often assumed to be the T_b at which suborganismal components of performance (e.g., metabolic efficiency, enzymatic function, tetanic tension) are optimized (12, 87). A non-mutually exclusive possibility is that hyperthermia and hypothermia trigger thermoregulatory behaviors that are incompatible with performance-demanding activities like aerial foraging during nestling provisioning (52). Consistent with this hypothesis, we found that tree swallows were more likely to pant as Q decreased ($\beta = -17.25$, $z = -3.40$, $p = 0.005$; Fig. 1D), mirroring our hyperthermia results. Similarly, we found that tree swallows were more likely to have their feathers fully erected as Q increased ($\beta = 0.99$, $z = 8.50$, $p < 0.001$; Fig. 1D), mirroring our hypothermia results.

Correlative species distribution modeling

Using the ensemble modeling approach, we evaluated how varying the classification threshold affected model performance by applying probability quantile thresholds ranging from 0.1 to 0.9 in 0.1 increments. As the threshold increased, we observed an optimal quantile for overall model

performance, calculated as the mean of sensitivity and specificity, around 0.4 for the ensemble approach (Fig. S8A). This peak model performance of the correlative model (0.70) was lower than the biophysical model (0.83; see dotted line).

Model performance was highly similar across the complex MaxEnt model, the simplified MaxEnt model (restricted to linear and quadratic features), and the hybrid MaxEnt model. The highest performance was consistently observed at the intermediate quantile, with maximum performance values ranging from 0.71 to 0.74 across model types (Fig. S8B,C,D). These more customized models performed slightly better than the model ensemble approach but were still lower than the model performance achieved by the biophysical model.

In the hybrid MaxEnt model, net sensible heat flux (Q) emerged as the most influential variable, with the highest percent contribution and permutation importance (Fig. S21). Although the inclusion of hybrid layers did not improve overall model performance, these results suggest that such layers may enhance correlative SDMs by capturing key physiological or environmental constraints. Notably, predicted habitat suitability peaked when Q was near zero (Fig. 3), a pattern consistent with results from the provisioning rate analyses. This finding indicates that optimal values of Q (Q_{opt}) and the breadth of performance tolerance may, at least in part, be inferred from modeled heat flux and species occurrence data.

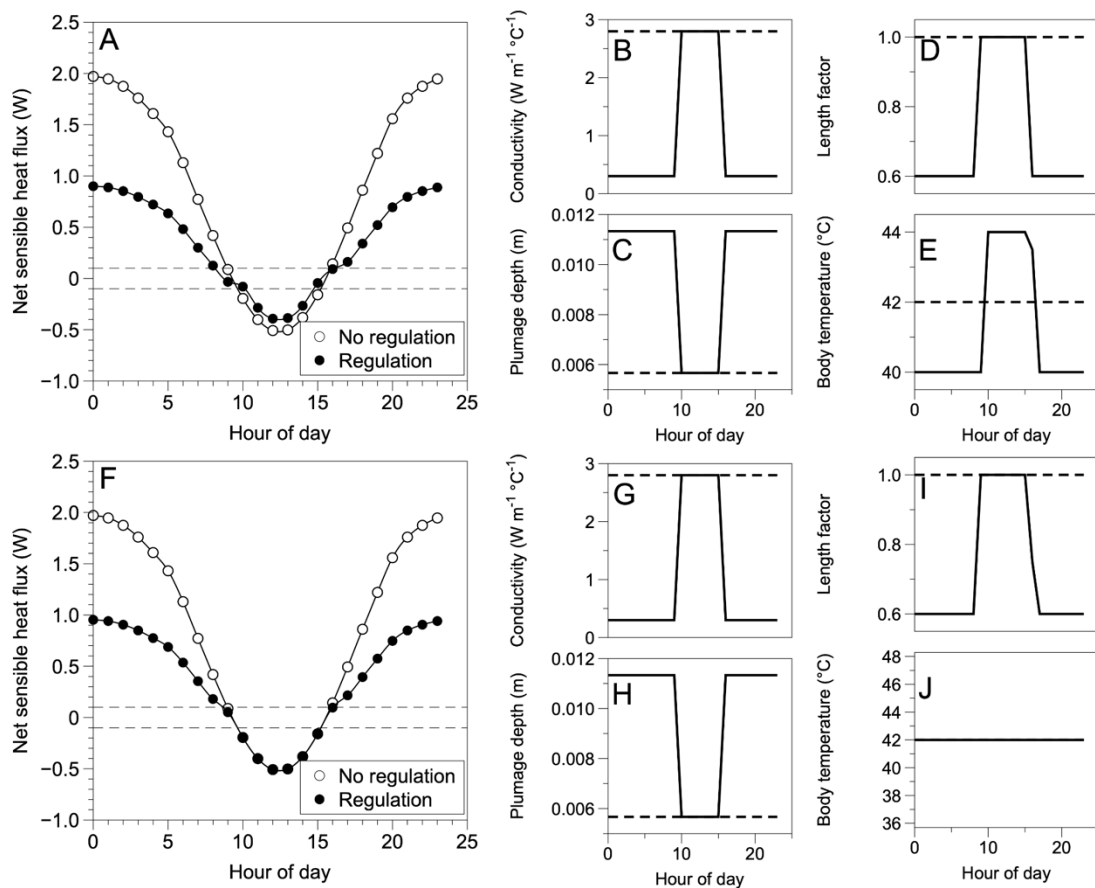


Fig. S1. Simulated thermoregulatory responses illustrating how behavioral and physiological adjustments can reduce net sensible heat flux (Q) toward thermal balance across the diel cycle. Panels A and F show hourly Q values for a tree swallow under unregulated (open circles) and regulated (filled circles) conditions. Dashed horizontal lines indicate the range considered to represent approximate thermal balance ($-0.1 < Q < 0.1$ W). In the upper simulation (A–E), birds were allowed to dynamically regulate skin conductivity (B), plumage depth (C), body shape through changes in body length (D), and body temperature (E). In the lower simulation (F–J), the same regulatory responses were permitted except that body temperature was held constant. Regulatory responses were applied sequentially until all possible changes could be made to minimize heat flux, demonstrating that realistic adjustments in physiology and morphology can substantially buffer thermal imbalance. Remaining deviations from thermal balance could likely be offset through additional thermoregulatory mechanisms not explicitly modeled here, including metabolic heat production, evaporative cooling, or microhabitat selection. Extrapolating empirical metabolic heat production measured below the lower critical temperature in tree swallows to an operative temperature of $5^\circ C$ suggests that birds could generate approximately 0.54–1.05 W of heat (69), which is sufficient to offset the remaining modeled imbalance after behavioral adjustments and observed changes in T_b are considered.

