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SYMPOSIUM

Integrating Spatial Analyses of Genomic and Physiological Data to Understand Avian Responses to Environmental Change

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Synopsis Projected rates of climate change over the next century are expected to force species to shift ranges, adapt, or acclimate to evade extinction. Predicting which of these scenarios may be most likely is a central challenge for conserving biodiversity in the immediate future. Modeling frameworks that take advantage of intraspecific variation across environmental gradients can be particularly important for meeting this challenge. While these space-for-time approaches are essential for climatic and genomic modeling approaches, mechanistic models that incorporate ecological physiology data into assessing species vulnerabilities rarely include intraspecific variation. A major reason for this gap is the general lack of empirical data on intraspecific geographic variation in avian physiological traits. In this review, we outline the evidence for and processes shaping geographic variation in avian traits. We use the example of evaporative water loss to underscore the lack of research on geographic variation, even in traits central to cooling costs in birds. We next demonstrate how shifting the focus of avian physiological research to intraspecific variation can facilitate greater integration with emerging genomics approaches. Finally, we outline important next steps for an integrative approach to advance understanding of avian physiological adaptation within species. Addressing the knowledge gaps outlined in this review will contribute to an improved predictive framework that synthesizes environmental, morphological, physiological, and genomic data to assess species specific vulnerabilities to a warming planet.

Introduction

Understanding animal responses to climate change is one of the most pressing conservation challenges in the 21st century. Detailed assessments of which populations may be the most vulnerable to ongoing warming trends will be essential for directing management efforts to mitigate the negative effects of climate change. To this end, researchers have studied the potential impacts of climate change across different biological and temporal scales. These range from community and ecosystem responses (Walther 2010; Riddell *et al.* 2021) to responses at the level of genotypes (Bay *et al.* 2018; Bi *et al.* 2019). Responses to climate change have also been evaluated at different temporal scales, ranging from a few decades (Araújo *et al.* 2005; Youngflesh *et al.* 2022) to paleoclimatic change using the fossil record (Veloz *et al.* 2012). Comparisons of intraspecific variation may be particularly relevant to understanding individual species’ responses to climate change. Evaluation of intraspecific variation across space contributes to a mechanistic understanding of how species adapt and acclimatize to environmental change at short evolutionary timescales that can inform predictive models (Hoffmann and Sgró 2011; Fitzpatrick and Keller 2015; Meek *et al.* 2023).

One of the most widely used modeling approaches are ecological niche models (ENMs) that link species occurrence data and environmental parameters to estimate the breadth of climatic conditions tolerable to a species (Elith and Leathwick 2009). An ENM can in turn be used to make predictions about the likelihood of species occupancy under changing climatic conditions (Hijmans and Graham 2006). However, there are limitations to ENM-based models of climate change responses (Buckley *et al.* 2018), and the incorporation

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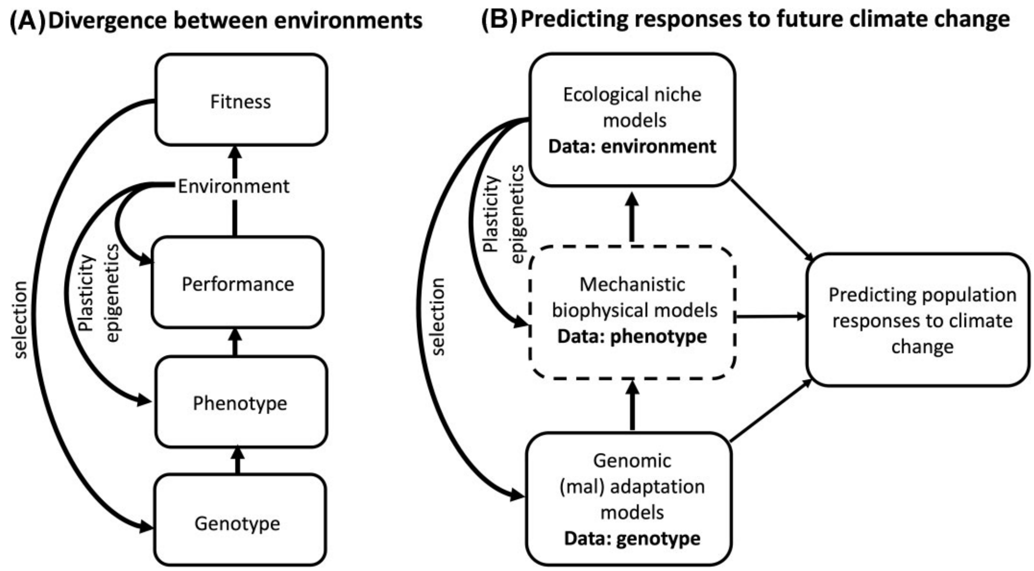

Fig. 1 Schematic showing the process of intraspecific divergence in response to environmental change. (A) The process of divergence between populations in response to environmental variation. Selection will favor individuals with higher fitness, which in turn causes allele frequency shifts at genes related to phenotypes underpinning differences in whole organism performance and fitness. Environment can also directly influence spatial variation at all levels of this hierarchy through developmental or reversible plasticity and trans-generational epigenetic mechanisms. (B) This framework can in turn guide integration of different modeling approaches to robustly infer species vulnerabilities to climate change in the near future. The dashed box highlights models that rarely incorporate intraspecific variation.

of additional genotypic and phenotypic data can contribute to improved predictions of species responses to climate change (Urban *et al.* 2016). For example, spatial associations between genotype and environment are increasingly being leveraged to understand mismatches between the genotypes of a local population and future environmental conditions (reviewed in Capblancq *et al.* 2020). These mismatches provide an assessment of genomic vulnerability and have been validated with population trends (Bay *et al.* 2018) or common garden experiments where genotypes that are more mismatched from local conditions exhibit reduced fitness (Lind *et al.* 2024). Finally, mechanistic models directly leverage data on the physiological capacity of animals to deal with heat stress and water limitations to assess species vulnerabilities to climate change (Chown *et al.* 2010; Bozinovic and Pörtner 2015; Briscoe *et al.* 2023).

