



OPEN ACCESS

EDITED AND REVIEWED BY
Jonathon H. Stillman,
San Francisco State University,
United States

*CORRESPONDENCE

Lin Zhang
lzhangss@msn.com
Buddhi Dayananda
b.dayananda@uq.edu.au
Ji-Gang Xia
jigangxia@163.com
Bao-Jun Sun
sunbaojun@ioz.ac.cn

SPECIALTY SECTION

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

RECEIVED 18 May 2022

ACCEPTED 30 June 2022

PUBLISHED 08 August 2022

CITATION

Zhang L, Dayananda B, Xia J-G and
Sun B-J (2022) Editorial:
Ecophysiological analysis of
vulnerability to climate warming in
ectotherms.
Front. Ecol. Evol. 10:946836.
doi: 10.3389/fevo.2022.946836

COPYRIGHT

© 2022 Zhang, Dayananda, Xia and
Sun. This is an open-access article
distributed under the terms of the
[Creative Commons Attribution License
\(CC BY\)](https://creativecommons.org/licenses/by/4.0/). The use, distribution or
reproduction in other forums is
permitted, provided the original
author(s) and the copyright owner(s)
are credited and that the original
publication in this journal is cited, in
accordance with accepted academic
practice. No use, distribution or
reproduction is permitted which does
not comply with these terms.

Editorial: Ecophysiological analysis of vulnerability to climate warming in ectotherms

Lin Zhang^{1*}, Buddhi Dayananda^{2*}, Ji-Gang Xia^{3*} and
Bao-Jun Sun^{4*}

¹School of Basic Medical Sciences, Hubei University of Chinese Medicine, Wuhan, China, ²School of Agriculture and Food Sciences, The University of Queensland, Brisbane, QLD, Australia, ³Laboratory of Evolutionary Physiology and Behavior, Chongqing Key Laboratory of Animal Biology, College of Life Sciences, Chongqing Normal University, Chongqing, China, ⁴Key Laboratory of Animal Ecology and Conservation Biology, Institute of Zoology, Chinese Academy of Sciences, Beijing, China

KEYWORDS

climate warming, physiological responses, adaptive evolution, life history, thermal physiology, thermal ecology

Editorial on the Research Topic

Ecophysiological analysis of vulnerability to climate warming in ectotherms

Identifying the species most vulnerable to extinction due to climate warming is the first step in their conservation and mitigating the impacts of climate change (Riddell et al., 2021; Song et al., 2021). However, organismal vulnerability to climate warming depends on the sensitivity of the organism to environmental changes, its exposure to those changes, its ability to recover from them, and its potential to adapt to the changes (Huey et al., 2012; van Heerwaarden and Sgro, 2021). The complexity of organismal response to temperature change makes predicting the effects of climate warming a great challenge for ecologists. Developing a deeper knowledge of the vulnerability of ectotherms to climate warming enhances our understanding of extinction processes, thereby aiding conservation efforts through the implementation of better policies and management strategies to prevent the extinction of remaining populations (Dayananda et al., 2016). The main objective of this interdisciplinary Research Topic is to collate research on how ectotherms respond to climate warming at various levels. This topic comprises investigations conducted at multiple research scales from meta-analyses to molecular determination, and focuses on insects, amphibians, and reptiles, combining some novel ecophysiological evidence with the considerations for evaluating the vulnerabilities of ectotherms to climate change.

Changes in environmental temperature can alter the body temperature of ectotherms and thus their physiological performance (Huey et al., 2012; Seebacher et al., 2015). Ectotherms have been found to shift their geographic range to higher latitudes or altitudes in response to climate change (Jacobsen, 2020). Body temperatures above the thermal optimum create physiological

stress, reduced performance, and increased disease susceptibility, ultimately leading to population declines and extinction (Buckley et al., 2021).

The magnitude of the effects of climate warming on ectotherms depends on their physiological and/or behavioral plasticity (Paaijmans et al., 2013; Dayananda et al., 2016) as well as their evolutionary adaptations, which enhance the fitness of an organism and whose current beneficial characteristics reflect the selective advantage of the trait at the time of its origin (Hochachka and Somero, 2002). Most ectotherms can precisely control their body temperature *via* behavioral and postural adjustments; thus, plasticity is a significant factor in ectotherms' response to fluctuating environmental conditions (Huey et al., 2003). Phenotypic plasticity can occur faster than evolutionary genetic changes in ectotherms and is therefore likely to directly influence their responses to climate change (Chevin et al., 2010). However, if plasticity is inadequate in response to climate warming, or if the adaptive change is too slow, ectotherms face a greater risk of extinction (Lafuente and Beldade, 2019; Logan and Cox, 2020). Furthermore, species with a low capacity for plasticity are expected to be vulnerable to climate warming (Rohr et al., 2018; Norin and Metcalfe, 2019), particularly tropical ectotherms (Morley et al., 2019) which already live close to their physiological thermal optima (Deutsch et al., 2008).

