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SYMPOSIUM INTRODUCTION

Recent Advances in the Mechanistic Understanding of Avian Responses to Environmental Challenges

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Synopsis Endothermic species have evolved strategies to maximize survival in highly variable or extreme environments. Birds are exemplary as they are among the most widely distributed endotherms on the planet, living in all manner of inhospitable environments. As an example, winter in temperate regions is characterized by cold temperatures and low food availability. Some birds have evolved to tolerate these conditions by seasonally increasing thermogenic capacity, increasing heterothermy, and displaying highly flexible phenotypes. Other species have evolved to avoid the inhospitable conditions of winter altogether by migrating—again requiring a unique set of physiological adaptations that allow success in this challenging endeavor. In these examples and in many others, the organismal requirements for success share similarities, but the underlying mechanisms, physiological requirements, and selection on those traits can differ significantly, as can their ecological and evolutionary impacts. In recent years, a suite of novel and established tools has become widely available and more accessible, allowing insights into long-standing questions. Genomic tools, new approaches to measure organismal performance, the use of citizen science data, easier access to metabolite assays or hormone detection, to name a few, have spurred rapid advances in our understanding of avian physiology. These new tools have been leveraged to investigate important questions regarding avian responses to our rapidly changing climate in an attempt to understand species resilience and limits.

Introduction

Birds live in all corners of the globe and are successful despite all manner of environmental challenges. They live in the hottest places on earth, as well as some of the coldest. They live in marine and terrestrial environments and can persist on fresh and salt water. They migrate thousands of kilometers across continents, oceans, and hemispheres to exploit seasonally abundant food to breed successfully, but they also breed opportunistically in harsh conditions. They live at high altitude and in this environment simultaneously push the limits of the physics of flight and the vertebrate oxygen transport cascade. In all of these cases, birds display an incredible capacity for short- and long-term phenotypic plasticity, adaptation, and evolution. The mechanistic study of avian physiological adaptations to environmental challenges has been a cornerstone of organismal biology for a long time (Calder and King 1974). Birds have evolved a vast diversity of complex physiological, morphological, and behavioral traits that have allowed their success. An emerging theme—one that became even more apparent during our symposium and the associated discussions—is that phenotypic flexibility, either in response to challenges or in anticipation of them, has allowed birds to respond appropriately to environmental challenges (Forsman 2015).

The myriad of challenges organisms face in the Anthropocene has amplified the importance of understanding how birds live where they live and do what they do. Further, advancements in the understanding of behavioral and physiological responses are increasingly important in applied conservation science, and predictive modeling approaches now incorporate physiological traits (e.g., Riddell et al. 2021). Many of the themes presented in our symposium are not new *per se* but are, of course, the natural evolution from what came

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before—as new information came to light and as approaches and techniques progressed. Thus, the content included in this symposium provides novel insights to broader long-standing questions, while also investigating more nuanced, focused questions for the first time. To make progress toward these long-standing questions and to develop and pursue new questions that have recently been brought to light, we require innovation in our approaches, techniques, instrumentation, and data analysis. When we conceived of this symposium, we therefore aimed to highlight new insights into avian responses to environmental challenges, but we specifically focused on innovation in each of the following areas—questions, approaches, techniques, data analysis, and data synthesis—and we wanted to highlight mechanistic investigations across multiple biological scales. The talks featured innovative approaches and analyses investigating important questions in avian biology at the cellular, molecular, and biochemical levels (Elowe and Stager 2024; Hood 2024; Rhodes et al. 2024), tissue and whole organism levels (Ivy and Guglielmo 2023; Cornelius et al. 2024; Elowe and Stager 2024; Pastres et al. 2024), as well as at the population level (Benham et al. 2024; Stager 2024). Although these manuscripts offer only a small glimpse into the recent progress in our field, they highlight innovation and progress that is broadly important.

Classic questions—renewed urgency for a changing world

Anthropogenic activities are leading to unprecedented rates of climate change, habitat loss, and pollution that are substantially affecting bird populations (Rosenberg et al. 2019). While curtailing these activities to stave off continued losses around the globe is imperative, conservation efforts are also focused on uncovering the most effective investments to buffer species and populations from steep declines (Bateman et al. 2020; Saunders et al. 2023). In this respect, decades of research into the physiological capacity of birds to withstand environmental challenges is helping us to understand which species are most vulnerable and where these directed conservation efforts can be most impactful. Classic questions about avian tolerance to hot and cold temperatures, harsh weather extremes, high altitude flight, long-distance migratory movements, and changing habitats have generated a wealth of knowledge about how birds respond to their environments (McWilliams and Karasov 2014; Swanson et al. 2014; Bishop et al. 2015; Scott et al. 2015; Senner et al. 2018; Gerson et al. 2019; Wolf et al. 2020; McKechnie et al. 2021; Stager et al. 2021; Elowe et al. 2023). However, the urgency of the environmental challenges posed by the Anthropocene has demanded a continued interest in these questions today.

As habitats are degraded or altered by human impacts, changes at the population and species level have become clear. However, in some cases the reasons for population changes are not immediately apparent, obfuscating the most effective targets of conservation efforts. This is complicated by the global nature of bird ranges, which, in migratory species, may span hemispheres, and thus face hazards across breeding and non-breeding habitats as well as the threats en route (Bay et al. 2021). Therefore, a major focus of new research is to understand the capacity for birds to respond to environmental change through physiological or behavioral changes. This capacity is partly determined by the potential for genetic diversity to support rapid adaptation, leading to a substantial effort to investigate adaptations to past changes in climate and project this capacity toward predicted changes in the future (e.g., Turbek et al. 2023; Benham et al. 2024). This work has already elucidated the potentially adaptive role of admixture in responding to climatic changes (Turbek et al. 2023), as well as identification of particularly vulnerable populations (Bay et al. 2021).