Although both ENMs and genomic offset approaches incorporate spatial data, few mechanistic models that include physiological data account for intraspecific spatial variation in measured traits. Data from a single locality without acclimation or acclimatization data are commonly assumed to represent a fixed trait across a species distribution and in response to different treatments (McKechnie and Wolf 2010; Albright *et al.* 2017). This assumption is likely to be false in many species with broader geographic ranges (Prosser 1955; Garland and Adolph 1991; McKechnie 2008). Failure to account for intraspecific variation when making inferences about climate change vulnerability could mislead predictions in serious ways. For instance, Albright *et al.* (2017) use empirical data on evaporative cooling capacity of six songbird species from a single locality characterized by hot, dry conditions to project lethal dehydration risk across the distribution of these taxa. By assuming that no differences in evaporative cooling capacity exist among populations exposed to mesic versus dry conditions, the model may be underestimating vulnerability to future climatic conditions.

An integrated understanding of how environmental variation contributes to intraspecific divergence will be essential for predicting species responses to climate change (Fig. 1A; Dalziel *et al.* 2009; Storz and Wheat 2010; Storz *et al.* 2015). This will enable the development of a modeling framework that integrates current genomic, mechanistic, and environmental approaches (Fig. 1B). However, an in-depth understanding of how phenotypic divergence across environmental gradients contributes to physiological performance is lacking. In this review, we argue for an expansion of research on avian physiological divergence across environmental gradients. Centering research on geographic variation, which we define as intraspecific spatial variation, will provide a strong framework for investigating the mechanistic underpinnings of avian adaptation to environmental challenges and global change. We specifically discuss: (1) the evidence for geographic variation in avian physiological characters; (2) the different ecological and evolutionary processes that can shape observed patterns of geographic variation; (3) how knowledge of intraspecific variation in key physiological traits remains sparse; (4) opportunities for combining intraspecific studies with genomic datasets to advance understanding of avian physiology; and (5) how integrating physiological, morphological, and genomic data can improve predictive frameworks for evaluating adaptation to environmental change through space and time.

Evidence for geographic variation in avian physiology

Over two centuries of research have generated abundant evidence for geographic variation in avian morphology, plumage, life history, diet, migratory behavior, physiology, and allele frequencies (Mayr 1963; Zink and Remsen 1986; Avise 2000). The often strong associations between phenotype and environment have led ornithologists to interpret patterns of spatial variation as evidence for adaptation to different climatic pressures (Johnston and Selander 1964; James 1970; Youngflesh *et al.* 2022; Mason *et al.* 2023). For example, variation along latitudinal and thermal gradients in body size and appendage length (*e.g.*, bill and tarsus length) has classically been interpreted in the context of heat dissipation rates across the surface of objects with smaller or larger surface-to-volume ratios (Bergmann 1847; Allen 1877; but see Scholander 1955). However, traits like bill size also vary in relation to diet and foraging ecology and can play important roles in song production (Tattersall *et al.* 2017). Similarly, plumage characters may contribute to thermoregulatory performance in birds, but also play critical roles in camouflage, resistance to wear, flight performance, foraging behavior, and sexual selection (Terrill and Shultz 2023). Ultimately, a deeper, mechanistic understanding of avian adaptation to different environments requires an exploration of geographic variation in whole organism physiological performance and the traits underlying divergence in performance.

Few studies have explored geographic variation in physiological characters beyond the external morphological and plumage characters described above. However, available research suggests that geographic variation in a variety of additional physiological traits may be common (Table 1). These studies identified spatial, intraspecific variation in physiological characters across gradients in elevation (Carey *et al.* 1983; Dubay and Witt 2014), temperature (Blem 1974; Dawson *et al.* 1983; Burger and Denver 2002), aridity (Ambrose and Bradshaw 1988; Noakes *et al.* 2016; Ribeiro *et al.* 2019), salinity (Benham and Cheviron 2020), urbanization (Giraudeau and McGraw 2014), and pollution (Bauerová *et al.* 2017). Divergence across these environmental gradients occurs in a diversity of traits contributing to physiological performance. This includes divergence in kidney size and medullary tissue in response to environments that pose osmotic challenges (Benham and Cheviron 2020). Mesic and arid-adapted house sparrows demonstrate differences in lipid composition of epidermal tissue that underpins differences in cutaneous water loss rates (*Passer domesticus*; Muñoz-Garcia and Williams 2008; Williams *et al.* 2012). Changes in biochemical functions, such as increased hemoglobin oxygen binding affinity, have been tied to allele frequency shifts across elevation gradients (Galen *et al.* 2015; Kumar *et al.* 2017). Last, differences in hormonal levels and hormone receptor activity vary across latitude in white-crowned sparrows (*Zonotrichia leucophrys*; Breuner *et al.* 2003).

Survival and reproduction in different environments will also necessitate adaptive divergence in physiological performance across life stages. Along elevation gradients, the reductions in atmospheric pressure lead to increased diffusivity of water vapor; in response, researchers have documented decreases in egg water vapor conductance with increasing elevation (Sotherland *et al.* 1980; Carey *et al.* 1983). House sparrows in mesic and arid environments also exhibit divergence in cutaneous water loss during development (Muñoz-Garcia and Williams 2011; Clement *et al.* 2012). Finally, recent work suggests that the low partial pressures of oxygen at high elevation also contribute to divergence in hemoglobin loci expressed only in embryos (Beckman *et al.* 2022a). Together, these studies demonstrate that many different ecological pressures will drive within species divergence in physiological performance and subordinate traits at all life stages.

Understanding the ecological and evolutionary processes shaping geographic variation

Following documentation of spatial variation, a major challenge will be determining the degree to which trait variation reflects genotypic divergence, plasticity, maternal effects, or genotype-by-environment interactions (Cheviron *et al.* 2013). Discerning among plastic versus genetic contributions to trait variation is challenging as it often necessitates maintaining birds in captivity (Wikelski *et al.* 2003; Stager *et al.* 2020) or quantitative genetics approaches applied to long-term studies of pedigreed populations (Teplitsky *et al.* 2008; Nafstad *et al.* 2023). A direct contribution of the environment to physiological trait variation within adult animals has been widely demonstrated for metabolic rates (McKechnie 2008), evaporative water loss (EWL)

Table 1 Examples of studies that measure physiological traits across three or more populations