The effects of increasing temperature on ectotherms occur on multiple dimensions, across life-history stages, and temporal and spatial scales (Dayananda et al., 2016). Incubation temperature strongly influences the development of ectotherms with important consequences for hatchling fitness (Noble et al., 2018). In oviparous species, the thermal environment for embryonic development depends on the location and depth of the nest, however, in viviparous species, the thermal environment for embryonic development depends on the mother's body temperature (Zhang et al., 2018). Incubation experiments suggest that incubation temperature affects the incubation length, embryo survival, size, shape, behavior, sex, and performance of hatchlings (Angilletta, 2009). Thus, assessing the oviparous embryonic responses to ongoing climate warming and understanding their effects will provide crucial information that can aid in their conservation (Mitchell et al., 2016; Sun et al., 2021).

The oviparous incubation process was interactively modulated by the warming and precipitation. For example, high soil temperature and low soil moisture had a significant negative effect on egg development, survival, and egg hatching of three dominant grasshopper species (*Dasyhippus barbipes*, *Oedaleus asiaticus*, and *Chorthippus fallax*) in the Inner Mongolian grasslands (Wu et al.).

Ectotherms are sensitive to seasonal variations in environmental temperature (Taylor et al., 2020; Liu et al., 2022). In particular, tropical ectotherms already live in temperatures close to their optimum physiological levels

(Deutsch et al., 2008). Body temperatures higher than the optimum create physiological stress, reduce performance, and increase disease susceptibility, ultimately leading to population declines and extinction (Huey et al., 2010; Sinervo et al., 2010). For instance, reptiles in Sri Lanka are highly vulnerable to extinction due to the severity of anthropogenic disturbances, however, no research has been conducted thus far to assess how they are affected by climate warming (Dayananda et al.). Furthermore, climate change could have strong potential effects on amphibians in China. A recent analysis found that 54 species are moderately vulnerable, including *Echinotriton chinhaiensis* and *Hynobius chinensis*, and 14 species are highly vulnerable, including *Ichthyophis kohtaoensis* and *Zhangixalus prasinatus* (Zhao et al.).

Climate warming has increased the frequency, duration, and intensity of heat waves during summer, causing greater impacts on species than increased average temperatures (Breitenbach et al., 2020). The physiological and biochemical responses of ectotherms to heat waves remain poorly understood. However, a recent study on the oxidant physiology of ectotherms after exposure to a simulated heat wave found heat waves did not lead to oxidative damage in ectotherms with low metabolic rates. For example, *Mauremys mutica* (Li et al.) and *Nanorana pleskei* (He et al.) did not suffer any oxidative damage after exposure to heat waves. However, the physiological responses to heat waves differed between the two species.

Lizards from medium and high latitudes could respond to thermal variation through multiple levels of metabolic acclimation, whereas their congeners from low latitudes lacked any level of modification and are thus more vulnerable to global warming (Sun et al., 2022). Embryonic and hatchling development can be improved by moderate warming in *Lacerta agilis* from the low-latitude margin population of a high-altitude species (Cui et al.), and moderate warming benefits hatchling fitness in the cold-climate lizard, *Takydromus amurensis* (Liu et al., 2022). In tropical regions, species with limited dispersal abilities, small geographic ranges, and restrictions to high altitudes are particularly vulnerable to extinction (Huey et al., 2012). However, the thermal biology traits of a tropical lizard (*Takydromus kuehnei*) are not severely threatened by ongoing climate change, highlighting the importance of thermal biology traits in evaluating the vulnerability of a species to climate change (Tao et al.). Furthermore, a study on Asiatic toads (*Bufo gargarizans*) from two altitudinal zones found that low-altitude toads might enhance their hypothermic reaction if they shift their ranges to higher altitudes to survive the warming climate (Yao et al.). Two low-altitude lizards (the oviparous *Phrynocephalus axillaris* and the viviparous *P. forsythii*) may live at high altitudes by reducing behavioral activity and increasing energy efficiency (Qi et al.). Taken together, more studies are required to understand how the species with limited dispersal abilities, small geographic ranges, and restriction to

high altitudes shift their phenotypic plasticity to adapt to climate warming.

In the future, investigations of species' vulnerability to climate warming are likely to benefit from measurements of environmental conditions, taken at the scale experienced by the organisms (Williams et al., 2008). Moreover, a comparison of intra- and inter- species vulnerability provides a variety of adaptive strategies for global warming (Huey et al., 2009). However, predicting the effects of climate warming on species is extraordinarily difficult owing to the complex nature of ecosystems; thus, this remains a major challenge for ecologists.