While genomic approaches can help to understand broad-scale shifts in populations and predict future responses, these efforts are bolstered by direct studies of the capacity for both behavioral and physiological flexibility. In this respect, current efforts are expanding on classic questions of environmental tolerance by considering the effects of multiple stressors or environmental variables (Cornelius 2022) and evaluating the amount of intraspecific variation in physiological flexibility that exists (Stager et al. 2021). Because climate effects do not occur in isolation, these studies are providing particularly valuable insights into the spatial and temporal vulnerability of birds.

Additionally, due to their spectacular migratory journeys and their worldwide distribution across harsh habitats, understanding performance limits in birds has always been a driving factor in avian physiology research. In that vein, Ivy and Williamson (2024) review the physiological traits that allow birds to perform in low-oxygen environments experienced during transient high-altitude flight and altitudinal migration. However, these performance limits become even more relevant when combined with the challenges imposed by anthropogenic stressors. Even within related species, there is substantial variation, suggesting that species- or population-specific responses to the environment may be constrained in different ways. To that end, Benham and Beckman (2024) emphasize the need for integrating across data types (environmental, physiological, morphological, and genomic) and incorporating intraspecific variation when predicting species vulnerabilities to global change. Integrative approaches are vital in this endeavor, combining environmental, physiological, morphological, and genomic data can provide a more accurate and comprehensive understanding of species vulnerabilities, but such approaches require effective collaboration and the use of novel and innovative methods to be successful.

New approaches

Recent advancements in the pursuit of the above questions can, in part, be attributed to new technologies that allow us to overcome previously insurmountable obstacles in physiological data collection and hypothesis testing. In some cases these innovations have become indispensable to our various sub-disciplines. We highlight only a few obvious and important new technologies here. Some of these are established and have transformed the way we approach our scientific inquiry, while others are just in their infancy but have great potential to allow novel insights, broader participation, or may have impacts in ways yet to be seen.

Respirometry

Flow-through respirometry has been a staple technique in understanding avian metabolism in response to environmental challenges for decades. This approach continues to be important to determine the metabolic response to high (Gerson et al. 2019) and low temperatures (Swanson and Liknes 2006; Petit et al. 2013), hypoxia (Scott 2011), short- and long-term exercise (Zhang et al. 2015; Gerson et al. 2020), and humidity (Pierce et al. 2005; Gerson et al. 2014, 2020), and to investigate allometric scaling relationships (Rezende et al. 2002; McKechnie et al. 2021). This approach is also being used to quantify the energetic costs/savings of specific behavioral responses. For instance, by comparing oxygen consumption under different behavioral states, Pastres et al. (2024) demonstrate that postural changes result in energetic savings for individuals with low energy reserves. Much of this information can then be used to inform biophysical models predicting responses to climatic change (Riddell et al. 2019, 2021), or to investigate how metabolic parameters, such as the width of the thermal neutral zone, vary geographically (Pollock et al. 2019, 2021). While there is no doubt that basic respirometry has contributed enormously to the advancement of our field, recent advancements in sensor accuracy and response times, as well as improvements in design have allowed accurate and more rapid multiplexing, which allows rapid switching among animal chambers to increase the time-resolution of measurements on multiple animals simultaneously (Lighton and Halsey 2011). This has led to the development of metabolic phenotyping systems that allow for continuous, direct measurement of metabolism in numerous animals over long periods of time—days to weeks or longer (Fig. 1). These measures of daily energy expenditure can be combined with simultaneous assays of activity, as well as food and water consumption, and allow impressively detailed energy budgets. This approach was originally detailed in Lighton and Halsey (2011) and has since become popular among small mammal researchers through the availability of commercial systems. However, it is possible to develop these systems using standard respirometry equipment with careful design considerations. In addition to whole-animal respirometry, advances in techniques to measure tissue-level energetics through mitochondrial respirometry (Hood 2024; Rhodes et al. 2024) allow for a mechanistic interrogation of the factors that contribute to variation in avian metabolic rates. In this case, high-resolution mitochondrial respirometry was taken to the field, allowing an accurate assessment of differences in mitochondrial energetics and substrate preferences of migratory birds. Such approaches have traditionally been difficult since mitochondrial measurements must be completed in traditional lab space and, as a result have typically done with captive birds. Bringing a mobile lab to the field in this case provides a more accurate representation of mitochondrial function.

Open electronics

An associated but independent new development that has had tremendous impact already in many fields is the availability of cheap, user-friendly open electronics (Arduinos and Raspberry Pis) that are seemingly infinitely flexible, easy to code, and able to produce accurate data for any number of applications. Such devices, for instance, allow for autonomous assays of behavioral and physiological responses to temperature in wild birds at bird feeders (Bridge et al. 2019) and nest boxes (Zimmer et al. 2020). We have also recently used these to measure food and water consumption during metabolic phenotyping in captive sparrows during a temperature manipulation while also continuously measuring metabolism and water loss (Fig. 1). These example data show the high-resolution data generated with this custom system. When paired with a USB microphone and existing acoustic bird classification platforms (i.e., BirdNet; Kahl et al. 2021), these circuits are also being used for continuous bird localization and species detection (https://github.com/mcguirepr89/BirdNET-Pi). Many other examples can be found, and this topic has recently been the focus of its own conference workshop (Morozov 2022), but the relative low cost and ease of

