2006). This view is supported by exciting new research from wild birds. Bäckman et al. (2016) have provided the first annual-cycle data of activity of a free-living migratory bird, a red-backed shrike Lanius collurio. Intriguingly, the same species had earlier been recorded in captivity (Gwinner and Biebach 1977). The overall timing of migration is wellmatched in both studies. However, in agreement with observations from stop-over sites, the wild bird showed relatively few nights with migratory flights, whereas its captive conspecifics showed several months of continued Zugunruhe. Another recent study, on European blackbirds *Turdus merula* (Zúñiga et al. 2016), found that radio-tracked wild migrants showed no increase in nocturnal activity until the night of departure from the breeding grounds, whereas captive birds slowly built up Zugunruhe over several weeks. The physiological and ecological mechanisms that affect alternations between flight and stopover mode are now under intense investigation, using both Zugunruhe and tracks of free-flying birds (Fusani et al. 2009, 2013, Goymann et al. 2010, Eikenaar et al. 2014, Skrip et al. 2015). Dissection of the genetic and environmental regulators of migration will not only aid migration research, but also allow important advances for understanding how genes and environment interact to shape complex behaviour.

We believe that *Zugunruhe* will continue to be a powerful tool in the study of avian migration. If used with circumspection and in combination with new tools, from molecular methods to new tracking technologies (Alerstam 2011, Liedvogel and Lundberg 2014, Ketterson et al. 2015), *Zugunruhe* will reveal new answers to ancient questions about the migration of birds (Alerstam 1990).

Acknowledgements — We thank Jérémie Huguenin, Katharina Foerster, Hans Winkler, and Irby Lovette for earlier work with the stonechat data, for valuable discussions, and for support. We thank Anders Hedenström and Åke Lindström for helpful feedback. Funding was provided by the Max Planck Society and the Hunter R. Rawlings III Cornell Presidential Research Scholars Program at Cornell Univ. BH thanks Lotte Helm for her kind support. We could not write about stonechats without acknowledging the friendship of Eberhard Gwinner, who initiated these studies at the Max-Planck Institute in Andechs. Our article is dedicated to Thomas Alerstam, who has so greatly inspired migration biology, intellectually and through his kindness and enthusiasm.

## References

- Alerstam, T. 1990. Bird migration. Cambridge Univ. Press. Alerstam, T. 2006. Strategies for the transition to breeding in time-selected bird migration. Ardea 94: 347–357.
- Alerstam, T. 2011. Optimal bird migration revisited. J. Ornithol. 152: 5–23.
- Bäckman, J., Andersson, A., Alerstam, T., Pedersen, L., Sjöberg, S., Thorup, K. and Tøttrup, A. P. 2016. Activity and migratory flights of individual free-flying songbirds throughout the annual cycle: method and first case study. – J. Avian Biol. doi:10.1111/jav.01068
- Baldwin, M. W., Winkler, H., Organ, C. L. and Helm, B. 2010. Wing pointedness associated with migratory distance in common-garden and comparative studies of stonechats (Saxicola torquata). – J. Evol. Biol. 23: 1050–1063.

- Bates, D., Maechler, M., Bolker, B. and Walker, S. 2015. Fitting linear mixed-effects models using lme4. J. Stat. Softw. 67: 1–48.
- Berthold, P. 1988a. Evolutionary aspects of migratory behavior in European warblers. J. Evol. Biol. 1: 195–209.
- Berthold, P. 1988b. Unruhe-Aktivität bei Vögeln: eine Übersicht. Vogelwarte 34: 249–259.
- Berthold, P. 2001. Bird migration. A general survey. Oxford Ornithol. Ser. 12: 1–253.
- Birkhead, T. R. 2008. The wisdom of birds. An illustrated history of ornithology. Bloomsbury.
- Both, C., Artemyev, A. V., Blaauw, B., Cowie, R. J., Dekhuijzen, A. J., Eeva, T. and Visser, M. E. 2004. Large-scale geographical variation confirms that climate change causes birds to lay earlier. Proc. R. Soc. B 271: 1657–1662.
- Briedis, M., Hahn, S., Gustafsson, L., Henshaw, I., Träff, J., Král, M. and Adamík, P. 2016. Breeding latitude leads to different temporal but not spatial organization of the annual cycle in a long-distance migrant. J. Avian Biol. 47: 743–748.
- Brown, M. J. and Taylor, P. D. 2015. Adult and hatch-year blackpoll warblers exhibit radically different regional-scale movements during post-fledging dispersal. Biol. Lett. 11: 20150593.
- Chan, K. 2005. Partial migration in the silvereye (Zosteropidae: Aves): pattern, synthesis, and theories. Ethol. Ecol. Evol. 17: 449–363.
- Conklin, J. R., Battley, P. F., Potter, M. A. and Fox, J. W. 2010. Breeding latitude drives individual schedules in a trans-hemispheric migrant bird. – Nat. Commun. 1: 67.
- Coppack, T. and Pulido, F. 2009. Proximate control and adaptive potential of protandrous migration in birds. Integr. Comp. Biol. doi: 10.1093/icb/icp029
- Delmore, K. E. and Irwin, D. E. 2014. Hybrid songbirds employ intermediate routes in a migratory divide. Ecol. Lett. 17: 1211.
- Deregnaucourt, S., Guyomarc'h, J.-C. and Belhamra, M. 2005. Comparison of migratory tendency in European quail *Coturnix c. coturnix*, domestic Japanese quail *Coturnix c. japonica* and their hybrids. Ibis 147: 25–36.
- Eikenaar, Ć., Klinner, T., Szostek, K. L. and Bairlein, F. 2014. Migratory restlessness in captive individuals predicts actual departure in the wild. Biol. Lett. 10: 20140154.
- Farner, D. 1955. The annual stimulus for migration: experimental and physiologic aspects. – In: Wolfson, A. (ed.), Recent studies in avian biology. Univ. of Illinois Press, pp. 198–237.
- Fuchs, R., Winkler, H., Bingman, V. P., Ross, J. D. and Bernroider, G. 2014. Brain geometry and its relation to migratory behavior in birds. – J. Adv. Neurosci. Res. 1: 1–9.
- Fuchs, T., Haney, A., Jechura, T. J., Moore, F. R. and Bingman, V. P. 2006. Daytime naps in night-migrating birds: behavioural adaptation to seasonal sleep deprivation in the Swainson's thrush, *Catharus ustulatus*. Anim. Behav. 72: 951–958.
- Fusani, L. and Gwinner, E. 2005. Melatonin and nocturnal migration. Ann. N. Y. Acad. Sci. 1046: 264–270.
- Fusani, L., Cardinale, M., Carere, C. and Goymann, W. 2009. Stopover decision during migration: physiological conditions predict nocturnal restlessness in wild passerines. – Biol. Lett. 5: 302–305.
- Fusani, L., Coccon, F., Mora, A. R. and Goymann, W. 2013. Melatonin reduces migratory restlessness in *Sylvia* warblers during autumnal migration. – Front. Zool. 10: 79.
- Goymann, W., Spina, F., Ferri, A. and Fusani, L. 2010. Body fat influences departure from stopover sites in migratory birds: evidence from whole-island telemetry. Biol. Lett. 6: 478–481.
- Gwinner, E. 1986. Circannual rhythms. Springer.
- Gwinner, E. 1990. Circannual rhythms in bird migration: control of temporal patterns and interactions with photoperiod. In: