

et al. 2010). In future genetic experiments on *Zugunruhe*, data should be collected on traits that shed light on the migratory context of behaviour (Noordwijk et al. 2006).

Changepoint analysis as a quantitative tool for *Zugunruhe*

Our analytic approach allowed us both to classify presumed migrants and non-migrants and identify periods of *Zugunruhe* on the individual level for the vast majority of birds from all taxa and age groups. Overall, the algorithm performed equally well for classifying *Zugunruhe* regardless of a population's migratory phenotype. The parameters of the method can easily be adjusted to fit other phenotypes or answer different questions. In contrast to fixed exclusion criteria (Maggini and Bairlein 2010), changepoint analysis has the advantage of assessing changes in nocturnal activity in the context of a given bird's behavioural profile, thus accommodating individual differences by using an individual-specific baseline. Consequently, changepoint analysis is presumably less prone to bias from behavioural differences or recording methods. Some studies have applied individual-specific criteria, e.g. nocturnal activity relative to diurnal activity (Ramenofsky et al. 2008), or white-noise techniques (Helm and Gwinner 2006). However, unlike changepoint analysis, these measures were not specific to the seasonal features of *Zugunruhe*. In comparison to autocorrelation techniques (Helm and Gwinner 2006), changepoint analysis classified fewer birds as exhibiting *Zugunruhe*, presumably because of its focus on major changes in nocturnal activity profiles. Importantly, and in contrast to commonly used 'eyeballing' methods, changepoint analysis is objective and repeatable as long as its settings are documented. Strong contrasts and sharp delineation between *Zugunruhe* and neutral periods, especially during spring migration, were easiest to measure unambiguously (Supplementary material Appendix 2, Fig. A1A, C). However, even in cases with noisy data, the decisions made by the analytic approach were objective compared to methods of manual classification of raw data. Delineation of *Zugunruhe* by changepoint analysis was also more adaptable to the features of *Zugunruhe* than methods based on fixed thresholds (Pulido et al. 1996, Owen and Moore 2008), and general algorithms such as 'edge detectors' (Helm and Gwinner 2005).

Our findings on *Zugunruhe* intensity were robust to variation in analysis method: population-level comparisons of raw activity data largely mirrored results of *Zugunruhe* intensity. This suggests that more conventional analytic methods are sufficient for detecting coarse intensity patterns. Overall, we feel that the main advantage of our approach is its general applicability, and we hope to aid its implementation with our provided R script (Dryad Digital Repository, <<http://dx.doi.org/10.5061/dryad.484m0>>).

Conclusions: implications for avian migration studies

Our study shows that *Zugunruhe* is a robust component of the annual cycle in the stonechat complex: the behaviour was present in four populations with drastically different migratory phenotypes. Characteristic differences in *Zugunruhe* between the populations were apparent in our

common-garden set-up, supporting the view that genetic variation underlies differences in the migration programme (see also Berthold 2001, Maggini and Bairlein 2010, Ketterson et al. 2015). A heritable basis of the main features of *Zugunruhe* was further indicated by intermediate patterns in hybrids, in line with findings from other crossbreeding studies of migratory birds, and matching evidence from wild species. For example, tracking data from wild Swainson's thrushes *Catharus ustulatus* revealed intermediate routes taken by hybrids from a migratory divide (Delmore and Irwin 2014). The largely consistent evidence for genetic migration programmes is encouraging for future studies of the evolutionary architecture of movement behaviour (e.g. identifying the specific genes that are responsible for such variation, their regulation, and their interactions), which could combine *Zugunruhe* with genomic tools (Peterson et al. 2013, Liedvogel and Lundberg 2014).

In our stonechat study, the differences between populations imply high evolutionary lability of migratory traits as well as some phenotypic plasticity of individuals, for example with increasing age. In agreement with findings from other species, *Zugunruhe* levels were higher and more robustly programmed in spring than in autumn (Helms 1963, Maggini and Bairlein 2010). Several comparisons between populations indicated that the timing of spring and autumn migration can be modified independently. Remarkably, however, we observed an apparent coupled change across seasons within European stonechats: Irish birds showed a consistent phase shift in timing compared to Austrian birds throughout the annual cycle, despite their overlapping wintering ranges (Helm et al. 2006, Helm 2009). Similarly consistent phase differences (often referred to as carry-over effects) within species have recently also been reported in field studies of migratory waders and songbirds (Conklin et al. 2010, Briedis et al. 2016) and may thus have an inherited basis.

We also found patterns that are not commonly reported, despite possibly being widespread. For example, stonechats of all groups showed juvenile nocturnal restlessness during their postfledging phase, sometimes even before the start of moult (Mukhin 1999). A better understanding of this behaviour could provide important cues for studies of avian navigation, prospecting and dispersal. In addition, the striking reductions of *Zugunruhe* with age could indicate plasticity and learning processes that are yet to be understood, requiring testing in wild birds over several years of their life. Furthermore, our comparisons of diurnal and nocturnal activity across the annual cycle suggest that individuals that showed higher levels of *Zugunruhe* were also generally more active birds. This calls for closer study of relationships between *Zugunruhe* and other behaviours, including personality traits (van Oers and Naguib 2013), and for cautious interpretation of findings from selective breeding experiments (Berthold et al. 1988a).

Clearly, many questions remain about the interpretation of *Zugunruhe*. Our findings of undiminished *Zugunruhe* in partially migrant Irish stonechats and confirmation of *Zugunruhe* in Kenyan residents underscore an urgent concern: the parts of this behaviour that align with actual migration need to be distinguished from those that indicate an environmentally sensitive preparedness to migrate (Merkel 1956, Helms 1963, Gwinner and Czeschlik 1978, Helm