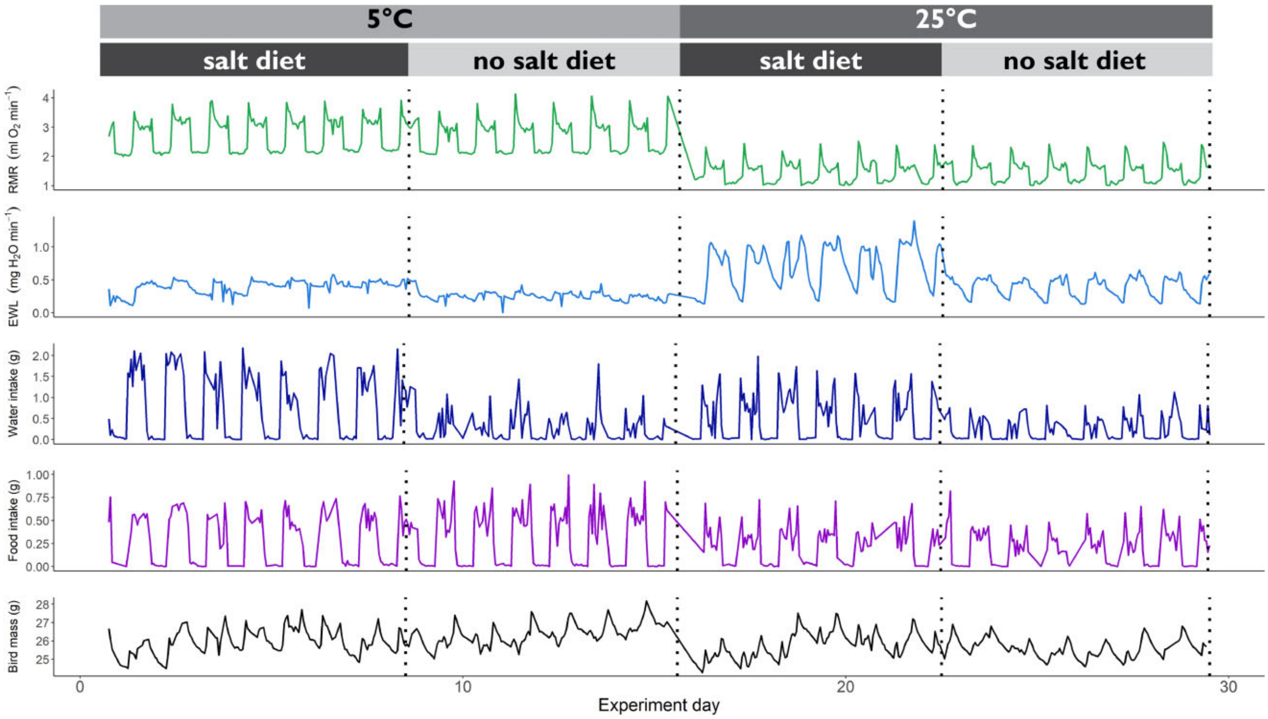

Fig. 1 Example data from a custom metabolic phenotyping system that simultaneously measures resting metabolic rate (RMR), evaporative water loss (EWL), drinking water intake, food intake, and animal mass through a 30-day experiment where temperature and dietary salt were manipulated. Such systems combine rapid multiplexing and standard respirometry equipment with custom, low-cost Arduino-driven load cells.

customization make open electronics an appealing approach for many biological questions.

Biologging devices

The advent of miniaturized biologging devices has additionally revolutionized our ability to track and monitor birds in the wild. Perhaps most notably, these devices have uncovered exceptional feats of performance during migration (e.g., Gill et al. 2009; Egevang et al. 2010; Hedenström 2010; Hawkes et al. 2013; Hedenström et al. 2016). They have also revealed behavioral responses of birds to extreme weather events (Senner et al. 2015; Watts et al. 2021), habitat alterations (Chan et al. 2023), and artificial light at night (McGlade et al. 2023). In addition to documenting patterns of movement and activity, biologgers can record acceleration (Brown et al. 2022), flight altitude (Senner et al. 2018), diving depth (Guilford et al. 2022), body temperature (Andreasson et al. 2023), heart rate (Bishop et al. 2015), wingbeat frequency (Bouten et al. 2013), and even eye movements in flight (Lapsansky et al. 2024). Some of these devices are now even small enough to put on hummingbirds (Williamson and Witt 2021). Several of the talks in our symposium and complementary session demonstrated the power of pairing biologgers with physiological assays to better understand how birds cope with environmental challenges. For example, Williamson and colleagues (Williamson et al. 2024) combined tracking and respiratory trait data to reveal the time course of altitudinal acclimatization of Southern Giant Hummingbirds (*Patagona gigas*) as they ascend the Andes. Uehling and colleagues (2024) characterized activity patterns and dietary preferences of breeding Tree Swallows (*Tachycineta bicolor*) after manipulating their glucocorticoid levels to simulate an environmental challenge, demonstrating that endocrine mediators of the stress response can induce changes in activity and foraging. Moreover, Young and colleagues (2024) quantified the energetic costs of diet alterations by simultaneously assaying oxygen consumption and body temperature (using implanted PIT tags) in Western Sandpipers (*Calidris mauri*), showing that dietary factors are key to metabolic flexibility and energy savings. Finally, Dominoni and colleagues (2024) used automated biotelemetry to record both body temperature and activity of urban birds, revealing desynchronization of physiology and behavior in response to artificial light at night. These innovative uses of biologgers help us to address longstanding questions by linking experimental manipulations in the lab and real-world environmental conditions.