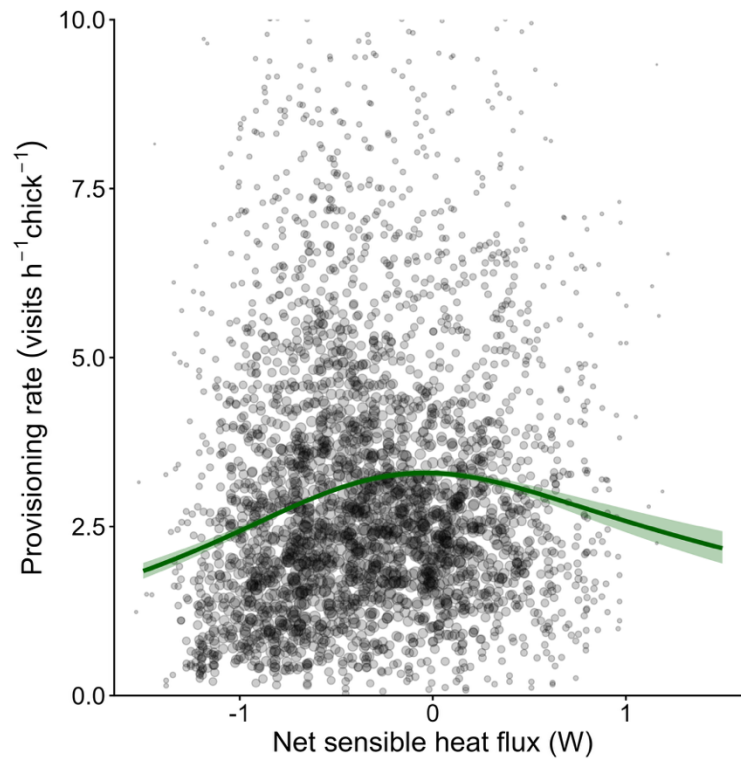


Fig. S2. Partial effect plot of the QPC in our Iowa population. Tree swallow hourly provisioning rates per nestling were highest at Q of -0.006 W (optimal $Q[Q_{opt}]$) and declined above and below this point. The solid curve represents the predicted marginal effects of Q on provisioning rate from a generalized additive mixed model (see SI for details) and the shaded band represents the model 95% confidence intervals. The points represent partial residuals and are size-scaled according to local observation density (kernel-smoothed).

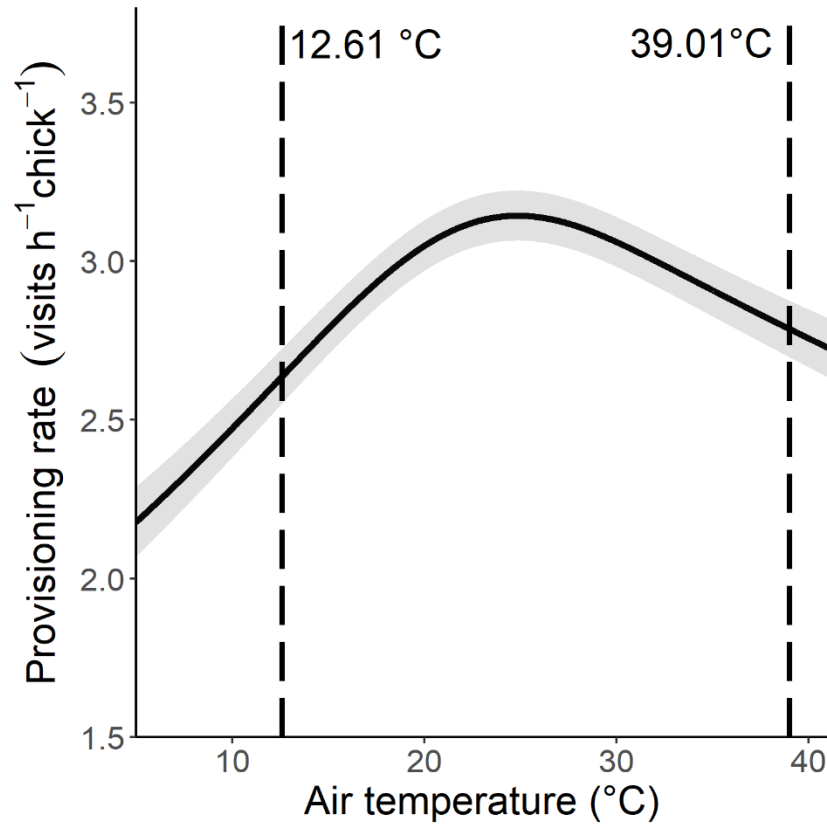


Fig. S3. Performance curve based on air temperature for tree swallows. Tree swallow hourly provisioning rates per nestling were highest at an air temperature of 25.94 °C (optimal T_{air} [T_{opt}]) and declined above and below this point. The dashed vertical lines indicate the 80% performance breadth. The solid curve represents the predicted marginal effects of T_{air} on provisioning rate from a generalized additive mixed models (see SI for details) and the shaded band represents the model 95% confidence intervals.

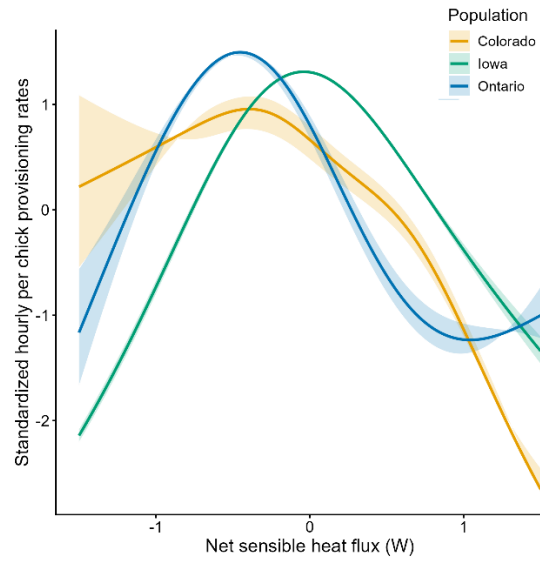


Fig. S4. Performance curves built on net sensible heat flux were similar across three tree swallow populations. Specifically, the estimated optimal heat flux for provisioning nestlings (Q_{opt}) was close to heat balance ($Q \sim 0$) in all populations (*Iowa*: $Q_{\text{opt}} = -0.006$ W; *Ontario*: $Q_{\text{opt}} = -0.654$ W; *Colorado*: $Q_{\text{opt}} = -0.445$ W). Moreover, the 80% performance breadths in all populations overlapped $Q = 0$ (*Iowa*: 80% performance breadth = -1.11, 1.09 W; *Ontario*: 80% performance breadth = -2.15, 0.85 W; *Colorado*: 80% performance breadth = -1.58, 0.68 W). The y-axis represents hourly per chick provisioning rates standardized across populations, given interpopulation variation in absolute provisioning rates. The solid curves represent the predicted marginal effects of Q on provisioning rate from generalized additive mixed models (see SI for details) and the shaded bands represent model 95% confidence intervals.