Environmental gradient	Species	Continent	Populations	Traits	Acclimation experiment?	Observed change	Citation
Aridity	Karoo scrub-robin (*Cercotrichas coryphaeus*)	Africa	7	BMR; metabolic expansibility	Seasonal differences	BMR highest in summer, lower in more arid populations, wider ME in arid habitats	Ribeiro et al. 2019
	White-browed scrubwren (*Sericornis frontalis*)	Australia	3	BMR	Seasonal differences	BMR lower in arid population and in summer	Ambrose and Bradshaw 1988
	Rufous-collared sparrow (*Zonotrichia capensis*)	South America	4	BMR, organ masses, isotopes	No	BMR increases with aridity and trophic level	Sabat et al. 2009
Elevation	Pied-crested tit-tyrant (*Anairetes reguloides*)	South America	7	Hemoglobin; HCT; MCHC; Heart mass	No	Most traits increase with elevation	Dubay and Witt 2014
	House wren (*Troglodytes aedon*)	South America	14	Hemoglobin AF; Oxygen binding afinity	No	Higher frequency allele at high elevation associated with increased O2 binding affinity	Galen et al. 2015
	Cliff swallow (*Petrochelidon pyrrhonota*)	North America	7	Egg water conductance	No	Decreases with elevation	Sotherland et al. 1980
	Red-winged blackbird (*Agelaius phoeniceus*)	North America	10	Egg water conductance, permeability, mass	No	Egg water conductance, permeability decrease with elevation; Egg mass increases with elevation	Carey et al. 1983
	American robin (*Turdus migratorius*)	North America	6	Egg water conductance, permeability, mass	No	Egg water conductance, permeability decrease with elevation; Egg mass increases with elevation	Carey et al. 1983
Latitude	Stonechat (*Saxicola torquata*)	Europe/Africa	4	BMR	Raised in common garden	RMR lower in tropical sedentary species	Wikelski et al. 2003
	House sparrow (*Passer domesticus*)	North America	8	Thermal conductance	No	Conductance higher in southern birds	Blem 1974
	White-crowned sparrow (*Zonotrichia leucophrys*)	North America	3	Corticosterone levels, Corticosteroid-binding globulin capacity, intracellular receptors	No	Northern breeders show: lower free cort, lower number of receptors, CBG binding capacity higher	Breuner et al. 2003

Table 1 Continued

Environmental gradient	Species	Continent	Populations	Traits	Acclimation experiment?	Observed change	Citation
	Rufous-collared sparrow (*Zonotrichia capensis*)	South America	3	Digestive track morphology, enzyme activity	Diet	More flexibility in digestive track in more variable environments	Maldonado et al. 2011
	Thorn-tailed rayadito (*Aphrastura spinicauda*)	South America	3	Baseline CORT, Stress response	No	Baseline but not stress CORT lower in southernmost population	Quirici et al. 2014
Salinity	Savannah sparrow (*Passerculus sandwichensis*)	North America	13	TEWL; kidney morphology; fluid osmolality	No	Kidneys larger, higher fluid osmolality in salt marshes; TEWL variable	Benham and Cheviron 2020
Thermal	Dark-eyed junco (*Junco hyemalis*)	North America	8	Thermogenic capacity (Msum)	Temperature acclimation	Greater Msum with higher daily temp range; more flexibility in more seasonally variable environments	Stager et al. 2021
	House finch (*Haemorhous mexicanus*)	North America	4	Cold tolerance	Seasonal acclimitization	Cold tolerance increases in winter and higher in Colorado	Dawson et al. 1983
	Northern cardinal (*Cardinalis cardinalis*)	North America	6	BMR; TH	TH treatments	T4 hormones vary with latitude; BMR tends to increase with latitude	Burger and Denver 2002
	Tree swallow (*Tachycineta bicolor*)	North America	4	Corticosterone levels	Breeding season stages	Higher CORT levels in unpredictable thermal environments	Zimmer et al. 2020
	Ostrich (*Struthio camelus*)	Africa	3	Thermoregulatory capacity	Raised in common garden	Thermoregulatory capacity higher in thermally more unpredictable environments	Svensson et al. 2023
Urban	House finch (*Haemorhous mexicanus*)	North America	8	Plasma carotenoids, vitamins, and oxidative stress	Seasonal differences	Decreases in vitamin A, certain carotenoid levels in urban environments	Giraudeau and McGraw 2014
	Great tit (*Parus major*)	Europe	13	Blood heavy metal concentration, total red blood cell count, heterophil/lymphocyte ratio, body condition	No	Increased H/L ratio and decreased red blood cell count with heavy metal contamination	Bauerová et al. 2017

Table shows intraspecific variation across a range of different gradients, species, and regions of the world. Trait abbreviations: basal metabolic rate (BMR), summit metabolic rate (Msum), hematocrit (HCT), mean cellular hemoglobin concentration (MCHC), corticosterone (CORT), total evaporative water loss (TEWL), thyroid hormone (TH).

(Tieleman *et al.* 2003; Noakes and McKechnie 2019), and organ sizes (Sabat *et al.* 2004; Peña-Villalobos *et al.* 2013). These experiments performed on adult birds provide evidence for reversible phenotypic plasticity, but the environment can also shape phenotypic variation irreversibly during development (Piersma and Drent 2003). In this case, common garden experiments have been essential for showing that genetic variation likely influences differences in metabolic rates (Wikelski *et al.* 2003). Effects of the environment can also persist across generations via a range of epigenetic mechanisms and maternal effects (Hu and Barrett 2017). Ostriches (*Struthio camelus*) raised in a common garden for multiple generations provide strong evidence for a genetic basis to differences in thermogenic capacity among subspecies from different environments (Svensson *et al.* 2023). Finally, selection can also operate on the degree of plasticity with individuals from more temporally heterogenous environments exhibiting greater levels of plasticity (Stager *et al.* 2021).

A further challenge to interpreting patterns of geographic variation in physiological traits will be determining whether the observed trait variation is adaptive. Gene flow rates, variation in effective population sizes, and divergence times among populations can influence both local adaptation (Kawecki and Ebert 2004; Savolainen *et al.* 2013) and plasticity (Sultan and Spencer 2002; Chevin and Lande 2011). Further, environmental plasticity can improve or impair physiological performance, adaptive or maladaptive plasticity, respectively. For example, humans exposed to low environmental oxygen (hypoxia) increase hemoglobin concentration, which may contribute to mountain sickness, cardiac strain, and reproductive costs (Storz et al. 2010; Storz and Scott 2021). Humans with Himalayan Sherpa ancestry compensate for this apparent maladaptive plasticity by increasing blood plasma volume, resulting in high total blood volume with hemoglobin concentrations similar to individuals at sea level (Stembridge *et al.* 2019). Thus, across elevation, humans with lowland ancestry in hypoxic conditions exhibit maladaptive phenotypic plasticity, while genetic compensation in humans with Himalayan Sherpa ancestry leads to a lack of observable phenotypic variation across space. Within bird species, hemoglobin concentration also increases along elevation gradients (Dubay and Witt 2014; Linck *et al.* 2023; Williamson *et al.* 2023). However, the extent to which these phenotypic trends can be maladaptive in high elevation bird populations remains an outstanding question.