Additional new technologies

Several other recent technologies are being applied to better understand avian responses to environmental change. Here, we only mention two tools, as examples, that have recently been adopted and both fill an important niche in our collective quantitative toolbox. However, there are numerous additional technologies applied by contributors to this symposium, such as thermography (Zuluaga and Danner 2023), that are greatly contributing to our toolkit.

Quantitative magnetic resonance body composition analysis has now been available to researchers for 20 years, and many lab groups have adopted this new technology, which allows non-invasive and rapid quantitative measurement of fat mass, lean body mass, and total body water (Seewagen and Guglielmo 2011). Since it is rapid and non-invasive, conducting repeated measures on individuals to quantify changes in body condition over time (Gerson and Guglielmo 2011) has been one of the most impactful applications of this technology. More recently, it has been shown that the changes in fat mass and lean mass over time are accurate enough to be used to determine energy expenditure, with a similar accuracy to doubly labeled water (Elowe et al. 2023). Further, accurate quantification of fat mass and lean mass has been used to estimate flight ranges in free-living birds, investigate phenotypic flexibility during breeding (Boyle et al. 2012), or provide a quantitative assessment of body condition at stopover in multiple species (Kennedy et al. 2016). One drawback of this technology is the high cost, but the versatility and low per-scan operating cost have made it an important new technology in avian biology.

Cavity ring-down spectroscopy has become popular to measure ^{13}C isotope concentrations in CO_2, or deuterium, and ^{18}O concentrations in liquid water samples. These instruments are much more accessible and user-friendly than traditional mass spectrometry used for the measurement of natural and experimentally enriched isotope samples. This has allowed the rapid development of $^{13}CO_2$ breath testing to investigate dietary shifts, or fuel use when animals are fed labeled amino acids, sugars, or fats, and (McCue et al. 2010; McCue and Welch 2015; Welch et al. 2017; Rogers and Gerson 2024) all provide detailed descriptions of the instruments and technique. Energy expenditure over short periods of time using the ^{13}C-sodium bicarbonate method is also now more readily available and accurate (Hambly and Voigt 2011; Busse et al. 2013; Hedh et al. 2020) and allows accurate determination of activity costs in free-living animals over very short periods of time. These instruments have also allowed the accurate measurement of both ^{2}H and ^{18}O in liquid water or breath, allowing the more cost-effective use of the doubly labeled water technique (Berman et al. 2012; Mitchell et al. 2015), and recent advances in the accuracy of these instruments have allowed novel pursuits into isotopic methods for determining water fluxes in birds and mammals (Whiteman et al. 2019; Sabat et al. 2021).

Genomic tools

An obvious development that has had a profound impact across biological disciplines is the dramatic reduction in the cost of genomic library preparation and sequencing, as well as the availability of analysis platforms to process such large volumes of data. This has already resulted in a wealth of publicly available avian genomic resources, including comprehensive phylogenies (e.g., Kimball et al. 2019) that allow for phylogenetically informed analyses in comparative physiological investigations (e.g., Londoño et al. 2015; Stager et al. 2016; Linck et al. 2023; Uehling et al. 2024). Several studies are now further highlighting the power of sequencing approaches for investigating questions related to avian environmental adaptation and/or coping with environmental challenges. For instance, Williamson and colleagues (Williamson et al. 2024) provide new context for physiological variation occurring across the broad elevational distribution of the Giant Hummingbirds (*Patagona spp.*) by defining deep evolutionary divergence among migratory and high-elevation resident populations using genomic data. At the same time, both genomic and transcriptomic data are being employed to generate hypotheses about the biochemical mechanisms underlying avian physiological and behavioral adaptations (Branch et al. 2022; Benham et al. 2024) and acclimation capacity (Stager et al. 2015; Sharma et al. 2021). When paired with detailed physiological assays, these datasets can provide new insight into long-sought-after questions in avian physiology, such as the molecular mechanisms underlying avian non-shivering thermogenesis (Elowe and Stager 2024). Moreover, genomic tools are underscoring the unrivaled value of natural history collections for addressing fundamental questions about adaptation to environmental change (Benham and Bowie 2022). Benham and colleagues (Benham et al. 2024) employed genomic data from both contemporary and historic samples to understand the evolution of avian physiological adaptation to saltmarsh habitats and the influence of gene flow on traits important for water conservation in these environments over the past 150 years. We look forward to more exciting advancements in the field as these technologies continue to become increasingly accessible and cost-effective.

Citizen science datasets

One advantage to studying wild birds that cannot be overstated is the huge popularity of birdwatching around the globe. This has resulted in several long-running programs that harness the power of citizen scientists to amass high-quality bird observations across space and time. For instance, eBird (CornellLab) is an online portal for documenting bird sightings with over 100 million observations contributed annually worldwide (Sullivan et al. 2009). Its data and associated scientific products, and those of many other avian citizen science projects, are freely available for biological applications. These extensive resources are now being employed to inform our understanding of avian responses to environmental challenges at unprecedented geographic, temporal, and taxonomic scales. For example, eBird occurrence data can be used to populate species-distribution models and project bird ranges under future climate-warming scenarios (Bateman et al. 2020). A number of exciting new applications demonstrate that, by pairing these observation data with climatic data, physiological tolerance can also be investigated. This was recently illustrated by Cohen et al. (2023), who characterized both spatial and seasonal thermal sensitivity in 21 bird species across North America. At the same time, by combining these datasets with physiological trait data, the ecological and evolutionary effects of physiological variation can be explored in novel ways. For instance, Latimer and Zuckerberg (2021) use weekly occurrence data to determine how avian thermal tolerance influences winter occupancy dynamics at regional scales. These datasets are also being used to understand responses to extreme weather events (Cohen et al. 2021) and, further, the effects of these events on avian fitness (Taff and Shipley 2023). As these datasets continue to amass observations from all across the globe, the power of these approaches seems infinite.

