Assessing the functional significance of metabolism and activity in niche diversification

Jonathan A. Green

School of Environmental Sciences, University of Liverpool, Liverpool, UK

Correspondence
Jonathan A. Green
Email: jonathan.green@liverpool.ac.uk

Since its conception over 100 years ago, the idea of the ecological niche remains a topic of enduring interest (Pocheville, 2015). The continued coexistence of multiple species and the myriad ways in which species adapt to, and survive, the environments in which they make their home continues to fascinate not only fully time ecologists, but those simply interested in the natural world. Among scientists, understanding a species or population’s niche brings together those interested in behaviour, ecology and physiology and in particular those who seek to link these disciplines together and understand the life-history consequences of physiological adaptation (Ricklefs & Wikelski, 2002). Such questions are particularly important in the context of environmental change and there is a critical lack of mechanistic understanding of the capacity that animals have to alter their behaviour, within the limits of their physiology and hence buffer against change (Urban et al., 2016). Indeed physiological ‘markers’ have recently been proposed as sensitive indicators of biodiversity challenges, in their role as links from environment to demography (Bergman et al., 2019).

In understanding an animal species’ niche, there is a temptation to generalise and understand patterns in behaviour and physiology based on simple traits such as body size (Brown et al., 2004) or broad-scale patterns in the environment (Boyles et al., 2013). However, if there were single and simple answers to how species exist in their local environment and in particular how species appear to coexist in the same environment, then as functional ecologists we would soon be out of a job. Instead, it is clear that the strategies by which animals are able to survive and reproduce and the niches they occupy are as diverse as the animal kingdom itself. This diversity is elegantly characterised in a recent study by Menzies et al. (2020) which defines the contrasting functional niches of two sympatric herbivorous mammal species (the snowshoe hare and the red squirrel) that allow them to survive and coexist in the extreme conditions of winter in the Canadian Yukon.

Winter temperatures at the study site ranged from 10 to −30°C, superimposed with short-term variation within and between days. Both study species are described appropriately by the authors as ‘too big to be small, and too small to be big’ (Lovegrove, 2000), thus must remain active above the snow throughout winter while remaining homeothermic, yet without the thermoregulatory advantages of large size. Menzies et al. (2020) used biologging tags to record physiological characteristics (body temperature, heart rate) and behaviour (activity levels) of both species in the same place at the same time. This allowed them to reveal differential responses to the same environmental challenge. While small in scale in comparison to differences between generalists and specialists or autotrophs and heterotrophs, the differences between the species were stark and sufficient to easily define two very different niches. The hares are nocturnal and worked hard to defend and maintain a constant body temperature at all times, via variation in heart rate, reflective of thermogenesis. They maintained constant, relatively high, levels of activity as they foraged continually during the night and crepuscular periods. They responded to supplemental food by reducing activity and to colder temperatures by increasing heart rate, again reflecting the role of thermogenesis. In contrast the squirrels remained primarily inactive in their insulated nests, particularly during cold periods and at night. Their body temperature was far more labile and varied in proportion to activity and heart rate. In warmer temperatures, the squirrels were more active and had higher body temperatures. They responded to food supplementation by reducing activity but increasing heart rate and temperature.

The differing niches that are described and the strategies that define them are both ultimately successful and highlight how studies that might be dismissed as descriptive, actually provide critical insights into evolution by clearly demonstrating divergent adaptation to
common problems. Next steps would be to ascertain precisely which of these strategies might provide better protection to these species in the face of environmental change. This goes beyond the biology of these two species, however, and it would be interesting to determine whether the species which favoured metabolic regulation of body temperature (the hare) fared more successfully than the one favouring behavioural regulation (the squirrel) and whether these findings are generalisable to other species and systems. Indeed looking across seasons there is some evidence that both metabolic and behavioural approaches may be balanced in some species (Dunn et al., 2020), again illustrating the diversity of solutions to nature’s challenges. This is particularly important for species facing limits to their metabolic rates and/or activity levels on either a seasonal or annual basis (Halsey et al., 2019).

Biologging approaches such as those used in this study are now an established mechanism by which to understand the behaviour and ecology of animals in their natural environments (Cooke et al., 2004). As such they are increasingly proposed as key tools for conservation management (Hays et al., 2019; McGowan et al., 2017), with the potential to define a species or population’s niche and hence provide the link from environment to demography (Bergman et al., 2019). Indeed researchers across taxa with extensive biologging datasets might continue to examine or re-examine how, when and why homeotherms defend body temperature or allow it to vary (Butler & Woakes, 2001). The work of Menzies et al. (2020) promotes the use of such physiological, alongside behavioural, data streams in defining the functional niche, in order to better understand adaptation and coexistence. This further supports the idea that the drivers of species distributions and coexistence are unique, complex and multi-dimensional. As ecologists and policy-makers know, further exploration of this niche diversity will continue to reap rewards.

