



Figure 8. Comparison between overall nocturnal and diurnal activity levels by season for each population. Boxplots show activity levels for each migration season flanked by activity levels during summer and winter ‘neutral’ seasons (for definitions, see Fig. 6). The boxplots show daily activity levels as the number of 10-min active periods for night (top row) and day (bottom row); boxplots as in Fig. 2).

differences in many traits of life history, physiology, morphology, and biological time-keeping (Gwinner et al. 1983, 1995, Helm et al. 2005, 2009, Helm 2009, Tieleman et al. 2009, Baldwin et al. 2010, Fuchs et al. 2014, Versteegh et al. 2014). These population-level differences were largely consistent with our predictions: long-distance migratory Siberian stonechats showed by far the strongest migratory tendencies and most consistent behaviour. Siberian birds rarely failed to engage in *Zugunruhe* and consistently showed high *Zugunruhe* intensities in both spring and autumn. Among the migrant populations, Siberian stonechats were the first to initiate *Zugunruhe* in autumn and the last to do so in spring. Siberian birds had the longest *Zugunruhe* period in autumn and the shortest in spring. This extended autumn *Zugunruhe* period is likely related to the long distances travelled by this population, paired with a possibly slower pace of autumn migration (Yamaura et al. 2016, but see Raess 2008). Alternatively, the long fall *Zugunruhe* may reflect a necessity to facultatively remain in migratory condition because of unpredictable resource availability (Helms 1963). Although short, the spring *Zugunruhe* periods of Siberian stonechats were exceptionally intense (peak activities were near 100% of the night length). This may reflect the need for a rapid long-distance return journey to the breeding grounds within a tightly constrained time window (i.e. late enough that spring has arrived – but not too late for breeding in a short season, Alerstam 2006, 2011). This view is supported by spring field records from stonechats (Raess 2008).

On the other end of the migration spectrum, resident Kenyan stonechats clearly showed the weakest migratory tendencies, but they still regularly engaged in *Zugunruhe*,

especially first-year birds (Helm 2006, Helm and Gwinner 2006). Most Kenyan birds showed *Zugunruhe* at least once, but also refrained from engaging in *Zugunruhe* at least once, including the overwhelming majority of older birds. Under temperate photoperiods in the laboratory, Kenyan birds showed well-defined population timing, starting at about the same time as Austrian birds in autumn, but significantly later in spring. In both seasons, *Zugunruhe* profiles of Kenyan birds had relatively short durations and low intensities. Although the present analysis finds relatively low levels, it corroborates the persistence of *Zugunruhe* and several of its features in African stonechats. The interpretation of this behaviour is still unclear and merits further investigation (Zink 2011).

The Irish and Austrian populations are currently classified as members of the same species (European stonechat), and are both medium distance migrants that reach Mediterranean winter quarters. However, in contrast to obligate Austrian migrants, British Isles stonechats are partial migrants, with roughly half of the birds remaining at or near the breeding sites in winter (Helm et al. 2006). Our study population originated from a coastal site in Ireland where birds overwinter, such that our sample could have been biased towards resident phenotypes (Helm 2003). Nonetheless, we found that *Zugunruhe* behaviours in these two populations were generally similar, showing intermediate phenotypes of timing and incidence compared to Kenyan and Siberian birds. Counter to predictions for partial migrants (Berthold 1988a, Pulido et al. 1996, Pulido and Berthold 2010), we could not detect a heightened proportion of Irish stonechats showing no *Zugunruhe*. Most unexpectedly, Irish birds exhibited