Looking to the future

As we and the other symposium contributors have shown, the imaginative application of innovative tools can help us address longstanding and timely questions about the capacity for birds to respond to a rapidly changing world. However, the success of these tools will depend on accessibility and collaborations that facilitate their widespread application. For example, the use of custom-made measurement systems can be encouraged by open-access publication of designs and resources, as well as collaborations with colleagues with computer science and engineering backgrounds. Likewise, our understanding of widespread intraspecific variation may be accelerated by open sharing of physiological data for meta-analyses, driven by collaborations between physiologists and evolutionary biologists that can ensure appropriate analyses that address important questions. In doing so, we will be better able to conduct truly integrative work that propels our understanding of the mechanistic responses of birds to environmental challenges across biological levels.

Author contributions

All authors contributed equally to the conceptualization, funding acquisition for this symposium. All authors contributed equally to writing this manuscript.

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Conflict of interest

The authors declare no conflicts of interest..

Data availability

Please contact the authors to request any referenced data.

References

Andreasson F, Rostedt E, Nord A. 2023. Measuring body temperature in birds—the effects of sensor type and placement on estimated temperature and metabolic rate. J Exp Biol 226:jeb246321.

Bateman BL, Taylor L, Wilsey C, Wu J, LeBaron GS, Langham G. 2020. Risk to North American birds from climate change-related threats. Conserv Sci Pract 2:e243.

Bay RA, Karp DS, Saracco JF, Anderegg WRL, Frishkoff LO, Wiedenfeld D, Smith TB, Ruegg K. 2021. Genetic variation reveals individual-level climate tracking across the annual cycle of a migratory bird. Ecol Lett 24:819–28.

Benham PM, Beckman EJ. 2024. Integrating spatial analyses of genomic and physiological data to understand avian responses to environmental change. Integr Comp Biol 64. https://doi.org/10.1093/icb/icae059.

Benham PM, Bowie RCK. 2023. Natural history collections as a resource for conservation genomics: understanding the past to preserve the future. J Hered 114:367–84.

Benham PM, Walsh J, Bowie RCK. 2024. Spatial variation in population genomic responses to over a century of anthropogenic change within a tidal marsh songbird. Glob Chang Biol 30:e17126.

Berman ESF, Fortson SL, Snaith SP, Gupta M, Baer DS, Chery I, Blanc S, Melanson EL, Thomson PJ, Speakman JR. 2012. Direct analysis of δ 2H and δ 18O in natural and enriched human urine using laser-based, off-axis integrated cavity output spectroscopy. Anal Chem 84:9768–73.

Bishop CM, Spivey RJ, Hawkes LA, Batbayar N, Chua B, Frappell PB, Milsom WK, Natsagdorj T, Newman SH, Scott GR et al. 2015. The roller coaster flight strategy of bar-headed geese conserves energy during Himalayan migrations. Science 347:250–4.

Bouten W, Baaij EW, Shamoun-Baranes J, Camphuysen KCJ. 2013. A flexible GPS tracking system for studying bird behaviour at multiple scales. J Ornithol 154:571–80.

Boyle WA, Winkler DW, Guglielmo CG. 2012. Rapid loss of fat but not lean mass prior to chick provisioning supports the flight efficiency hypothesis in tree swallows. Funct Ecol 26:895–903.

Branch CL, Semenov GA, Wagner DN, Sonnenberg BR, Pitera AM, Bridge ES, Taylor SA, Pravosudov VV. 2022. The genetic basis of spatial cognitive variation in a food-caching bird. Curr Biol 32:210–219.e4.e4.

Bridge ES, Wilhelm J, Pandit MM, Moreno A, Curry CM, Pearson TD, Proppe DS, Holwerda C, Eadie JM, Stair TF et al. 2019. An Arduino-based RFID platform for animal research. Front Ecol Evol 7:257.

Brown JM, Bouten W, Camphuysen KCJ, Nolet BA, Shamoun-Baranes J. 2022. Acceleration as a proxy for energy expenditure in a facultative-soaring bird: comparing dynamic body acceleration and time-energy budgets to heart rate. Funct Ecol 36:1627–38.

Calder WA, King JR. 1974. Thermal and caloric relations of birds. In: Farner DS, King JR, editors. Avian biology IV. p. 259–413.

Chan Y-C, Chan DTC, Tibbitts TL, Hassell CJ, Piersma T. 2023. Site fidelity of migratory shorebirds facing habitat deterioration: insights from satellite tracking and mark-resighting. Mov Ecol 11:79.

Cohen JM, Fink D, Zuckerberg B. 2021. Extreme winter weather disrupts bird occurrence and abundance patterns at geographic scales. Ecography 44:1143–55.

Cohen JM, Fink D, Zuckerberg B. 2023. Spatial and seasonal variation in thermal sensitivity within North American bird species. Proc Biol Sci 290:20231398.

Cornelius JM, Vernasco BJ, Mori N, Watts HE. 2024. Response to food restriction, but not social information use, varies seasonally in captive cardueline finches. Integr Comp Biol 12. https://doi.org/10.1093/icb/icae016.

Cornelius JM. 2022. Advance social information allows red crossbills (*Loxia curvirostra*) to better conserve body mass and intestinal mass during food stress. Proc Biol Sci 289:20220516.