A broader understanding of the ecological and evolutionary context shaping geographic variation in avian responses to different environments will require expanding research efforts across taxonomic groups, latitudes, and hierarchical levels of biological organization. This will be especially important for assessing how variation in physiological traits critical to coping with thermal stress may contribute to adaptation and acclimatization to future climate regimes. However, as we demonstrate in the next section, we lack a broad understanding of how traits vary within species, even for those central to coping with hot and dry conditions.

Lack of geographic variation studies in avian EWL

Analyses of geographic variation for any given physiological trait have rarely been replicated across multiple species. Here, we focus on a key physiological trait widely measured in birds: EWL. The EWL of an individual is often reported as the rate of water lost due to respiration, the rate of water lost from across the skin barrier, or the total evaporative water loss (TEWL) that combines cutaneous and respiratory losses. Birds lose water to the atmosphere even at relatively moderate temperatures. As birds experience rising ambient temperatures, EWL rates begin to steeply increase as an individual comes to rely exclusively on evaporative cooling to thermoregulate. Ultimately, loss of water to keep cool can impose costs on birds and result in lethal dehydration. Vulnerability to lethal dehydration will depend on mode of water loss, body size, rates of water loss, and access to standing water (Bartholomew and Cade 1963; Dawson 1982; McKechnie *et al.* 2021). Understanding patterns of EWL variation among and within species will thus be critically important for evaluating vulnerabilities of different species to climate change (McKechnie and Wolf 2010; Williams *et al.* 2012; Albright *et al.* 2017).

Given the direct importance of EWL to avian responses to thermal stress, we searched the literature for avian studies where rates of EWL were reported. We performed an opportunistic literature search using Google Scholar and a series of search terms, such as avian water economy, avian EWL, and avian water budget. We additionally surveyed all studies included in large meta-analyses of avian EWL (Williams 1996; Song and Beissinger 2020). We restricted our analyses to studies of wild-caught birds and studies that clearly indicated a geographic locality for measured birds. For each study that met these criteria, we assigned the number of localities within species based on how the authors analyzed the data. Specifically, if authors recognized different populations in analyses, we considered those distinct localities, whereas birds analyzed as a single population were considered one locality. We noted whether EWL was

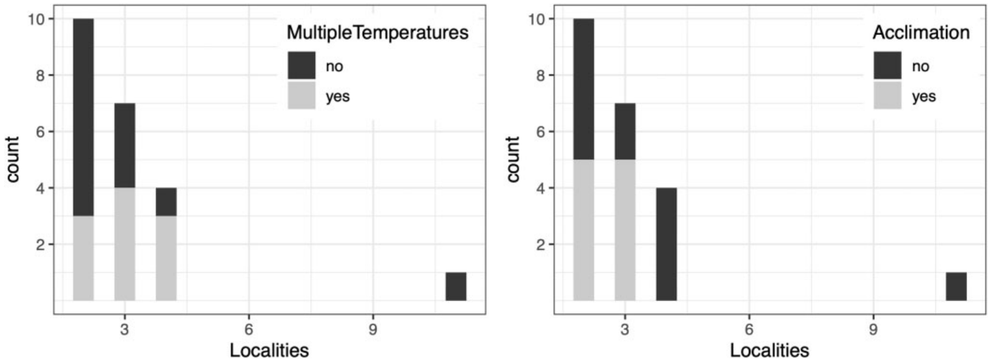

Fig. 2 Summary of studies quantifying EWL from two or more localities. Number of localities sampled is along the x-axis and number of studies on the y-axis. Left panel distinguishes studies that only measured EWL at a single temperature (typically within the thermal neutral zone; black) versus across multiple temperatures (gray). The right panel shows the number of studies where the effects of acclimation or acclimatization to different environmental variables were considered (gray) or not (black).

measured at a single ambient temperature (typically within the thermal neutral zone) or if EWL rates were measured across a range of ambient temperatures. Finally, we noted whether authors considered EWL responses to seasonal acclimatization, experimental acclimation, different temperatures, or water restrictions.

In total, we identified 187 studies that met our criteria; these included 262 species (Supplementary Table S1). Of these, only 22 studies (11.8%), including 13 species (5.0% of 262 species), reported intraspecific data from two or more localities. Nearly half of the studies included comparisons between only two populations ($n = 10$), and a maximum of 11 localities were analyzed in a single study (Fig. 2; Table 2). Approximately half of the studies included measurements of EWL from multiple temperatures. Of the nine studies that measured effects of a treatment on EWL, four measured temperature differences, two seasonal differences, two humidity, and one hydration state.

The scarcity of geographic variation studies in traits like EWL makes it difficult to draw conclusions about how EWL rates may shift in response to environmental change. Over half of the studies ($n = 14$) report statistically significant differences in EWL rates among populations. Among the studies that did not find evidence for spatial variation in EWL were several that accounted for the effects of plasticity. For instance, white-browed sparrow-weavers (*Plocepasser mahali*) did show evidence for spatial and seasonal variation in EWL (Noakes *et al.* 2016), but this stemmed entirely from plastic responses to different temperature regimes (Noakes and McKechnie 2019; Noakes and McKechnie 2020). In contrast, spatial differences in EWL among rufous-collared sparrow (*Zonotrichia capensis*) populations persisted in adult birds exposed to different temperature extremes (Cavieres and Sabat 2008). In both cases, studies explored acclimation responses in adult birds and did not account for environmental contributions during development or due to maternal effects. Only a single study raised birds in a common garden environment to account for developmental plasticity and found no differences in EWL among stonechats (*Saxicola torquata* sensu lato) from different environments (Tieleman 2007). Predicting vulnerability of avian populations to changes in thermal and precipitation regimes will necessitate further research on the ecological and evolutionary mechanisms contributing to variation in evaporative cooling capacity within species. Further, combining investigations on spatial variation in EWL with genomic and transcriptomic data will provide important insights into avian responses to future climatic regimes.