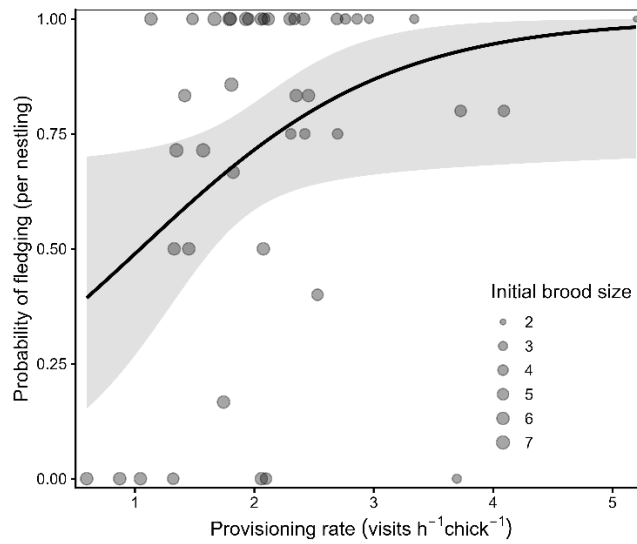


Fig. S5. Provisioning rate is related to fledging success. Per chick provisioning rates were positively correlated with the probability of a nestling successfully fledging from its nest. The solid line represents the generalized linear model prediction and the shaded area corresponds to the 95% confidence interval. Each data point is a separate nest and variation in point size represents variation in the number of nestlings initially present in the nest (initial brood size).

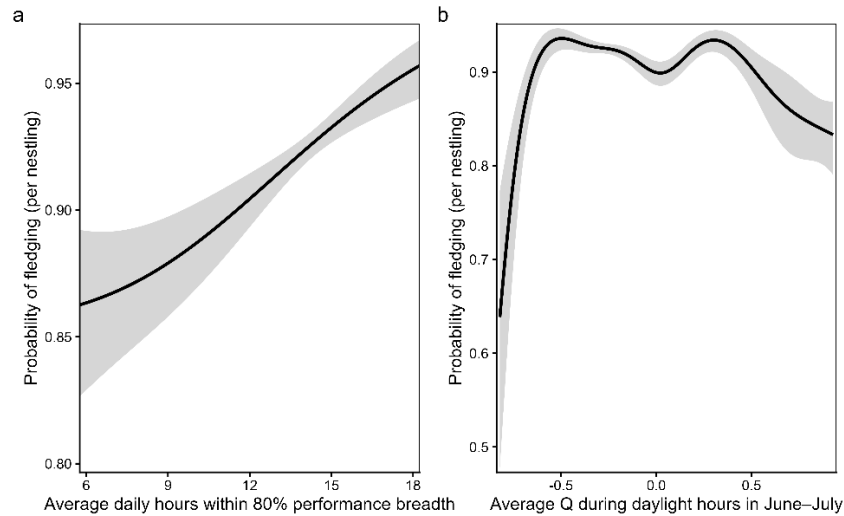


Fig. S6. The effects of heat flux across tree swallow populations in North America. Analyses of reproductive fitness across the tree swallow breeding range suggest that Q influences geographic variation in tree swallow fitness. A) Tree swallows inhabiting regions with more hours per day within the 80% performance breadth (of our Iowa population) were more likely to have higher fledgling success than tree swallows from regions with fewer hours per day in optimal heat flux conditions. B) Tree swallows inhabiting regions where average hourly Q was near zero ($Q_{\text{opt}} = -0.32$; 80% performance breadth = $-1.18, 0.53$ W) had higher fledgling success than tree swallows in regions with higher or lower average hourly Q . Both analyses are based on 83,484 nest records from the NestWatch database. The solid curves represent the predicted marginal effects of Q on provisioning rate from generalized additive mixed models (see SI for details) and the shaded bands represent model 95% confidence intervals.

