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Published in:
Frontiers in Ecology and Evolution

DOI:
10.3389/fevo.2022.1034659

2022

Citation for published version (APA):
Swanson, D. L., Vezina, F., McKechnie, A., & Nord, A. (2022). Editorial: Avian behavioral and physiological responses to challenging thermal environments and extreme weather events. *Frontiers in Ecology and Evolution*, *10*, 4-7. Artikel 1034659. https://doi.org/10.3389/fevo.2022.1034659

Total number of authors:
4

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frontiers | Frontiers in Ecology and Evolution

TYPE Editorial
PUBLISHED 16 September 2022
DOI 10.3389/fevo.2022.1034659

Editorial: Avian behavioral and physiological responses to challenging thermal environments and extreme weather events

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SPECIALTY SECTION
This article was submitted to Ecophysiology, a section of the journal Frontiers in Ecology and Evolution

RECEIVED 01 September 2022
ACCEPTED 06 September 2022
PUBLISHED 16 September 2022

CITATION
Swanson DL, Vézina F, McKechnie AE and Nord A (2022) Editorial: Avian behavioral and physiological responses to challenging thermal environments and extreme weather events. *Front. Ecol. Evol.* 10:1034659. doi: 10.3389/fevo.2022.1034659

KEYWORDS

thermoregulation, phenotypic flexibility, evaporative cooling, cold tolerance, heat tolerance, birds

Editorial on the Research Topic
Avian behavioral and physiological responses to challenging thermal environments and extreme weather events

Introduction

Birds occupy habitats ranging from Antarctic ice shelfs to tropical deserts and lowland rainforests, so are exposed to the full range of climates on Earth (Dawson and O'Connor, 1996). Cold, hot or spatially and temporally variable thermal conditions can present significant thermoregulatory challenges to birds, which typically must maintain body temperatures (T_b) within narrow physiological limits (McKechnie, 2022). Such challenges may occur throughout the year (Parr et al., 2019) and in all life stages (DuRant et al., 2012; Nord and Giroud, 2020), so adjustments to these conditions are required to maintain fitness and, ultimately, stable populations. Here, we broadly define a challenging thermal environment as one requiring physiological acclimation or behavioral adjustments that modify rates of thermogenesis or heat loss to maintain long-term ecological function.

Avian abilities to respond physiologically to extreme temperatures are defined by capacities for heat production or dissipation (Swanson, 2010; McKechnie et al., 2021a). Behavioral responses to environmental temperature reduce the magnitude of physiological adjustments, although potentially with opportunity costs (Cunningham et al., 2021). It is this combination of behavioral and physiological responses at multiple levels of organization that determines the survival probability of birds in thermally challenging situations (e.g., Albright et al., 2017; Petit et al., 2017). Moreover, thermal conditions experienced during reproduction can affect parental investment and nestling development, with potentially long-term consequences (Nord and Giroud, 2020; van de Ven et al., 2020; Broggi et al., 2022). Our knowledge of response mechanisms, their time courses, and their impacts on fitness, however, remains incomplete. Behavioral and physiological responses of birds to extreme and/or seasonally variable climates have been a research focus for decades (Chaffee and Roberts, 1971; Dawson et al., 1983), but recent methodological and analytical advances for studies of physiology and behavior have produced novel findings regarding patterns and mechanisms of avian adjustments to challenging thermal environments (e.g., McCafferty et al., 2015; Cheviron and Swanson, 2017; McKechnie et al., 2021a).

Avian responses to heat and aridity

Physiological and behavioral responses permit the maintenance of sublethal T_b under hot conditions, but water is required for evaporative cooling, so interactions between temperature and water availability are important considerations for thermoregulation in the heat (Conradie et al., 2020). Large birds have greater thermal inertia and lower surface area to volume ratios than small species, so body mass may impact the magnitude of heat tolerance responses (McKechnie et al., 2021a), but this has been little studied. Czenze et al. found that heat tolerance, maximum T_b, and evaporative cooling capacities in three larger-bodied South African non-passerines approximated those in other non-passerines and exceeded capacities in passerines (McKechnie et al., 2021a). Sabat et al. tested a new method to estimate metabolic and pre-formed water contributions to the body water pool and detected isotopic differences under cold temperatures and between species using freshwater and saltwater resources, thereby validating the method for future studies of water balance. Navarette et al. experimentally manipulated water availability in rufous-collared sparrows (*Zonotrichia capensis*) and identified trade-offs involving water restriction-induced increases in basal metabolic rate (BMR) and erythrocyte oxidative enzyme activities at the expense of skeletal muscle oxidative damage. Sharpe et al. documented reduced foraging and increased use of thermally buffered microhabitats by Jacky Winters (*Microeca fascinans*) during hot weather; nevertheless, 29% of the study population died when air temperature reached 49°C, demonstrating limits to physiological and behavioral capacities for responding to extreme heat events.