Dominoni D, Helm B, Capilla-Lacheras P. 2024. Chronobiology of urban life: new insights from parallel recording of activity and body temperature. Society for integrative and comparative biology annual meeting. Seattle, WA, USA. Jan 2–6 2024.

Egevang C, Stenhouse IJ, Phillips RA, Petersen A, Fox JW, Silk JRD. 2010. Tracking of Arctic terns *Sterna paradisaea* reveals longest animal migration. Proc Natl Acad Sci USA 107:2078–81.

Elowe CR, Groom DJE, Slezacek J, Gerson AR. 2023. Long-duration wind tunnel flights reveal exponential declines in protein catabolism over time in short- and long-distance migratory warblers. Proc Natl Acad Sci USA 120:e2216016120.

Elowe CR, Stager M. 2024. SERCA uncoupling may facilitate cold acclimation in dark-eyed juncos (*Junco hyemalis*) without regulation by sarcolipin or phospholamban. Integr Comp Biol. https://doi.org/10.1093/icb/icae022.

Forsman A. 2015. Rethinking phenotypic plasticity and its consequences for individuals, populations and species. Heredity 115:276–84.

Gerson AR, Desimone JG, Black EC, Dick MF, Groom DJ. 2020. Metabolic reduction after long-duration flight is not related to fat-free mass loss or flight duration in a migratory passerine. J Exp Biol 223:jeb215384.

Gerson AR, Guglielmo CG. 2011. Flight at low ambient humidity increases protein catabolism in migratory birds. Science 333:1434–6.

Gerson AR, Mckechnie AE, Smit B, Whitfield MC, Smith EK, Talbot WA, Mcwhorter TJ, Wolf BO. 2019. The functional significance of facultative hyperthermia varies with body size and phylogeny in birds. Funct Ecol 33:597–607.

Gerson AR, Smith EK, Smit B, Mckechnie AE, Wolf BO. 2014. The impact of humidity on evaporative cooling in small desert birds exposed to high air temperatures. Physiol Biochem Zool 87:782–95.

Gill RE, Tibbitts TL, Douglas DC, Handel CM, Mulcahy DM, Gottschalck JC, Warnock N, Mccaffery BJ, Battley PF, Piersma T. 2009. Extreme endurance flights by landbirds crossing the Pacific Ocean: ecological corridor rather than barrier? Proc Biol Sci 276:447–57.

Guilford T, Padget O, Maurice L, Catry P. 2022. Unexpectedly deep diving in an albatross. Curr Biol 32:R26–8.

Hambly C, Voigt CC. 2011. Measuring energy expenditure in birds using bolus injections of 13C-labelled Na-bicarbonate. Comp Biochem Physiol A Mol Integr Physiol 158:323–8.

Hawkes LA, Balachandran S, Batbayar N, Butler PJ, Chua B, Douglas DC, Frappell PB, Hou Y, Milsom WK, Newman SH et al. 2013. The paradox of extreme high-altitude migration in bar-headed geese *Anser indicus*. Proc Biol Sci 280:20122114.

Hedenström A, Norevik G, Warfvinge K, Andersson A, Bäckman J, Åkesson S. 2016. Annual 10-month aerial life phase in the common swift *Apus apus*. Curr Biol 26:3066–70.

Hedenström A. 2010. Extreme endurance migration: what is the limit to non-stop flight? PLoS Biol 8:e1000362–6.

Hedh L, Guglielmo CG, Johansson LC, Deakin JE, Voigt CC, Hedenström A. 2020. Measuring power input, power output and energy conversion efficiency in un-instrumented flying birds. J Exp Biol 223:jeb223545.

Hood WR. 2024. A mitochondrial perspective on the demands of reproduction. Integr Comp Biol. https://doi.org/10.1093/icb/icae049.

Ivy CM, Guglielmo CG. 2023. Migratory songbirds exhibit seasonal modulation of the oxygen cascade. J Exp Biol 226:jeb245975.

Ivy CM, Williamson JL. 2024. On the physiology of high-altitude flight and altitudinal migration in birds. Integr Comp Biol 64. https://doi.org/10.1093/icb/icae062.

Kahl S, Wood CM, Eibl M, Klinch H. 2021. BirdNET: A deep learning solution for avian diversity monitoring. Ecol Inform 61:101236.

Kennedy LV, Morbey YE, Mackenzie SA, Taylor PD, Guglielmo CG. 2016. A field test of the effects of body composition analysis by quantitative magnetic resonance on songbird stopover behaviour. J J Ornithol 158 1–9.

Kimball RT, Oliveros CH, Wang N, White ND, Barker FK, Field DJ, Ksepka DT, Chesser RT, Moyle RG, Braun MJ et al. 2019. A phylogenomic supertree of birds. Diversity 11:109.

Lapsansky A, Wylie D, Altshuler D. 2024. Unlocking the visual world of free-flying pigeons: insights from head-mounted cameras. Society for integrative and comparative biology annual meeting. Seattle, WA, USA. Jan 2–6 2024.

Latimer CE, Zuckerberg B. 2021. Habitat loss and thermal tolerances influence the sensitivity of resident bird populations to winter weather at regional scales. J Anim Ecol 90:317–29.

Lighton JRB, Halsey LG. 2011. Flow-through respirometry applied to chamber systems: pros and cons, hints and tips. Comp Biochem Physiol A Mol Integr Physiol 158:265–75.

Linck EB, Williamson JL, Bautista E, Beckman EJ, Benham PM, Dubay SG, Flores LM, Gadek CR, Johnson AB, Jones MR et al. 2023. Blood variation implicates respiratory limits on elevational ranges of Andean birds. Am Nat 201:741–54.