Intraspecific variation and omics approaches

A rapidly growing number of studies are applying omic approaches to understand the genetic basis of the adaptation in birds (reviewed in Campagna and Toews 2022). Focusing on geographic variation in traits associated with physiological performance could thus provide unique opportunities to integrate genomic approaches into studies of avian physiology. Many of the analytical approaches for establishing demographic context for phenotypic divergence, comparison of gene expression profiles, and linking phenotype to genotype, or genotype to environment have the greatest statistical power when making intraspecific comparisons (Hoban *et al.* 2016; Bernatchez *et al.* 2024). These genomic approaches will be most relevant for understanding the genetic contributions to physiological variation. Various omics approaches can be leveraged to understand

Table 2 Studies that measured EWL across two or more populations

Common name	Scientific name	Multiple Temps	Significant Differences Reported	Acclimation?	Localities	Citation
Blue tit	*Parus caeruleus*	Yes	No	No	3	Thomas *et al.* 2001
Cape white-eye	*Zosterops virens*	No	No	Season	2	Thompson and Downs 2017
Stonechat	*Saxicola torquata*	Yes	No	Common garden	3	Tieleman 2007
Freckled nightjar	*Caprimulgus tristigma*	Yes	Yes	Season	2	O'Connor *et al.* 2017
Horned lark	*Eremophila alpestris*	Yes	Yes	No	2	Trost 1972
House finch	*Haemorhous mexicanus*	No	Yes	Hydration	2	MacMillen and Hinds 1998
House sparrow	*Passer domesticus*	No	Yes	Humidity, ontogeny	2	Munoz-Garcia and Williams 2008
House sparrow	*Passer domesticus*	No	Yes	No	2	Munoz-Garcia and Williams 2005
House sparrow	*Passer domesticus*	Yes	No	No	4	Hudson and Kimzey 1966
House sparrow	*Passer domesticus*	No	Yes	Ontogeny	2	Munoz-Garcia and Williams 2011
House sparrow	*Passer domesticus*	No	Yes	Ontogeny, humidity	2	Clement *et al.* 2012
Rufous-collared sparrow	*Zonotrichia capensis*	Yes	Yes	No	2	Sabat *et al.* 2006
Rufous-collared sparrow	*Zonotrichia capensis*	No	Yes	Temperature	3	Cavieres and Sabat 2008
Rufous-collared sparrow	*Zonotrichia capensis*	No	Yes	No	3	Maldonado *et al.* 2012
Savannah sparrow	*Passerculus sandwichensis*	No	Yes	No	11	Benham and Cheviron 2020
Song sparrow	*Melospiza melodia*	Yes	Yes	No	4	Gamboa 2021
Southern fiscal	*Lanius collaris*	Yes	Yes	No	4	Soobramoney *et al.* 2003
Western screech-owl	*Megascops kennicottii*	No	Not determined	No	2	Bartholomew and Dawson 1953
White-browed sparrow-weaver	*Plocepasser mahali*	No	No	No	4	Noakes *et al.* 2017
White-browed sparrow-weaver	*Plocepasser mahali*	Yes	No	Temperature	3	Noakes and McKechnie 2019
White-browed sparrow-weaver	*Plocepasser mahali*	No	No	Temperature	3	Noakes and McKechnie 2020
White-browed sparrow-weaver	*Plocepasser mahali*	Yes	Yes	Temperature	3	Noakes *et al.* 2016

Also included is information on whether studies evaluated EWL at just one temperature (no) or range of temperatures (yes), whether or not statistically significant differences in EWL rates among populations were detected, and whether or not the authors accounted for plasticity using an acclimation experiment or seasonal acclimatization.

how plasticity and transgenerational epigenetic mechanisms also contribute to patterns of geographic variation (reviewed in Hu and Barrett 2017; Bernatchez *et al.* 2024). However, in the remainder of the paper, we focus primarily on methods aimed at illuminating the genetic basis of local adaptation. This focus will provide important advances in understanding how birds adapt to environmental challenges and can represent an important first step in species, like most birds, that are challenging to raise in captivity. We do not provide extensive details on different sequencing methods; however, we give a brief overview of the commonly used genomics approaches in avian studies and appropriate questions for each in the supplemental materials.

Interpreting geographic variation within a demographic and phylogeographic context

The relationship between ecological variation and trait variation can be confounded by phylogeographic structure and isolation-by-distance. This issue has long been recognized in interspecific comparisons where individual species are not independent units and phylogenetic relatedness needs to be accounted for when comparing trait variation across species (Garland 1992; Garland and Adolph 1994). Conspecific populations can also be connected by varying degrees of gene flow and differ in effective population size, which can both influence patterns of trait divergence (Stone *et al.* 2011; Savolainen *et al.* 2013) and confound studies of geographic variation (Garland and Adolph 1994; Stone *et al.* 2011). For instance, divergence in phenotypic traits between urban San Diego dark-eyed juncos (*Junco hyemalis*) and nearby montane birds (*J. h. thurberi*) was originally attributed to rapid adaptation and plasticity; however, phylogeographic analyses later showed the source population for the San Diego birds was from a more northern and phenotypically similar subspecies (*J. h. pinosus*, Friis *et al.* 2022).

A number of statistical approaches exist to account for the contributions of population genetic differentiation, gene flow, or genetic diversity on spatial patterns of phenotypic variation (reviewed in Stone *et al.* 2011). Many of these approaches, such as generalized linear mixed models, include an among population genetic distance matrix as a random effect to remove the confounding influences of gene flow and population structure, allowing for conclusions to be made on the influence of an environmental parameter on trait variation. This approach has been used to assess the environmental drivers of morphological variation in *Anolis* lizards (Jaffe et al. 2016) or spatial variation in thermogenic capacity of juncos (Stager *et al.* 2021). In another approach, Benham and Cheviron (2020) employed structural equation modeling to infer the relative contributions of gene flow and ecological variation on patterns of osmoregulatory trait divergence between Savannah sparrow populations adapted to freshwater and salt marshes. In this model, several environmental parameters from each population were used to generate a latent "ecological differences" variable, and the model included correlations among gene flow, trait divergence, and ecological differences. This analysis revealed that some osmoregulatory traits were constrained by gene flow, other traits varied in response to environmental variation, and some experienced contributions from both sources.