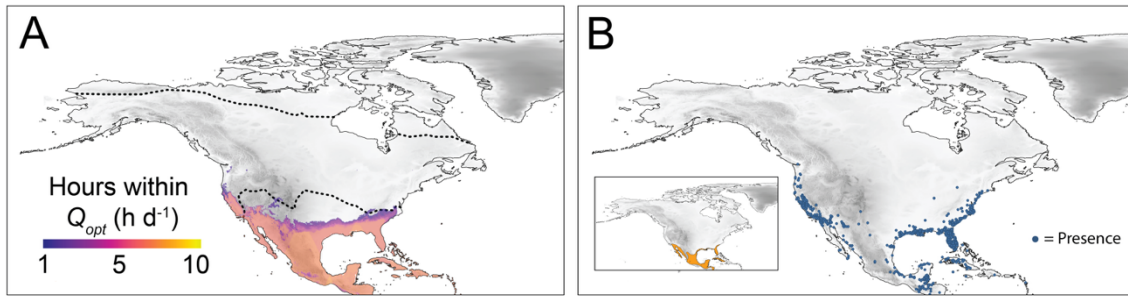
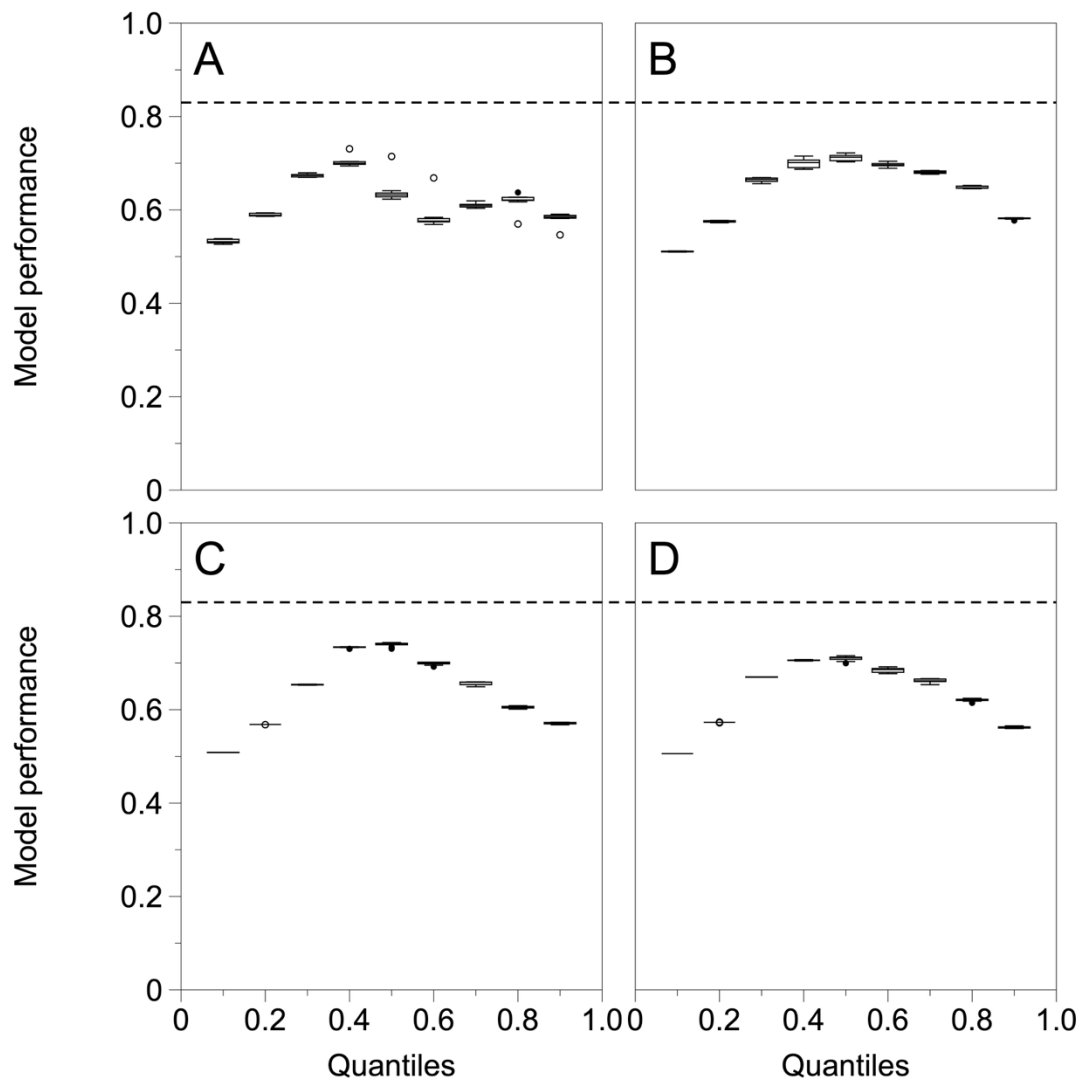


Fig. S7. Hours within optimal heat flux coincide with non-breeding range during winter months. (A) The spatial distribution of suitable habitat for tree swallows as determined by average hours within the 80% performance breadth for Q during January in contemporary climatic conditions. Dotted lines indicate the upper and lower latitudinal limits of the breeding distribution. (B) The geographic distribution of presences of tree swallows in January as determined by eBird observations as well as the shape file for the non-breeding range from eBird (inset). Of the 2,699 observations from eBird, 2,515 or 93.1% fell in regions predicted to experience substantial portions of the day (~ 10 h) within the 80% performance breadth of heat flux for tree swallows. The figure illustrates that tree swallows could track environmental conditions that maximize time experiencing heat balance between breeding and non-breeding grounds.

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1757 **Fig. S8. Model performance across thresholding quantiles for correlative species**
1758 **distribution models.** (A) Performance of the ensemble model across threshold quantiles. The
1759 dotted line represents the performance of the biophysical model using net sensible heat flux. (B)
1760 Performance of the MaxEnt model with the highest complexity settings. (C) Performance of the
1761 MaxEnt model constrained to linear and quadratic terms. (D) Performance of a hybrid MaxEnt
1762 model incorporating net sensible heat flux alongside uncorrelated bioclimatic predictors. Across
1763 all thresholding approaches, no correlative model exceeded the performance of the biophysical
1764 model.

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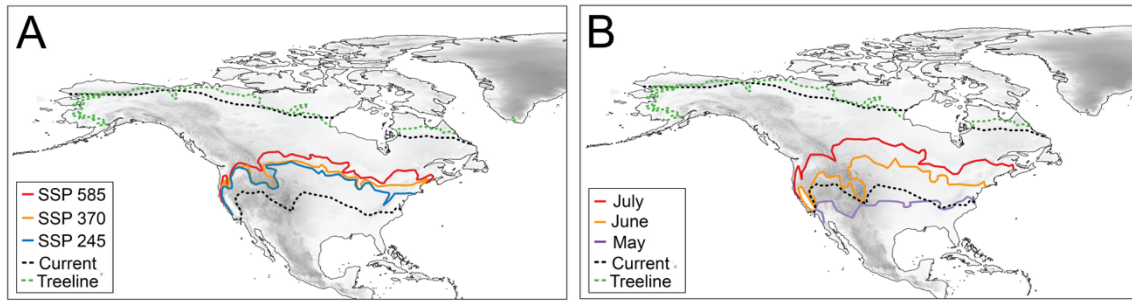


Fig. S9. Forecasts of tree swallow responses to climate change reveal importance of heat flux. (A) The spatial shift in the lower latitude limit of the tree swallow breeding range under three climate warming scenarios (SSP2-4.5 = blue; SSP3-7.0 = orange; SSP5-8.5 = red) assuming tree swallows continue to breed during June and July. The current upper and lower latitudinal limits are delineated by dashed black lines. The North American treeline (the northern limit of suitable tree swallow breeding habitat) is also displayed as a dashed green line. (B) The temporal shift in the lower latitude limit of the tree swallow breeding range as predicted by heat flux under SSP5-8.5. Displayed are the limits for July (red), June (orange), and May (purple) as well as the current range limits and treeline.