Londoño GA, Chappell MA, Castañeda MDR, Jankowski JE, Robinson SK. 2015. Basal metabolism in tropical birds: latitude, altitude, and the 'pace of life'. Funct Ecol 29:338–46.

Mccue MD, Sivan O, Mcwilliams SR, Pinshow B. 2010. Tracking the oxidative kinetics of carbohydrates, amino acids and fatty acids in the house sparrow using exhaled 13CO2. J Exp Biol 213:782–9

Mccue MD, Welch KC. 2016. 13C-Breath testing in animals: theory, applications, and future directions. J Comp Physiol B 186:265–85.

Mcglade CLO, Capilla-Lasheras P, Womack RJ, Helm B, Dominoni DM. 2023. Experimental light at night explains differences in activity onset between urban and forest great tits. Biol Lett 19:20230194.

Mckechnie AE, Gerson AR, Wolf BO. 2021. Thermoregulation in desert birds: scaling and phylogenetic variation in heat tolerance and evaporative cooling. J Exp Biology 224:jeb229211.

Mcwilliams SR, Karasov WH. 2014. Spare capacity and phenotypic flexibility in the digestive system of a migratory bird: defining the limits of animal design. Proc Biol Sci 281:20140308.

Mitchell GW, Guglielmo CG, Hobson KA. 2015. Measurement of whole-body CO_2 production in birds using real-time laser-derived measurements of hydrogen (δ^2H) and oxygen (δ^{18}O) isotope concentrations in water vapor from breath. Physiol Biochem Zool 88:599–606.

Morozov. 2022. Open electronics in comparative physiology workshop. In: American Physiological Society intersociety meeting in Comparative physiology: from organisms to omics in an uncertain world. San Diego California: American Physiological Society.

Pastres M, Maggini I, Cardinale M, Fusani L, Ferretti A. 2024. Sleep posture influences metabolic rate and vigilance in the common whitethroat (*Curruca communis*). Integr Comp Biol. https://doi.org/10.1093/icb/icae031.

Petit M, Lewden A, Vézina F. 2013. Intra-seasonal flexibility in avian metabolic performance highlights the uncoupling of basal metabolic rate and thermogenic capacity. PLoS One 8:e68292.

Pierce BJ, Mcwilliams SR, O'connor TP, Place AR, Guglielmo CG. 2005. Effect of dietary fatty acid composition on depot fat and exercise performance in a migrating songbird, the red-eyed vireo. J Exp Biol 208:1277–85.

Pollock HS, Brawn JD, Agin TJ, Cheviron ZA. 2019. Differences between temperate and tropical birds in seasonal acclimatization of thermoregulatory traits. J Avian Biol 50:e02067.

Pollock HS, Brawn JD, Cheviron ZA. 2021. Heat tolerances of temperate and tropical birds and their implications for susceptibility to climate warming. Funct Ecol 35:93–104.

Busse R, Swartz SM, Voigt C. 2013. Flight metabolism in relation to speed in Chiroptera: testing the U-shape paradigm in the short-tailed fruit bat, *Carollia perspicillata*. J Exp Biol 216:2073–80.

Rezende EL, Swanson DL, Novoa FF, Bozinovic F. 2002. Passerines versus nonpasserines: so far, no statistical differences in the scaling of avian energetics. J Exp Biol 205:101–7.

Rhodes EM, Yap KM, Hill GE, Hood WR. 2024. A comparison of the mitochondrial performance between migratory and sedentary mimid thrushes. Integr Comp Biol 62. https://doi.org/10.1093/icb/icae137.

Riddell EA, Iknayan KJ, Hargrove L, Tremor S, Patton JL, Ramirez R, Wolf BO, Beissinger SR. 2021. Exposure to climate change drives stability or collapse of desert mammal and bird communities. Science 371:633–6.

Riddell EA, Iknayan KJ, Wolf BO, Sinervo B, Beissinger SR. 2019. Cooling requirements fueled the collapse of a desert bird community from climate change. Proc Natl Acad Sci USA 116:21609–15.

Rogers EJ, Gerson AR. 2024. Water restriction increases oxidation of endogenous amino acids in house sparrows (*Passer domesticus*). J Exp Biol 227:jeb246483.

Rosenberg KV, Dokter AM, Blancher PJ, Sauer JR, Smith AC, Smith PA, Stanton JC, Panjabi A, Helft L, Parr M et al. 2019. Decline of the North American avifauna. Science 366:120–4.

Sabat P, Newsome SD, Pinochet S, Nespolo R, Sanchez-Hernandez JC, Maldonado K, Gerson AR, Sharp ZD, Whiteman JP. 2021. Triple oxygen isotope measurements (Δ'17O) of body water reflect water intake, metabolism, and δ18O of ingested water in Passerines. Front Physiol 12:710026.

Saunders SP, Grand J, Bateman BL, Meek M, Wilsey CB, Forstenhaeusler N, Graham E, Warren R, Price J. 2023. Integrating climate-change refugia into 30 by 30 conservation planning in North America. Front Ecol Environ 21:77–84.

Scott GR, Hawkes LA, Frappell PB, Butler PJ, Bishop CM, Milsom WK. 2015. How bar-headed geese fly over the Himalayas. Physiology 30:107–15.

Scott GR. 2011. Elevated performance: the unique physiology of birds that fly at high altitudes. J Exp Biol 214:2455–62.

Seewagen CL, Guglielmo CG. 2011. Quantitative magnetic resonance analysis and a morphometric predictive model reveal lean body mass changes in migrating Nearctic-Neotropical passerines. J Comp Physiol B 181:413–21.