Avian responses to heat during reproduction

The heat dissipation limits hypothesis (HDLH) posits that the capacity to dissipate heat loads acquired during sustained activities, such as breeding, limits performance and may negatively affect reproductive output and fitness (Speakman and Król, 2010). Several studies of free-living birds support the HDLH, even in comparatively cool habitats (Andreasson et al., 2020). Zagkle et al. found support for the HDLH by manipulating heat loss while increasing foraging costs in zebra finches (*Taeniopygia guttata*), documenting negative effects on reproduction under warm temperatures that were buffered by experimentally increased heat loss. Increasing temperatures over an 11-year study period were strongly negatively correlated with reproductive output in southern yellow-billed hornbills (*Tockus leucomelas*) (Pattinson et al.), suggesting that, if current warming trends continue, reproductive capacity will be sufficiently compromised to result in imminent nesting failure for this population. Pipoly et al. demonstrated that negative effects of high temperatures on nestling growth and survival were stronger in forest than urban populations of great tits (*Parus major*), suggesting that urban nestlings are less vulnerable to heat. Udino and Mariette experimentally documented that parental heat calls during the late *in ovo* period resulted in panting at lower temperatures, reduced panting at high temperatures, and higher activity at warm temperatures when the offspring had reached adulthood, highlighting the priming effects of early life conditions on later thermoregulatory patterns.

Avian responses to cold

Metabolic flexibility allows birds to match metabolic rates to environmental conditions (Swanson, 2010). Underlying mechanisms of metabolic flexibility include adjustments in muscle size (Swanson and Vézina, 2015; Swanson et al., 2022) and cellular aerobic and fat catabolism capacities (Swanson, 2010), but the contribution of other metabolic pathways to this flexibility is poorly known (Stager et al., 2015; Cheviron and Swanson, 2017). Wone and Swanson used integrated metabolomics/transcriptomics analyses to document seasonal changes in amino acid, lipid- and cellular metabolism pathways in two passerine birds and identified a potential role for nicotinamide-adenine-nucleotide derivatives in regulating cellular metabolism. In addition to heat production mechanisms, energy conservation strategies, including torpor

(Ruf and Geiser, 2015; Geiser, 2021) and ventilatory/respiratory adjustments (Arens and Cooper, 2005), can contribute to avian cold tolerance. Bech and Mariussen detected winter increases in BMR and the respiratory frequency/tidal volume ratio in great tits, allowing energy savings by reducing respiratory energetic costs and evaporative water losses. Aharon-Rotman et al. showed that winter-acclimatized eastern yellow robins (*Eopsaltria australis*) regularly entered torpor, expanding documentation of torpor use in the comparatively poorly studied passerine taxon.

Conclusions

As demonstrated by the studies in this Research Topic, behavioral and physiological flexibility can buffer temperature impacts on birds. In addition to changes in average temperatures, however, global change is predicted to increase climate variability, with more frequent extreme events for many locations (Jentsch et al., 2007; Wallace et al., 2014; Cohen et al., 2018). Increasing extreme summer maximum temperatures and more variable winter temperatures can have negative consequences for birds, including mass mortality events (McKechnie and Wolf, 2010; McKechnie et al., 2021b), phenotype-environment mismatches (Boyles et al., 2011; Jimenez et al., 2020; Vézina et al., 2020; Ruuskanen et al., 2021), reduced reproductive capacities (Carroll et al., 2018; Nord and Nilsson, 2019; van de Ven et al., 2020), and altered offspring physiology and behavior (Mariette and Buchanan, 2016; Mariette, 2020). Future research incorporating not only behavior and physiology, but also flexibility in these traits and their thermal reaction norms, into population and distribution models will be critical to understand impacts of climate change on avian biodiversity.

Author contributions

All authors listed have made a substantial, direct, and intellectual contribution to the work and approved it for publication.

Funding

This work was supported by the U.S. National Science Foundation (IOS 1021218 to DS) and the National Research Foundation of South Africa (Grant 119754 to AM). FV was supported by a Discovery grant from the Natural Sciences and Engineering Research Council of Canada (Number 2020-05628). AN was supported by the Swedish Research Council (Grant 2020-04686).

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

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