

Introduction. Adaptation to the annual cycle

Most large organisms have an annual routine; that is to say they schedule activities in a regular way over the year. Like any behaviour, annual routines can be explained in terms of either their causation or their contribution to reproductive success, that is their evolutionary function. Previous work on causal mechanisms has sometimes ignored the broader ecological context. Previous theoretical accounts of function have often ignored the physiological state of the animal. An aim of this issue is to highlight work that combines these approaches and to encourage further such work.

Life-history tradeoffs are central to functional accounts of behaviour. Several contributions to this volume draw attention to the physiological basis of various tradeoffs (e.g. Barta *et al.* 2008; Martin *et al.* 2008; McNamara & Houston 2008; Speakman 2008; Verhulst & Nilsson 2008). We believe that incorporating this basis will lead to a new generation of analysis that will provide a deeper understanding of life histories and suggest new lines of physiological research.

One major issue concerns the mechanisms (particularly hormonal) by which animals respond to seasonal environments (Ball & Ketterson 2008; Hahn & MacDougall-Shackleton 2008; Martin *et al.* 2008). In a seasonal environment, it is important for animals to control the timing of activities. Mechanisms for this are discussed by Paul *et al.* (2008) and Wikelski *et al.* (2008).

Seasonal environments may differ in their predictability and hence in the cues to which animals should respond. Individuals can also be expected to respond to their physiological condition. Cues and associated plasticity are central to most of the papers in this issue and are the main focus of Barta *et al.* (2008), Shine & Brown (2008) and Verhulst & Nilsson (2008).

Breeding is a crucial part of an annual cycle and is considered by all papers but is the particular concern of Shine & Brown (2008; year-to-year variation and cues), Ball & Ketterson (2008; sex differences), Verhulst & Nilsson (2008; timing) and Speakman (2008; costs).

Migration is a significant annual event for many species. It is discussed by Buehler & Piersma (2008; bottlenecks in the annual cycle of knots), Barta *et al.* (2008; optimal moult, migration and breeding) and Hedenström (2008; models based on minimizing time or energy on a migratory journey). Models are also at the heart of Wingfield (2008; life-history stages and annual routines) and McNamara & Houston (2008; incorporating physiology and behaviour in a common adaptive framework). The latter approach is illustrated by Barta *et al.* (2008).

By combining theoretical accounts of tradeoffs with physiological research across issues such as breeding, migration and seasonal responses, this collection offers a unique blend of perspectives on how to provide holistic accounts of adaptation to the annual cycle. The papers in this issue should encourage an approach that integrates physiology, individual behaviour and ecology. We believe that this is necessary rather than considering each in isolation.

John M. McNamara^{1,*}
Alasdair I. Houston²

June 2007

¹*Department of Mathematics, University of Bristol, Bristol BS8 1TW, UK*

(john.mcnamara@bristol.ac.uk)

²*School of Biological Sciences, University of Bristol, Bristol BS8 1UG, UK*

REFERENCES

- Barta, Z., McNamara, J. M., Houston, A. I., Weber, T. P., Hedenström, A. & Feró, O. 2008 Optimal moult strategies in migratory birds. *Phil. Trans. R. Soc. B* **363**, 211–229. (doi:10.1098/rstb.2007.2136)
- Ball, G. F. & Ketterson, E. D. 2008 Sex differences in the response to environmental cues regulating seasonal reproduction in birds. *Phil. Trans. R. Soc. B* **363**, 231–246. (doi:10.1098/rstb.2007.2137)
- Buehler, D. M. & Piersma, T. 2008 Travelling on a budget: predictions and ecological evidence for bottlenecks in the annual cycle of long-distance migrants. *Phil. Trans. R. Soc. B* **363**, 247–266. (doi:10.1098/rstb.2007.2138)
- Hahn, T. P. & MacDougall-Shackleton, S. A. 2008 Adaptive specialization, conditional plasticity, and phylogenetic history in the reproductive cue response systems of birds. *Phil. Trans. R. Soc. B* **363**, 267–286. (doi:10.1098/rstb.2007.2139)
- Hedenström, A. 2008 Adaptations to migration in birds: behavioural strategies, morphology and scaling effects. *Phil. Trans. R. Soc. B* **363**, 287–299. (doi:10.1098/rstb.2007.2140)
- McNamara, J. M. & Houston, A. I. 2008 Optimal annual routines: behaviour in the context of physiology and ecology. *Phil. Trans. R. Soc. B* **363**, 301–319. (doi:10.1098/rstb.2007.2141)
- Martin, L. B., Weil, Z. M. & Nelson, R. J. 2008 Seasonal changes in vertebrate immune activity: mediation by physiological trade-offs. *Phil. Trans. R. Soc. B* **363**, 321–339. (doi:10.1098/rstb.2007.2142)
- Paul, M. J., Zucker, I. & Schwartz, W. J. 2008 Tracking the seasons: the internal calendars of vertebrates. *Phil. Trans. R. Soc. B* **363**, 341–361. (doi:10.1098/rstb.2007.2143)
- Shine, R. & Brown, G. P. 2008 Adapting to the unpredictable: reproductive biology of vertebrates in the Australian wet-dry tropics. *Phil. Trans. R. Soc. B* **363**, 363–373. (doi:10.1098/rstb.2007.2144)
- Speakman, J. R. 2008 The physiological costs of reproduction in small mammals. *Phil. Trans. R. Soc. B* **363**, 375–398. (doi:10.1098/rstb.2007.2145)

One contribution of 14 to a Theme Issue 'Adaptation to the annual cycle'.

- Verhulst, S. & Nilsson, J.-Å. 2008 The timing of birds' breeding seasons; a review of experiments that manipulated timing of breeding. *Phil. Trans. R. Soc. B* **363**, 399–410. (doi:10.1098/rstb.2007.2146)
- Wikelski, M., Martin, L. B., Scheuerlein, A., Robinson, M. T., Robinson, N. D., Helm, B., Hau, M. & Gwinner, E. 2008 Avian circannual clocks: adaptive significance and possible involvement of energy turnover in their proximate control. *Phil. Trans. R. Soc. B* **363**, 411–423. (doi:10.1098/rstb.2007.2147)
- Wingfield, J. C. 2008 Organization of vertebrate annual cycles: implications for control mechanisms. *Phil. Trans. R. Soc. B* **363**, 425–441. (doi:10.1098/rstb.2007.2149)