All these methods depend on inferences of population genetic differentiation from molecular datasets. Unlike phylogenetic studies that require one individual per species, phylogeographic methods require dense sampling across space with some studies including dozens to hundreds of individuals (Ruegg *et al.* 2021; Klicka *et al.* 2023). This requirement may result in mismatches between population sampling of phylogeographic and physiological datasets. Consequently, physiologists may face the prospect of sequencing and analyzing genetic data from the populations where they collected physiological measures. These data can be expensive to generate from across a species distribution, and individual research teams may not have both the physiological and genomic expertise needed to synthesize these different kinds of datasets.

Despite these challenges, the continued decline in sequencing costs is making even whole genome sequencing (WGS) for large numbers of samples more affordable (Szarmach *et al.* 2021). Generating WGS data from a large number of individuals will enable finer-scale, spatial sampling. Coupling these data with the same individuals measured for physiological assays will allow researchers to account for the influence of both coarser phylogeographic structure patterns and finer-scale isolation-by-distance (e.g., using mantel tests) effects on physiological trait variation. This will also enable analyses linking genotypes with phenotypic and environmental variation.

Genomic approaches for linking phenotype to genotype

Identifying the genetic basis of physiological traits and mapping the allelic variation that contributes to these traits across geographic space is critical to understanding species vulnerabilities to climate change. A number of different approaches can be used to elucidate the genomic regions that contribute to physiological traits. Quantitative trait locus (QTL) mapping has been used to reveal the heritability and underlying genetic architecture of external morphological traits in birds (Tarka *et al.* 2010; Knief *et al.* 2012; Schielzeth *et al.* 2012). Tarka *et al.* (2010) used QTL mapping, combining genetic markers with pedigree information from a 30-year field program, to identify a locus of large effect impacting wing length among populations of great reed warblers (*Acrocephalus arundinaceus*) that differ in migration distance. QTL mapping is a powerful approach for linking genotype to phenotype, but is labor-intensive, requiring either long-term field studies or making experimental crosses of animals in captivity.

Another approach to elucidate the genetic underpinnings of a trait is through statistical associations between variation in the traits of interest and genotypic variation using genome-wide association studies (GWAS). GWAS methods have been used to identify regions of the genome that contribute to high-level phenotypes, such as tarsus length, wing morphology, and bill morphology (Duntsch *et al.* 2020, Huang *et al.* 2022), as well as life history traits like clutch size (Husby *et al.* 2015) and spatial cognitive ability (Branch *et al.* 2022). QTL mapping and GWAS are robust to the unique evolutionary histories of loci across the genome, including different histories of selection, and can reveal the genetic architecture of a trait. However, the high number of individuals required for these analyses, the difficulty of linking highly plastic traits to genotypes, the need for a pedigree or captive breeding population in the case of QTL mapping, and the importance of accounting for population structure can make these methods difficult for researchers studying non-model organisms (Santure and Garant 2018).

Genomic approaches to linking genotype with environment

Another approach to identifying the underlying genetic basis of physiological traits is to use methods that test for signatures of spatially varying selection within the genome, or significant associations between genetic and environmental variables. One approach is to explore divergence between two populations across genomic windows to detect regions that are significantly divergent between populations relative to the genome-wide background in certain statistics (e.g., Fst, Dxy, nucleotide diversity, Tajima's D; Irwin et al. 2018). Candidate outlier loci identified through these genome scan methods can then be queried against existing databases to assess known gene functions (The UniProt Consortium 2017) and pathways (The Gene Ontology Consortium 2019). Genome scan approaches can be used to compare patterns of genomic divergence among populations distributed in different environments and make inferences about which genes are diverging in response to selective pressures in each environment. For example, Walsh *et al.* (2019) used these approaches to explore patterns of intraspecific genomic divergence among upland and salt marsh populations in four sparrow species to understand the genomic basis of adaptation to high-salinity environments. Although experimental validation will be needed to conclusively link candidate genes with divergent phenotypes, genome scan approaches can also generate new hypotheses about the traits underlying physiological divergence among environments. In the salt marsh sparrow example, several species exhibited divergence in genes associated with cell shape regulation and cytoskeletal organization. Divergence in these genes could relate to an increased capacity to tolerate excess salt levels internally (Benham and Cheviron 2020).

Sequencing individuals that were densely sampled across an environmental gradient, allows researchers to perform genotype-environment associations (GEA; Capblancq *et al.* 2018). GEA methods differ based on whether they allow comparisons of just a single environmental variable (e.g., LFMM; Caye *et al.* 2019), multiple environmental variables (e.g., RDA; Capblancq and Forester 2021), and whether they account for population structure. BayPass (Gautier 2015) can both consider multiple environmental axes and account for population structure. Stonehouse *et al.* (2024) used this program to identify 36 candidate loci associated with different axes of climate variation in European great tits (*Parus major*); this included CALM2, which was strongly associated with precipitation-related variables and was previously identified as an outlier in other desert animals. Latent Factor Mixed Models (LFMM) have also been used in birds to link genotypic variation with thermal variation. Gamboa *et al.* (2022) used this approach in Channel Islands song sparrows (*Melospiza melodia*) to identify outlier loci associated with responses to thermal stress, water homeostasis, and feather development. They also found evidence for selection operating on a number of bill development genes that could be linked to the observed differences in bill size among populations.

When broad geographic sampling is paired with corresponding physiological data, experimental approaches, and biochemical methods, GEA approaches can provide a strong link between genotype and physiological variation. Stager *et al.* (2021) integrated physiological field measurements, acclimation experiments, and an RDA approach, including all junco species and subspecies, to show allelic variation and thermogenic capacity in juncos co-vary across the landscape with environmental thermogenic heterogeneity. As with QTL and GWAS studies, selection scans can reveal the genetic architecture underlying a physiological trait.

Using population genetic analyses, Qu *et al.* (2020) report a polygenic basis for the strong phenotypic differentiation in muscle type between high and low elevation Eurasian tree sparrows (*Passer montanus*). When loci of large effect contribute to the physiological trait, selection scans and GEA tests based on broad spatial sampling complement functional analyses on candidate loci. For example, Beckman *et al.* (2022a) report spatially varying selection on a non-synonymous site in a hemoglobin locus that results in a functional change in the oxygen-binding affinity of a major hemoglobin isoform (Natarajan *et al.* 2016). Further, broad spatial sampling can suggest patterns in the magnitude of selection pressure across an environmental gradient (Galen *et al.* 2015; Lim *et al.* 2021; Beckman *et al.* 2022a; Beckman *et al.* 2022b).