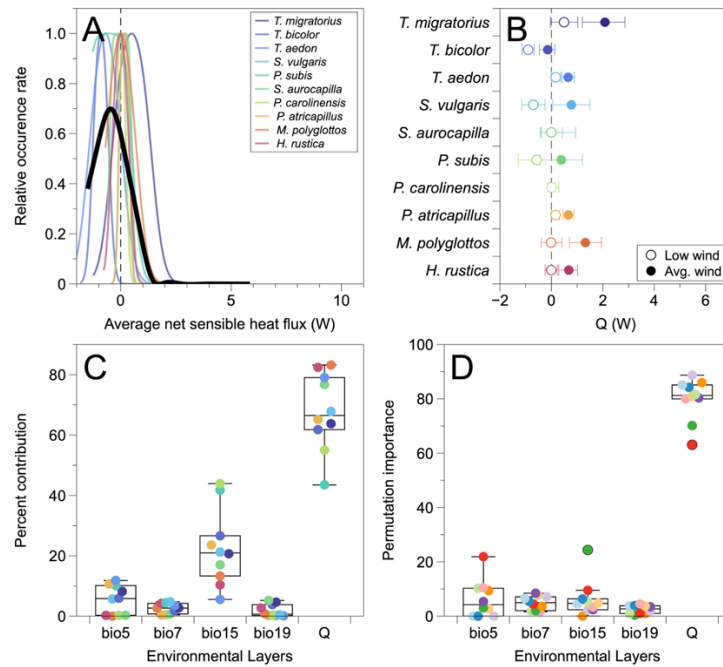


Fig. S10. Evidence for heat flux shaping breeding distributions in nine additional bird species at low wind speeds. (A) Response curves for net sensible heat flux at low wind speeds (0.1 m/s) predicting relative occurrence rate in tree swallows and nine additional species. The solid black line represents the average response curve across all species 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 at low wind speeds. (D) Permutation importance for the uncorrelated bioclimatic variables and net sensible heat flux at low wind speeds. 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).



Fig. S11. Panting behavior in tree swallows. Image from 10-second video clip showing an adult female tree swallow panting. The bill of this individual was held open as it rested at the nestbox in between provisioning trips and respired heavily. This video was recorded on 5 July 2021 at 14:24 when T_{air} was 33.57°C and Q was -1.37 W.

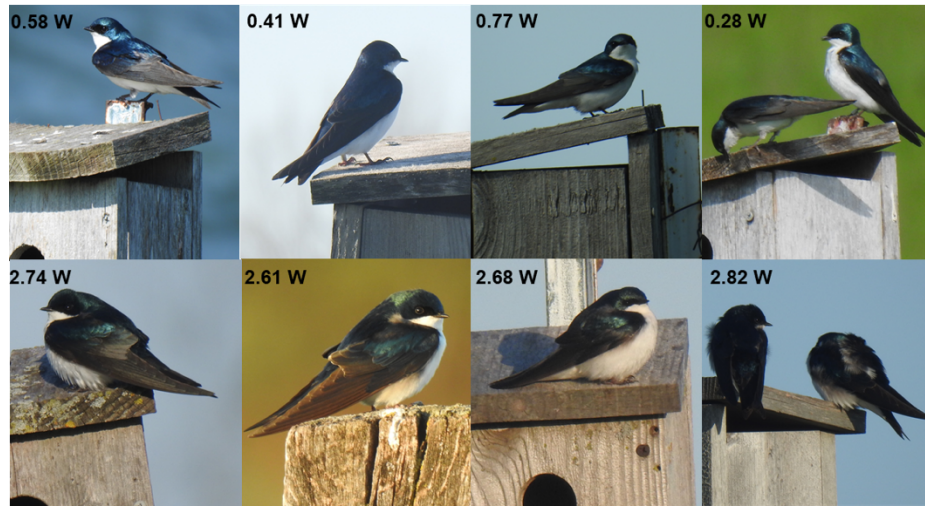


Fig. S12. Photographs of tree swallows perched on nest boxes illustrating variation in feather posture we used to define ptiloerection. We categorized all birds in the top row as “not fluffed” and all birds in the bottom row as “fluffed”. Note that the tarsometatarsus is clearly visible in the top row, while the tarsometatarsus is entirely or mostly covered by raised ventral feathers in the bottom row. Also note that birds in the bottom row show an obvious “hump” of raised feathers just behind the head around the nape. The estimate of Q from our biophysical model for each minute a bird was photographed is in the black text in the upper left of each photograph. All photographs were taken by CKP with a Nikon Coolpix P900 camera from 9 April 2024 to 18 May 2024 at our study site.

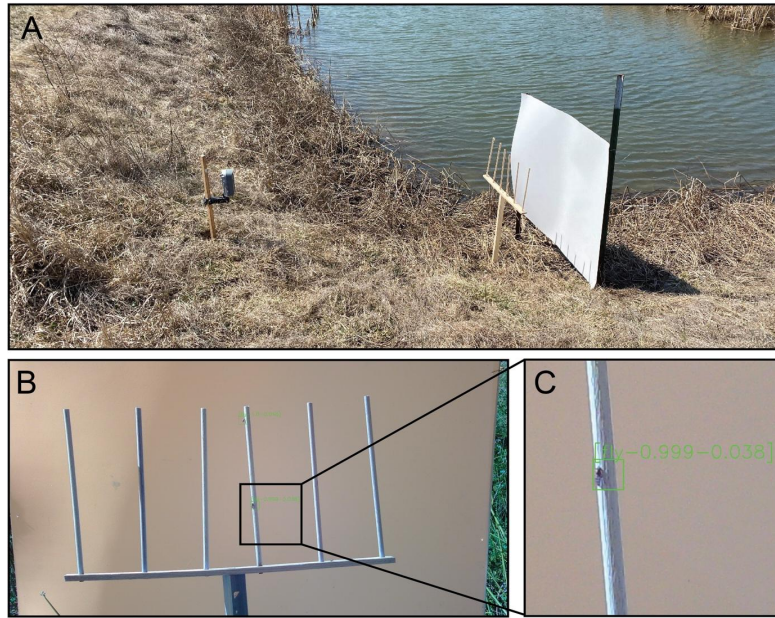


Fig. S13. Measurements of Dipteran activity using artificial intelligence. (A) The camera, wooden dowels, and background for recording insect activity in the field with a time-lapse camera (left) placed in front of a wooden perch array and large white board (right). We programmed cameras to take a picture of the board every 60 seconds, beginning at 0500 and ending at 2100 each day. This camera was deployed at the edge of an experimental pond, while the other camera was placed in a meadow approximately 0.18 km to the south. (B) An actual image from the camera with an inset (black box) showing the presence of a Dipteran. (C) The close-up of the image with the Dipteran illustrating the capacity of the artificial intelligence algorithm to accurately identify the insect.