ORCID
Jonathan A. Green https://orcid.org/0000-0001-8692-0163

TWITTER
Jonathan A. Green @jan_seabirds

REFERENCES
Bergman, J. N., Bennett, J. R., Binley, A. D., Cooke, S. J., Fryson, V., Hlina, B. L., Reid, C. H., Vala, M. A., & Madliger, C. L. (2019). Scaling from individual physiological measures to population-level demographic change: Case studies and future directions for conservation management. *Biological Conservation*, 238, 108242. https://doi.org/10.1016/j.biocon.2019.108242

Boyles, J. G., Thompson, A. B., McKechnie, A. E., Malan, E., Humphries, M. M., & Careau, V. (2013). A global heterothermic continuum in mammals. *Global Ecology and Biogeography*, 22, 1029–1039. https://doi.org/10.1111/geb.12077

Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M., & West, G. B. (2004). Toward a metabolic theory of ecology. *Ecology*, 85, 1771–1789. https://doi.org/10.1890/03-9000

Butler, P. J., & Woakes, A. J. (2001). Seasonal hypothermia in a large migrating bird: Saving energy for fat deposition? *Journal of Experimental Biology*, 204, 1361–1367.

Cooke, S. J., Hinch, S. G., Wikelski, M., Andrews, R. D., Kuchel, L. J., Wolcott, T. G., & Butler, P. J. (2004). Biotelemetry: A mechanistic approach to ecology. *Trends in Ecology & Evolution*, 19, 334–343. https://doi.org/10.1016/j.tree.2004.04.003

Dunn, R. E., Wanless, S., Daunt, F., Harris, M. P., & Green, J. A. (2020). A year in the life of a North Atlantic seabird: Behavioural and energetic adjustments during the annual cycle. *Scientific Reports*, 10, 5993. https://doi.org/10.1038/s41598-020-62842-x

Halsey, L. G., Green, J. A., Twiss, S. D., Arnold, W., Burthe, S., Butler, P. J., Cooke, S. J., Grémillet, D., Ruf, T., Hicks, O., Minta, K. J., Prystay, T. S., Wascher, C. A. F., & Careau, V. (2019). Flexibility, variability and constraint in energy management patterns across vertebrate taxa revealed by long-term heart rate measurements. *Functional Ecology*, 33, 260–272. https://doi.org/10.1111/1365-2435.13264

Hays, G. C., Bailey, H., Bograd, S. J., Bowen, W. D., Campagna, C., Carmichael, R. H., Casale, P., Chiaradia, A., Costa, D. A., Cuevas, E., Nico de Bruyn, P. J., Dias, M. P., Duarte, C. M., Dunn, D. C., Dutton, P. H., Esteban, N., Friedlaender, A., Goetz, K. T., Godley, B. J., Sequeira, A. M. M. (2019). Translating marine animal tracking data into conservation policy and management. *Trends in Ecology & Evolution*, 34, 459–473. https://doi.org/10.1016/j.tree.2019.01.009

Lovegrove, B. (2000). The zoogeography of mammalian basal metabolic rate. *The American Naturalist*, 156, 201–219. https://doi.org/10.1086/303383

McGowan, J., Beger, M., Lewison, R. L., Harcourt, R., Campbell, H., Priest, M., Dwyer, R. G., Lin, H.-Y., Lentini, P., Dudgeon, C., McMahon, C., Watts, M., & Possingham, H. P. (2017). Integrating research using animal-borne telemetry with the needs of conservation management. *Journal of Applied Ecology*, 54, 423–429. https://doi.org/10.1111/1365-2664.12755

Menzies, A. K., Studd, E. K., Majchrzak, Y. N., Peers, M. J. L., Boutin, S., Danzter, B., Lane, J. E., McAdam, A. G., & Humphries, M. M. (2020). Body temperature, heart rate, and activity patterns of two boreal homeotherms in winter: Homeostasis, allostasis, and ecological coexistence. *Functional Ecology*, 34, 2292–2301. https://doi.org/10.1111/1365-2435.13640

Pocheville, A. (2015). The ecological niche: History and recent controversies. In T. Heams, P. Huneman, G. Lecointre, & M. Silberstein (Eds.), *Handbook of evolutionary thinking in the sciences* (pp. 547–586). Springer.

Ricklefs, R. E., & Wikelski, M. (2002). The physiology/life-history nexus. *Trends in Ecology & Evolution*, 17, 462–468. https://doi.org/10.1016/S0169-5347(02)02578-8

Urban, M. C., Bocedi, G., Hendry, A. P., Mihoub, J.-B., Peer, G., Singer, A., Bridle, J. R., Crozier, L. G., De Meester, L., Godsoe, W., Gonzalez, A., Hellmann, J. J., Holt, R. D., Huth, A., Johst, K., Krug, C. B., Leadley, P. W., Palmer, S. C. F., Pantel, J. H., … Travis, J. M. J. (2016). Improving the forecast for biodiversity under climate change. *Science*, 353, 8466. https://doi.org/10.1126/science.aad8466