to first year birds. Decreases in overall activity with age are well known from many animal species, including vertebrates and invertebrates (Ingram 2000) and could well be unrelated to migration. We therefore used our data on activity outside of a migration context to assess whether the reductions in *Zugunruhe* represented general age-related patterns. We identified a consistent, but slight, reduction of activity levels with age for nocturnal activity also during summer and winter, and for diurnal activity around the annual cycle. In contrast to *Zugunruhe*, this reduction was consistent for the populations and seasons. Our findings thus suggest that the pronounced decrease in *Zugunruhe* in older birds was predominantly associated with migratory programming, rather than a general ageing process.

The magnitude of the age-related reductions in *Zugunruhe* was astonishing. Age effects on *Zugunruhe* are rarely discussed in the literature, and where they have been reported, patterns were inconsistent, for example between the sexes of European blackbirds (Lundberg 1988, Schwabl and Silverin 1990). It is possible that the reductions derived from long periods spent in captivity (Schwabl and Silverin 1990), or from modifications of the migration programme by prior experience (Ketterson and Nolan 1983, 1988). For example, based on experiments with dunnocks *Prunella modularis*, Schwabl et al. (1991) speculated that birds may recognise previous wintering locations and accordingly reduce *Zugunruhe* when exposed to them. Whatever the interpretation, it is interesting to note that in stonechats, age effects were absent in the most migratory population (i.e. Siberian stonechats).

We also found effects of age on the timing of *Zugunruhe*. Autumn timing was consistently earlier in older birds by approximately 2–3 weeks across populations, but duration did not change. These findings are consistent with those from other annual cycle events in stonechats, including earlier reproductive cycles and earlier moult in second-year compared to first-year stonechats (Helm et al. 2009). In the field, adults of many bird species commence autumn migration before juveniles (Newton 2008), presumably because juveniles benefit from a longer stay on the breeding grounds for maturation and the completion of postjuvenile moult. In spring, older stonechats started *Zugunruhe* slightly later but ended it earlier, possibly primed by previous photoperiodic experience (Sockman et al. 2004).

Seasons

Overall, our analysis demonstrates stark differences between spring and autumn *Zugunruhe*. *Zugunruhe* was more difficult to measure in autumn than in spring because of its more drawn out time profile and lower, more variable intensity. Autumn *Zugunruhe* was also confounded by juvenile restlessness and is known to be affected by other early-life effects, in particular by variation in hatching date (Fig. 1B; Helm and Gwinner 2006). Intensity of *Zugunruhe* was much higher in spring than in autumn for Austrian and Irish stonechats. Siberian birds appeared to make greater use of the available night time in spring than in autumn, but their high activity levels in both seasons were statistically inseparable.

These seasonal differences correspond well with *Zugunruhe* data of other species and with observations of wild birds. Many species migrate more rapidly during spring than autumn (Alerstam 2006, Newton 2008, Nilsson et al. 2013, Bäckman et al. 2016, Horton et al. 2016), and several aspects of migratory physiology reflect this faster pace. For example, when being re-fed after a fasting period, blackcaps pause *Zugunruhe* in autumn, but not in spring (Fusani and Gwinner 2005). Such differences may result from higher selection pressure on the timing of spring migration because of its proximity to the breeding season, relative to the apparently more 'casual' pace of autumn migration (Lack 1943, 1944, Helms 1963, Both et al. 2004, Alerstam 2006, Newton 2008). In our data, this interpretation is further supported by findings from diurnal activity. During *Zugunruhe*, mean diurnal activity was lower than before or after *Zugunruhe*, in accordance with the idea that birds require more rest to compensate for the increase in nocturnal activity (Rattenborg et al. 2004, Fuchs et al. 2006, Bäckman et al. 2016). The drop in mean diurnal activity during *Zugunruhe* was less pronounced during spring, indicating that birds generally maintained high diurnal activity levels in spring. However, in both seasons, stonechats compensated for increased nocturnal activity on a day-to-day basis by reducing diurnal activity levels after highly active nights, and this effect was at least as clear in spring as in autumn.

Finally, unlike for intensity, differences in the duration of *Zugunruhe* between the seasons were not consistent between populations (e.g. spring migration was shorter than autumn migration for Siberian stonechats, but the opposite was true for Irish stonechats); this type of heterogeneity might be expected from bird migration theory (Alerstam 2006, 2011).

Individual activity levels

Within individuals, *Zugunruhe* occupied a unique position in the annual cycle, with no significant elevations of nocturnal activity detected outside the migration seasons. However, intensity of *Zugunruhe* also covaried with individual differences in overall activity and was positively correlated with activity levels outside of the migration season, both during daytime and night-time. This finding implies that *Zugunruhe* intensity is not solely a measure of migratory tendency but also contains some information about a bird's overall behavioural phenotype, including, for example, possible differences in 'personality' or physiology (Mettke-Hofmann et al. 2005, Reale et al. 2007, van Oers and Naguib 2013). Breeding programs for high levels of *Zugunruhe* (e.g. in blackcaps, Berthold 1988a) may have thus selected in part for generally high locomotor activity, although in our study within-individual correlations between activities were low relative to the blackcaps' large selection response. Locomotor activity levels are known to be highly heritable. For example, genetic studies of mice found a QTL (quantitative trait locus) for the amount of activity, indicating high potential for selection (Mayeda and Hofstetter 1999).

Because variation in *Zugunruhe* intensity can predict variation in activity in other behavioural contexts, *Zugunruhe* intensity may be less useful than previously believed as a measure of migratory tendency. However, this depends on whether heightened overall activity levels covary with migration in the wild. Consequently, there is a need for further research on the relationship between *Zugunruhe* and other behavioural traits (Marchetti and Baldaccini 2003, Nilsson