Senner NR, Stager M, Verhoeven MA, Cheviron ZA, Piersma T, Bouten W. 2018. High-altitude shorebird migration in the absence of topographical barriers: avoiding high air temperatures and searching for profitable winds. Proc Biol Sci 285:20180569–9.

Senner NR, Verhoeven MA, Abad-Gómez JM, Gutiérrez JS, Hooijmeijer JCEW, Kentie R, Masero JA, Tibbitts TL, Piersma T. 2015. When Siberia came to the Netherlands: the response of continental black-tailed godwits to a rare spring weather event. J Anim Ecol 84:1164–76.

Sharma A, Das S, Sur S, Tiwari J, Chaturvedi K, Agarwal N, Malik S, Rani S, Kumar V. 2021. Photoperiodically driven transcriptome-wide changes in the hypothalamus reveal transcriptional differences between physiologically contrasting

seasonal life-history states in migratory songbirds. Sci Rep 11:12823.
Stager M, Pollock HS, Benham PM, Sly ND, Brawn JD, Cheviron ZA. 2016. Disentangling environmental drivers of metabolic flexibility in birds: the importance of temperature extremes versus temperature variability. Ecography 39:787–95.
Stager M, Senner NR, Swanson DL, Carling MD, Eddy DK, Greives TJ, Cheviron ZA. 2021. Temperature heterogeneity correlates with intraspecific variation in physiological flexibility in a small endotherm. Nat Commun 12:4401.
Stager M, Swanson DL, Cheviron ZA. 2015. Regulatory mechanisms of metabolic flexibility in the dark-eyed junco (*Junco hyemalis*). J Exp Biol 218:767–77.
Stager M. 2024. The genetic architecture underlying avian flexibility in a complex physiological trait. Society for integrative and comparative biology annual meeting. Seattle, WA, USA. Jan 2–6 2024.
Sullivan BL, Wood CL, Iliff MJ, Bonney RE, Fink D, Kelling S. 2009. eBird: A citizen-based bird observation network in the biological sciences. Biol Conserv 142:2282–92.
Swanson D, Zhang Y, King M. 2014. Mechanistic drivers of flexibility in summit metabolic rates of small birds. PLoS One 9:e101577.
Swanson DL, Liknes ET. 2006. A comparative analysis of thermogenic capacity and cold tolerance in small birds. J Exp Biol 209:466–74.
Taff CC, Shipley JR. 2023. Inconsistent shifts in warming and temperature variability are linked to reduced avian fitness. Nat Commun 14:7400.
Turbek SP, Bossu C, Rayne C, Gruppi C, Kus BE, Whitfield M, Smith TB, Paxton EH, Bay RA, Ruegg KC. 2023. Historical DNA reveals climate adaptation in an endangered songbird. Nat Clim Chang 13:735–41.
Uehling JJ, Taff CC, Houtz JL, Pipkin M, Becker P, Injaian A, Winkler D, Gabrielson RM, Vitousek M. 2024. Experimental glucocorticoid elevation alters activity and dietary choices in a wild songbird. Integr Comp Biol 64. https://doi.org/10.1093/icb/icae110.
Watts BD, Smith FM, Hines C, Duval L, Hamilton DJ, Keyes T, Paquet J, Pirie-Dominix L, Rausch J, Truitt B et al. 2021. Whimbrel populations differ in trans-atlantic pathways and cyclone encounters. Sci Rep 11:12919.
Welch KC, Péronnet F, Hatch KA, Voigt CC, Mccue MD. 2016. Carbon stable-isotope tracking in breath for comparative studies of fuel use. Ann NY Acad Sci 1365:15–32.
Whiteman JP, Sharp ZD, Gerson AR, Newsome SD. 2019. Relating Δ17O values of animal body water to exogenous water inputs and metabolism. Bioscience 69:658–68.
Williamson JL, Gyllenhaal EF, Bauernfeind SM, Bautista E, Baumann MJ, Gadek CR, Marra PP, Ricote N, Valqui T, Bozinovic F et al. 2024. Extreme elevational migration spurred cryptic speciation in giant hummingbirds. Proc Natl Acad Sci USA 121:e2313599121.
Williamson JL, Witt CC. 2021. A lightweight backpack harness for tracking hummingbirds. J Avian Biol 52:e02802.
Wolf BO, Mckechnie AE, Schmitt CJ, Czenze ZJ, Johnson AB, Witt CC. 2020. Extreme and variable torpor among high-elevation Andean hummingbird species. Biol Lett 16:20200428.
Young K, Dick MF, Ivy C, Guglielmo C. 2024. Do n-3 polyunsaturated fatty acids reduce energy costs in western sandpipers (*Calidris mauri*)? Society for integrative and comparative biology annual meeting. Seattle, WA, USA. Jan 2–6 2024.
Zhang Y, Eyster K, Liu J-S, Swanson DL. 2015. Cross-training in birds: cold and exercise training produce similar changes in maximal metabolic output, muscle masses and myostatin expression in House Sparrows (*Passer domesticus*). J Exp Biol 218:2190–200.
Zimmer C, Taff CC, Ardia DR, Rose AP, Aborn DA, Johnson LS, Vitousek MN. 2020. Environmental unpredictability shapes glucocorticoid regulation across populations of tree swallows. Sci Rep 10:13682.
Zuluaga JD, Danner RM. 2023. Novel approaches for assessing acclimatization in birds reveal seasonal changes in peripheral heat exchange and thermoregulatory behaviors. J Exp Biol 226:jeb245772.