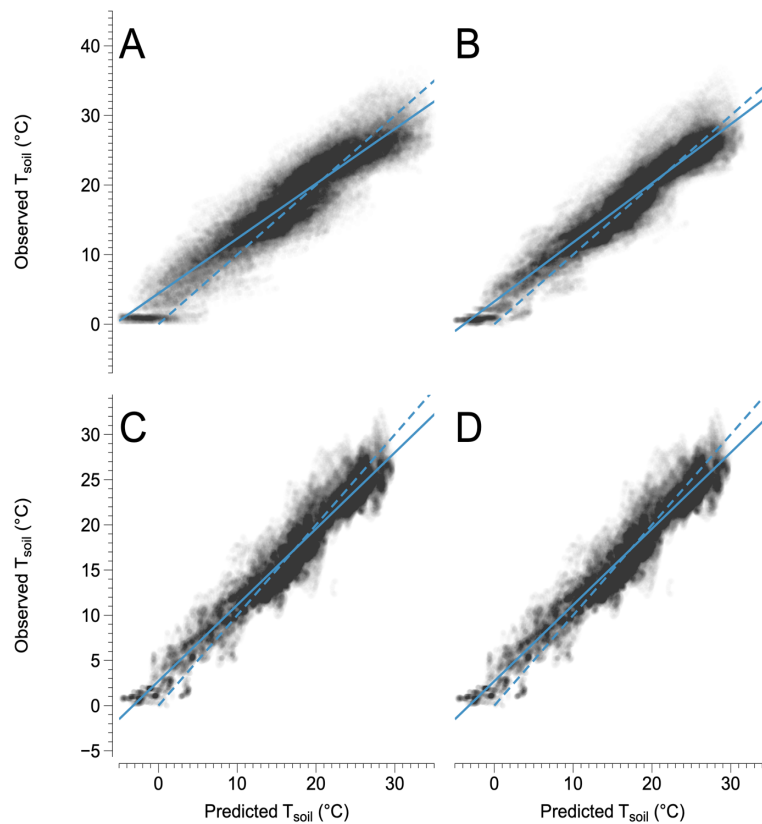


Fig. S14. Observed and predicted soil temperatures to validate the soil model. The figure illustrates that correlation between observed and predicted soil temperature at (A) 5 cm, (B) 10 cm, (C) 20 cm, and (D) 50 cm. The dotted blue line represents unity, and the solid blue line is the linear regression between observed and predicted values. Soil data were collected from 11 weather stations in the Soil Climate Analysis Network spanning 11° of latitude across North America.

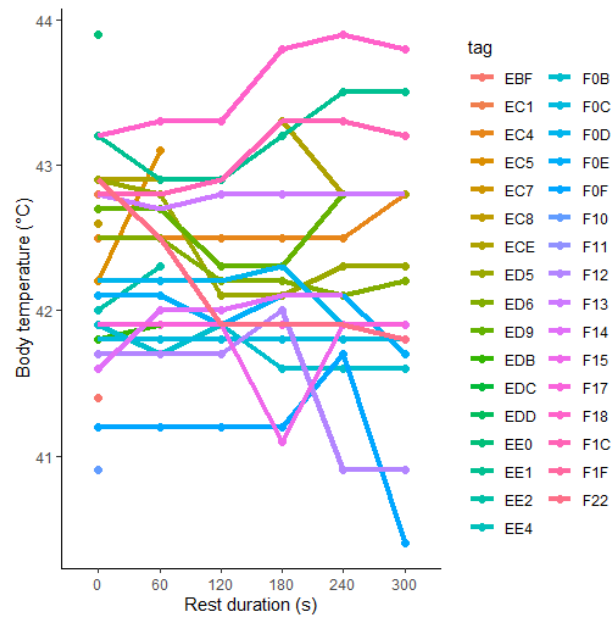


Fig. S15. Body temperature was not associated with rest time in tree swallows. Across individual tree swallows (separate, colored lines, with “tag” referring to the PIT tag identification number), we found no consistent relationship between body temperature and the amount of time the individual spent at rest near the nestbox (rest duration).

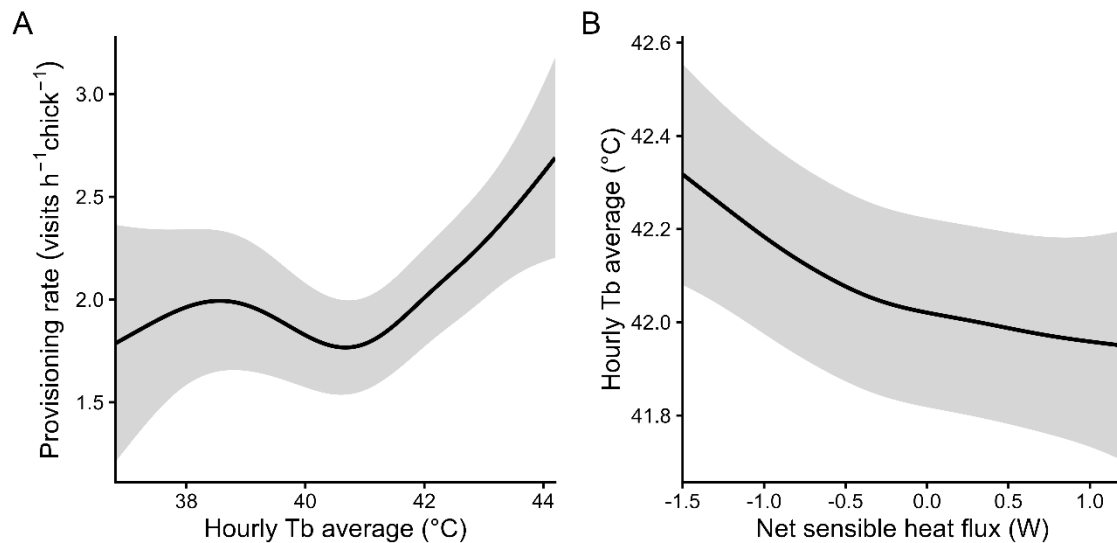


Fig. S16. The relationships between body temperature (T_b) and both provisioning rates and net sensible heat flux within our Iowa population. A) The relationship between T_b and provisioning rates does not show evidence of a typical TPC. Indeed, there is generally a positive correlation between T_b and provisioning rates, which we interpret as evidence of increased metabolic heat production with increased provisioning activity, leading to higher T_b . This illustrates one of the potential pitfalls with T_b -based performance curves in endotherms: feedback loops between performance and T_b , which complicate interpretations about the thermal-dependence of performance. B) The relationship between net sensible heat flux and T_b is negative, as expected. However, the typical within-individual variation in T_b is quite small across a range of heat flux values (just ~ 0.4 °C on average). Furthermore, T_b is relatively stable from ~ -0.5 to 1 W over which there is substantial variation in provisioning performance (Figure 1). The limited variation in T_b over a wide range of thermal conditions like reflects a suite of thermoregulatory responses that tree swallows use to tightly regulate T_b . Collectively, these results suggest that T_b -based TPCs may be difficult to implement in endotherms. The solid curves represent the predicted marginal effects from generalized additive mixed models (see SI for details) and the shaded bands represent model 95% confidence intervals.