Author contributions

LZ wrote the first draft. BD and B-JS edited the manuscript. J-GX advised the other authors. All authors reviewed and approved the manuscript.

Funding

LZ was supported by the National Natural Science Foundation of China (31800337) and Research Start-up Fund of Hubei University of Chinese Medicine. B-JS was supported by the National Natural Science Foundation of China (31870391) and Youth Innovation Promotion Association CAS (No. 2019085).

References

- Angilletta, M. J. (2009). *Thermal Adaptation: A Theoretical and Empirical Synthesis*. Oxford: Oxford University Press.
- Breitenbach, A. T., Carter, A. W., Paitz, R. T., and Bowden, R. M. (2020). Using naturalistic incubation temperatures to demonstrate how variation in the timing and continuity of heat wave exposure influences phenotype. *Proc. R. Soc. B Biol. Sci.* 287, 20200992. doi: 10.1098/rspb.2020.0992
- Buckley, L. B., Schoville, S. D., and Williams, C. M. (2021). Shifts in the relative fitness contributions of fecundity and survival in variable and changing environments. *J. Exp. Biol.* 224, jeb228031. doi: 10.1242/jeb.228031
- Chevin, L.-M., Lande, R., and Mace, G. M. (2010). Adaptation, plasticity, and extinction in a changing environment: towards a predictive theory. *PLoS Biol.* 8, e100357. doi: 10.1371/journal.pbio.1000357
- Dayananda, B., Gray, S., Pike, D., and Webb, J. K. (2016). Communal nesting under climate change: fitness consequences of higher nest temperatures for a nocturnal lizard. *Glob. Chang. Biol.* 22, 2405–2414. doi: 10.1111/gcb.13231
- Deutsch, C. A., Tewksbury, J. J., Huey, R. B., Sheldon, K. S., Ghalambor, C. K., Haak, D. C., et al. (2008). Impacts of climate warming on terrestrial ectotherms across latitude. *Proc. Natl. Acad. Sci. U.S.A.* 105, 6668–6672. doi: 10.1073/pnas.0709472105
- Hochachka, P. W., and Somero, G. N. (2002). *Biochemical Adaptation: Mechanism and Process in Physiological Evolution*. Oxford: Oxford University Press.
- Huey, R. B., Deutsch, C. A., Tewksbury, J. J., Vitt, L. J., Hertz, P. E., Álvarez Pérez, H. J., et al. (2009). Why tropical forest lizards are vulnerable to climate warming. *Proc. R. Soc. B Biol. Sci.* 276, 1939–1948. doi: 10.1098/rspb.2008.1957
- Huey, R. B., Hertz, P. E., and Sinervo, B. (2003). Behavioral drive versus behavioral inertia in evolution: a null model approach. *Am. Nat.* 161, 357–366. doi: 10.1086/346135
- Huey, R. B., Kearney, M. R., Krockenberger, A., Holtum, J. A. M., Jess, M., and Williams, S. E. (2012). Predicting organismal vulnerability to climate warming: roles of behaviour, physiology and adaptation. *Philos. Trans. R. Soc. B Biol. Sci.* 367, 1665–1679. doi: 10.1098/rstb.2012.0005
- Huey, R. B., Losos, J. B., and Moritz, C. (2010). Are lizards toast? *Science* 328, 832–833. doi: 10.1126/science.1190374
- Jacobsen, D. (2020). The dilemma of altitudinal shifts: caught between high temperature and low oxygen. *Front. Ecol. Environ.* 18, 211–218. doi: 10.1002/fee.2161
- Lafuente, E., and Beldade, P. (2019). Genomics of developmental plasticity in animals. *Front. Genet.* 10, 720. doi: 10.3389/fgene.2019.00720
- Liu, W.-L., Liu, P., Cui, L.-X., Meng, Y., Tao, S.-A., Han, X. Z., et al. (2022). Moderate climate warming scenarios during embryonic and post-embryonic stages benefit a cold-climate lizard. *Funct. Ecol.* 36, 1137–1130. doi: 10.1111/1365-2435.14032
- Logan, M. L., and Cox, C. L. (2020). Genetic constraints, transcriptome plasticity, and the evolutionary response to climate change. *Front. Genet.* 11, 538226. doi: 10.3389/fgene.2020.538226
- Mitchell, N. J., Rodriguez, N., Kuchling, G., Arnall, S. G., and Kearney, M. R. (2016). Reptile embryos and climate change: modelling limits of viability to inform translocation decisions. *Biol. Conserv.* 204, 134–147. doi: 10.1016/j.biocon.2016.04.004

Acknowledgments

We are very grateful to all the contributing authors for sharing with us their research findings to make this issue a great success. We thank all the referees, acknowledged on the first page of each article, for providing constructive and thoughtful comments on manuscript drafts. We also thank the Frontiers in Ecology and Evolution editorial and support teams for their patience and advice. We would like to thank Editage (www.editage.cn) for English language editing.