Integrating methods to understand complex traits

Integrating multiple genetic approaches with broad spatial sampling can reveal a deeper understanding of complex traits associated with thermal tolerance. To understand adaptation to novel thermal regimes in house mice (*Mus musculus*), Phifer-Rixey *et al.* (2018) combined phenotypic measures of body mass, GEA analyses, and clinal patterns in allelic variation in a latitudinal transect in eastern North America. They further used *cis*-expression quantitative trait loci (*cis*-eQTL) analysis using wild-derived, lab-born progeny to elucidate the candidates underlying the genetic basis of a complex trait, body mass. To better understand the contribution of expression variation to adaptive body size in house mice, Mack *et al.* (2018) used eQTL analysis and clinal variation in expression in wild-caught house mice from the latitudinal transect to identify two important genes (ADAM17, BCAT2) with expression variation associated with body mass. Additional analyses on house mice across latitude in western North America, including GWAS and GEA analyses, showed the genetic basis of body size is partly shared among eastern and western populations despite reciprocal monophyly between the transects (Ferris *et al.* 2021). The synthesis of these quantitative genetic, genome-environment, and expression analyses with phenotypic data provide a nuanced illustration of the genetic basis of body size in house mice across North America, and identified clear pathways for functional experiments relating to thermal tolerance (Ballinger *et al.* 2023). Similarly, integrative studies of birds across environmental gradients remain rare. Some of the best examples come from well-characterized loci, such as hemoglobin (Galen *et al.* 2015). In another exciting example, Gu *et al.* (2021) used tracking devices, genome scans, cell culture assays, and epigenetic approaches to demonstrate that a candidate gene associated with long-term memory, ADCY8, contributed to among population differences in migratory distance in peregrine falcons (*Falco peregrinus*).

An integrative framework for understanding intraspecific adaptation to environmental change

We expect the next several years to bring many exciting new advances in avian physiology as research groups take advantage of new technologies. Studies of geographic variation will play a significant role in these advances through evaluation of genotypic and functional phenotypic divergence across environmental gradients. This will in turn provide crucial predictive data for understanding the capacity of populations to adapt and acclimatize to climate change (Williams *et al.* 2008; Urban *et al.* 2016; Meek *et al.* 2023; Urban *et al.* 2024). Given the rapid rate in which global change is creating conservation challenges for many avian species, there is a pressing need for relevant physiological data that can improve predictive models now. Research that explicitly explores connections between external morphology and performance measures could serve as a critical bridge between the decades of research on geographic variation in external morphological characters and an understanding of the thermogenic and evaporative cooling capacity of birds. Towards this goal, we devote the remainder of the review to discussing opportunities for linking morphology, performance, and genotype across spatial and temporal environmental gradients.

Spatial analyses

Geographic variation in body size, bill size, tarsus length, and plumage variation is frequently interpreted within the context of contributions to thermoregulation (see above), yet empirical work connecting these traits to performance remains incomplete. Avian bill size is an example of a trait well known to vary along thermal gradients in birds (Zink and Remsen 1986; Tattersall *et al.* 2017). This pattern may relate to heat loss patterns with smaller-billed birds potentially losing less heat in cold environments and larger-billed birds dissipating more heat in hot environments. A larger bill may also enable birds to rely less on evaporative cooling (at least at moderate temperatures) and allow them to conserve water in water-limited environments like deserts and salt marshes (Greenberg *et al.* 2012a). Thermal imaging confirms that birds regulate blood flow to vascularized regions of the bill to dissipate heat (Hagan and Heath 1980; Tattersall *et al.* 2009) and that

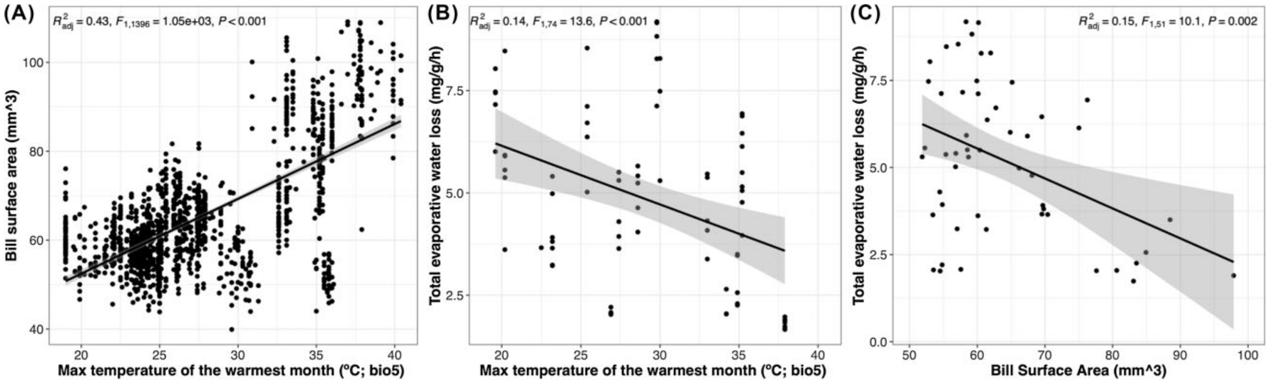

Fig. 3 Comparison of morphological, TEWL, and maximum temperature across Savannah sparrow populations. Both (A) bill surface area (approximated from bill length, width, and depth measures) and (B) TEWL within the thermal neutral zone were significantly correlated with maximum temperature variation across space. (C) Bill size and TEWL were significantly correlated with one another. Benham and Bowie (2021) took advantage of this spatial correlation to infer the amount of water savings that could be gained from a given increase in bill surface area through time. Bill measurements ($n = 1398$), TEWL measurements ($n = 76$), and 53 individuals had data for both. Data from Benham and Cheviron (2020) and Benham and Bowie (2021).

larger-billed birds can dissipate more heat across the bill surface (Greenberg *et al.* 2012b). In song sparrows, larger-billed subspecies could dissipate 33% more heat across the bill surface, and this was predicted to allow EWL reductions of 7.7%. These predictions have not been tested. To relate differences in heat dissipation across the bill surface to thermogenic capacity would require measurements of bill size variation with measures of thermogenic performance. For instance, can smaller-billed birds guard body temperatures and maintain functioning in response to cold challenges for longer or vice versa for large-billed birds in hot environments? Similarly, few data exist attempting to confirm a relationship between bill size and levels of EWL. Within Savannah sparrows, we have re-analyzed data from Benham and Cheviron (2020) and Benham and Bowie (2021) to show that both bill surface area (Fig. 3A) and TEWL within the thermal neutral zone (Fig. 3B) significantly vary in association with maximum annual temperature. Further, a significant negative correlation between bill size and TEWL exists for Savannah sparrows (Fig. 3C). In contrast, bill size variation in great tits (*Parus major*) does not relate to measures of evaporative cooling capacity (Playá-Montmany *et al.* 2021). Further work will be needed to establish when and where correlations between bill size and TEWL may be expected.