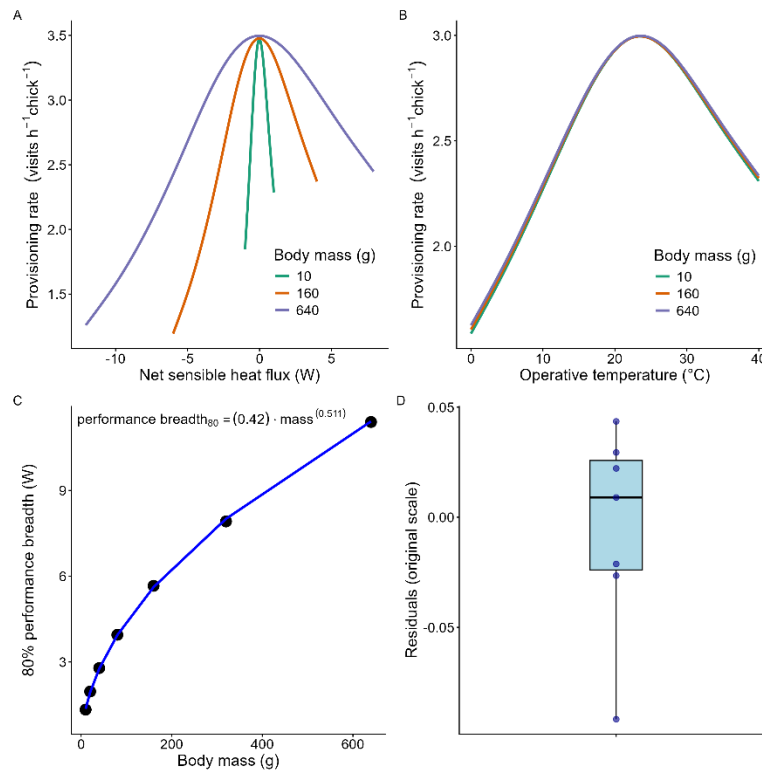
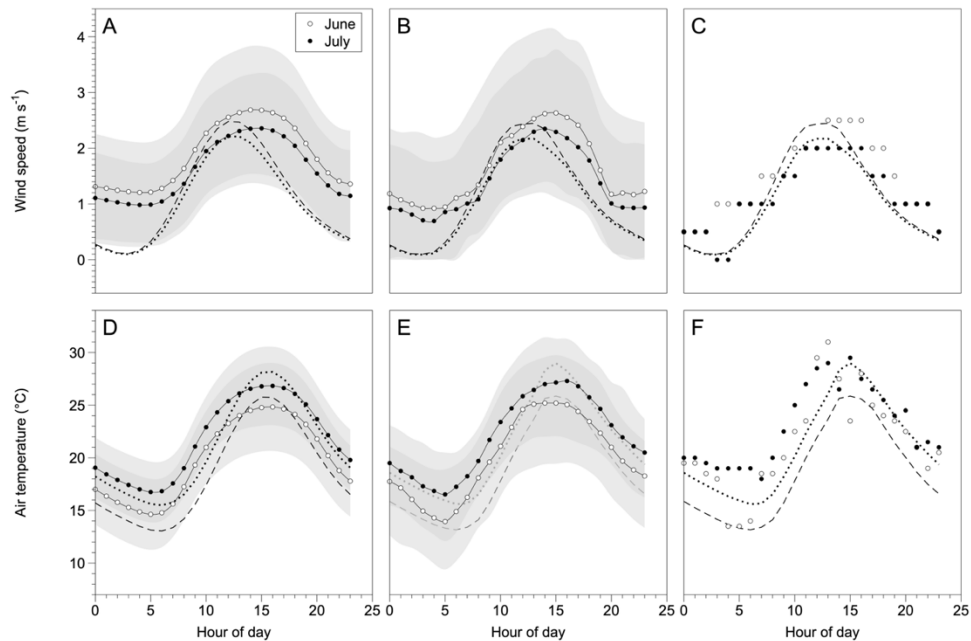


Fig. S17. Simulations illustrating potential challenges and solutions to comparing QPCs across species that differ in body size. Note that all analyses are based on our Iowa tree swallow QPC data, though they model variation in body size and allometric variation in size-related biophysical traits such as plumage depth (see SI). A) Larger species will inherently experience a wider range of Q values than smaller species, leading to wider performance breadths. B) One potential solution is to build performance curves based on operative temperature, which only models variation in external sources of heat flux, yet yields comparable performance curves across a wide range of body sizes. C) Another solution is to statistically correct for the relationship between body size and Q (in this case, the 80% performance breadth, estimated using the *rTPC* package described in the SM). The equation in panel C is the power law function fit to the data (blue line). Note that the exponent in this equation is close to the exponent in power law functions describing the relationship between body mass and metabolic rate across animals ($\sim 0.66 - 0.75$; 121). D) The residuals from the curve in panel C are centered around 0, indicating that this statistical approach successfully standardizes the 80% performance breadth around Q_{opt} for body mass.

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1869 **Fig. S18. Observed and predicted diel variation in wind speed and air temperature across**
1870 **North America.** (A-C) Observed and predicted hourly variation in wind speed and (D-F) air
1871 temperature across 20 weather stations distributed throughout North America during June and
1872 July. Open circles represent June observations and closed circles represent July observations.
1873 Panels A and D show hourly means, panels B and E show hourly medians, and panels C and F
1874 show hourly modes. Error ribbons in panels A, B, D, and E indicate ± 1 standard deviation around
1875 observed values. Dashed lines represent predicted June values and dotted lines represent
1876 predicted July values generated from the environmental model. Wind speed predictions were
1877 calibrated using 4,448,596 empirical observations collected from USCRN weather stations over
1878 an 18-year period.