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

All claims expressed in this article are solely those of the authors and do not necessarily represent those of their affiliated organizations, or those of the publisher, the editors and the reviewers. Any product that may be evaluated in this article, or claim that may be made by its manufacturer, is not guaranteed or endorsed by the publisher.

- Morley, S. A., Peck, L. S., Sunday, J. M., Heiser, S., and Bates, A. E. (2019). Physiological acclimation and persistence of ectothermic species under extreme heat events. *Glob. Ecol. Biogeogr.* 28, 1018–1037. doi: 10.1111/geb.12911
- Noble, D. W. A., Stenhouse, V., and Schwanz, L. E. (2018). Developmental temperatures and phenotypic plasticity in reptiles: a systematic review and meta-analysis. *Biol. Rev.* 93, 72–97. doi: 10.1111/brv.12333
- Norin, T., and Metcalfe, N. B. (2019). Ecological and evolutionary consequences of metabolic rate plasticity in response to environmental change. *Philos. Trans. R. Soc. B Biol. Sci.* 374: 20180180. doi: 10.1098/rstb.2018.0180
- Paaïmans, K. P., Heinig, R. L., Seliga, R. A., Blanford, J. I., Blanford, S., Murdock, C. C., et al. (2013). Temperature variation makes ectotherms more sensitive to climate change. *Glob. Chang Biol.* 19, 2373–2380. doi: 10.1111/gcb.12240
- Riddell, E. A., Iknayan, K. J., Hargrove, L., Tremor, S., Patton, J. L., Ramirez, R., et al. (2021). Exposure to climate change drives stability or collapse of desert mammal and bird communities. *Science* 371, 633–636. doi: 10.1126/science.abd4605
- Rohr, J. R., Civitello, D. J., Cohen, J. M., Roznik, E. A., Sinervo, B., and Dell, A. I. (2018). The complex drivers of thermal acclimation and breadth in ectotherms. *Ecol. Lett.* 21, 1425–1439. doi: 10.1111/ele.13107
- Seebacher, F., White, C. R., and Franklin, C. E. (2015). Physiological plasticity increases resilience of ectothermic animals to climate change. *Nat. Clim. Chang* 5, 61–66. doi: 10.1038/nclimate2457
- Sinervo, B., Méndez-de-la-Cruz, F., Miles, D. B., Heulin, B., Bastiaans, E., Villagrán-Santa Cruz, M., et al. (2010). Erosion of lizard diversity by climate change and altered thermal niches. *Science* 328, 894–899. doi: 10.1126/science.1184695
- Song, H., Kemp, D. B., Tian, L., Chu, D., Song, H., and Dai, X. (2021). Threshold of temperature change for mass extinctions. *Nat. Commun.* 12, 4694. doi: 10.1038/s41467-021-25019-2
- Sun, B.-J., Ma, L., Wang, Y., Mi, C.-R., Buckley, L. B., Levy, O., Lu, H.-L., and Du, W.-G. (2021). Latitudinal embryonic thermal tolerance and plasticity shape the vulnerability of oviparous species to climate change. *Ecol. Monogr.* 91, e01468. doi: 10.1002/ecm.1468
- Sun, B.-J., Williams, C. M., Li, T., Speakman, J. R., Jin, Z.-G., Lu, H.-L., et al. (2022). Higher metabolic plasticity in temperate compared to tropical lizards suggests increased resilience to climate change. *Ecol. Monogr.* 92, e1512. doi: 10.1002/ecm.1512
- Taylor, E. N., Diele-Viegas, L. M., Gangloff, E. J., Hall, J. M., Halpern, B., Massey, M. D., et al. (2020). The thermal ecology and physiology of reptiles and amphibians: a user's guide. *J. Exp. Zool. A Ecol. Integr. Physiol.* 335, 13–44. doi: 10.1002/jez.2396
- van Heerwaarden, B., and Sgro, C. M. (2021). Male fertility thermal limits predict vulnerability to climate warming. *Nat. Commun.* 12, 2214. doi: 10.1038/s41467-021-22546-w
- Williams, S. E., Shoo, L. P., Isaac, J. L., Hoffmann, A. A., and Langham, G. (2008). Towards an integrated framework for assessing the vulnerability of species to climate change. *PLoS Biol.* 6, e325. doi: 10.1371/journal.pbio.0060325
- Zhang, L., Guo, K., Zhang, G.-Z., Lin, L.-H., and Ji, X. (2018). Evolutionary transitions in body plan and reproductive mode alter maintenance metabolism in squamates. *BMC Evol. Biol.* 18, 45. doi: 10.1186/s12862-018-1166-5