It is unlikely that birds ever rely on change in a single trait (external or internal) such as bill size or body size to increase performance in response to novel thermal challenges. Different species may also arrive at different solutions to common problems due to constraints imposed on certain traits or differences in the genetic variation available for selection to act on. Thermoregulatory capacity is a complex trait that could ultimately be influenced by body size and shape, appendage length, changes in plumage structure, metabolic rates, and behavioral responses (Briscoe *et al.* 2023). Few intraspecific studies explore how variation in insulative characters (e.g., feather length) varies with climatic gradients, despite the relative ease with which these traits can be measured on museum specimens and a long history of authors suggesting they may be more important for enhancing thermoregulatory performance (Scholander 1955). Across species, plumage length increases in cold environments (Pap *et al.* 2020) and with elevation (Barve *et al.* 2021). Insulative properties of feathers have also been shown to change seasonally with greater feather mass and density in winter relative to summer (Swanson 1991; Nord *et a l.* 2023). Intraspecific increases in plumage length have also been documented along elevation gradients (de Zwaan *et al.* 2017; Barve and Cadena 2022). Geographic variation in plumage color may additionally contribute to thermoregulatory adaptation in horned larks (Mason *et al.* 2023). Jointly considering geographic variation in a number of external traits alongside thermoregulatory performance measures will be important for understanding which traits contribute the most to performance in any given species.

Linking these analyses to genomic datasets using methods outlined above can provide insights into the genetic basis of certain traits relevant to thermoregulation. In birds, there is a much better understanding of the genes involved in many external morphological and plumage traits (Toews *et al.* 2016; Bosse *et al.* 2017; Moreira and Smith 2023) than other traits of physiological relevance. While many physiological measures are complex traits shaped by both genetic variation and plastic responses, traits such as basal metabolic rates have been found to be heritable in several bird species (Ronning *et al.* 2007; Bushuev *et al.* 2012; Nafstad *et al.* 2023). Many of these traits are also likely to be highly polygenic, making it difficult to pinpoint specific loci impacting inter-individual variation (Storz *et al.* 2015), yet within mammalian systems genes influencing complex traits such as metabolic rates (Montaigne *et al.* 2021) and EWL (Hirabayashi *et al.* 2017) have been identified. Future work exploring genomic variation in relation to thermal and precipitation gradients, along with efforts to link genotypes to phenotypes using approaches outlined above will be important for understanding the potential contributions of different traits to physiological performance in response to climate change.

Temporal analyses

A detailed understanding of how external morphological characters and genotypes contribute to physiological measures of performance across spatial gradients will provide essential context for evaluating temporal trends. Analysis of long-term datasets has already revealed temporal declines in body size across dozens of bird species (Jirinic *et al.* 2021; Youngflesh *et al.* 2022). Natural history collections provide another source of time series data with millions of specimens collected between ca. 1850 and the present (Billerman and Walsh 2019). These collections have been used to demonstrate widespread morphological changes in birds related to body size (Gardner *et al.* 2019), bill size (Campbell-Tennant *et al.* 2015), and plumage pigmentation (Mason and Unitt 2018). In many cases, the observed changes are correlated with changing temperature over the past century and recapitulate expectations from Bergmann's and Allen's rules. However, whether these temporal changes are enough to keep up with the rate of climate change and the physiological significance of these changes has been questioned (Nord *et al.* 2024). The extent to which these changes reflect plasticity or genetic adaptations remains poorly known as well (Teplitsky and Millien 2014). Although measuring physiological performance in historical materials is largely impossible, researchers could use spatial analyses to evaluate how variation in certain morphological traits that can be measured on specimens (e.g., feather length, body size) directly contribute to performance differences. Studies could then quantify temporal morphological change in traits over time using museum specimens to make inferences about changes in performance over time. For example, Benham and Bowie (2021) took advantage of spatial correlations between bill size and TEWL in Savannah sparrows (Fig. 3C) to project how much daily water savings birds may gain from the observed magnitude of bill size change over the past century.

Technological advances are also making it increasingly feasible to extract DNA from historic museum specimens (reviewed in Benham and Bowie 2023). When compared to modern samples, these data can be used to infer genomic responses to climate and landscape change over the past century (Bi *et al.* 2019; Turbek *et al.* 2023). Efforts to connect genotypic variation with spatial variation in physiological traits along climatic gradients can help illuminate the functional significance of certain loci. Follow-up studies using time-series data can then ask whether temporal changes in allele frequency have occurred at these same loci in association with climate change in the recent past. In the absence of genes with a large effect on the phenotype, time-series data can also be leveraged to assess the importance of selection on many loci of small effect in adaptation to environmental change (Reid *et al.* 2023). Making connections between spatial and temporal allele frequency changes at loci underlying physiological and morphological traits would provide powerful support for the importance of certain genes in responding to climate change.

Conclusions

The central goal of this review is to urge avian physiologists to consider patterns of spatial variation in traits that may be directly involved in organismal responses to climate change. By quantifying the extent of geographic variation in functionally relevant traits across a species range, we can work towards predictive models that integrate across levels of biological organization to understand the capacity of populations to adapt to ongoing warming trends. Despite the inherent challenges in conducting rigorous physiological research involving multiple populations of the same species, technological advances related to sequencing, tracking devices, imaging, and more will provide a host of new opportunities to investigate the mechanisms underpinning avian adaptations to environmental challenges. Additionally, this research agenda will be advanced through the establishment of collaborations among avian biologists with diverse expertise in genomics, physiology, modeling, ecology, and evolution. As anthropogenic changes impacting climate, landscape, and other facets proceed at a rapid pace, we want to echo with renewed urgency the same conclusion made by Prosser (1955) nearly 70 years ago: There is "*An immediate need for the description of phenotypic and genotypic variation of physiological characters within known species. This can only be accomplished by the cooperative effort of physiologists, ecologists, geneticists and systematists.*"

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Supplementary data

Supplementary data available at *ICB* online.

Conflict of interest

The authors have no conflict of interest to declare.

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