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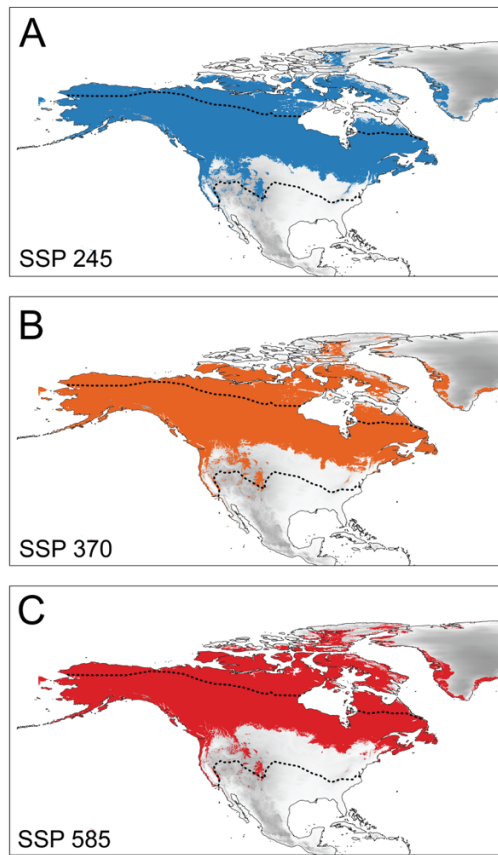
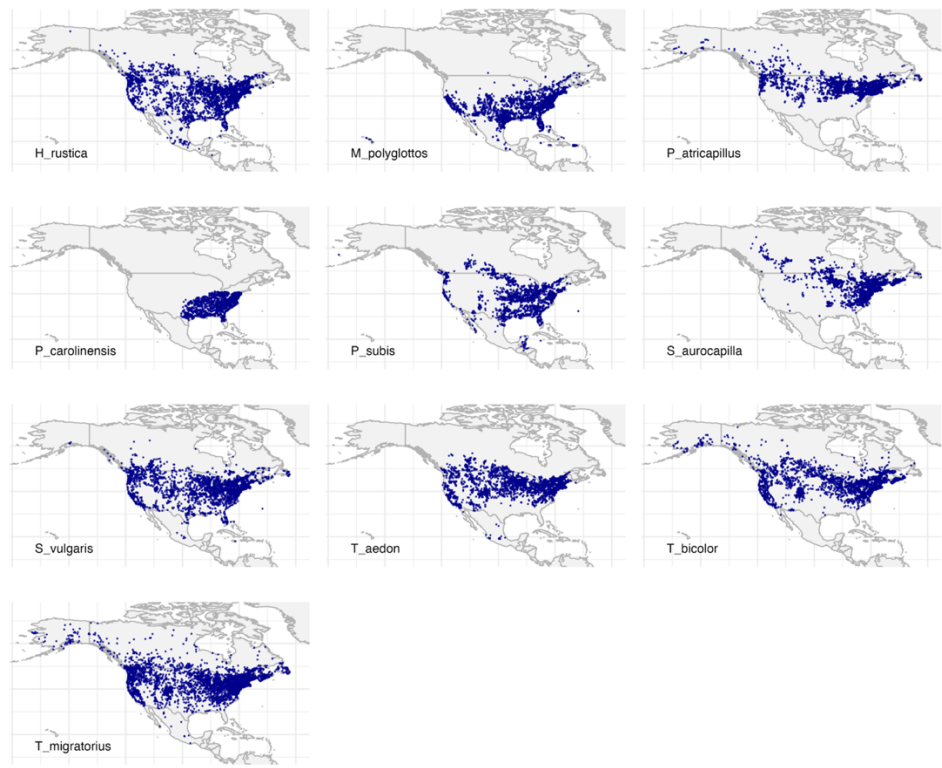


Fig. S19. Tree swallow suitable habitat as predicted by net sensible heat flux under future warming scenarios. These maps illustrate the extent of suitable habitat under climate change scenarios (A) SSP 245, (B) SSP 370, and (C) SSP 585, assuming tree swallows continue to breed in June. These maps also illustrate isolated regions of suitable habitat at high elevations that were not included in determining the lower latitudinal limits of tree swallows.

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1888

1889 **Fig. S20. Presences during the breeding season for the ten species used in the correlative**
1890 **modeling framework.** The presence locations downloaded from eBird for the ten species used in
1891 the hybrid modeling framework to determine if net sensible heat flux (Q) emerged as an
1892 important predictor of breeding distributions. Point locations are filtered for North America in
1893 June and July and thinned using a 20-km distance matrix.

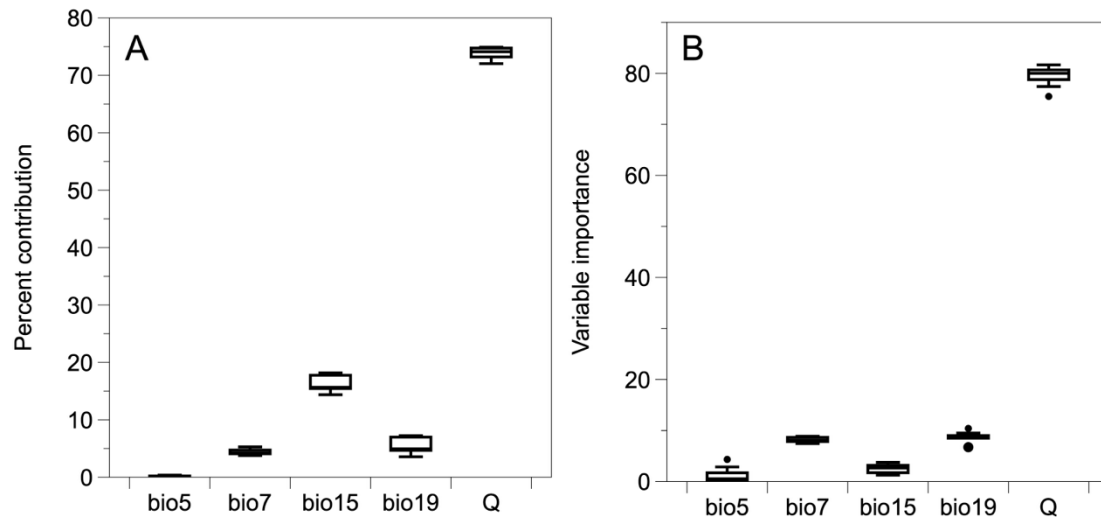


Fig. S21. Net sensible heat flux (Q) identified as most important variable influencing the geographic distribution of tree swallows during the breeding season. (A) Percent contribution of uncorrelated bioclimatic variables (bio5, bio7, bio15, bio19) and net sensible heat flux (Q). (B) Variable importance of uncorrelated bioclimatic variables and net sensible heat flux (Q). Both analyses ranked Q as the most important variable explaining the distribution of tree swallows during the breeding season.

Table S1. Sensitivity analysis for the biophysical model. The analysis evaluates the variability in model sensitivity and specificity in response to body temperature, feather absorptance, feather conductivity, wind speed, and body mass. Values are reported as the sensitivity and specificity for abundance data collected from eBird during the breeding season. Variation in body mass also incorporates concurrent variation in shape (see *Sensitivity analyses* above).

<i>Simulation</i>	<i>Sensitivity</i>	<i>Specificity</i>
Baseline	0.94	0.71
T _b = 44	0.91	0.71
T _b = 40	0.90	0.66
Low Feather Absorptance	0.94	0.70
High Feather Absorptance	0.94	0.70
Low Feather Conductivity	0.92	0.54
High Feather Conductivity	0.86	0.77
High Wind Speed	0.93	0.73
Low Wind Speed	0.95	0.66
Mass = 24	0.65	0.84
Mass = 16	0.95	0.69
T _b = body temperature (°C); Mass (g)		

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