

and Czeschlik 1978) and are often restless every night, whereas wild birds typically migrate for single nights and then refuel at stopover sites (Bäckman et al. 2016 compared to Gwinner and Biebach 1977). In light of these discrepancies, there is a need for more information on the relationship between *Zugunruhe* and diverse migratory phenotypes in the wild, and on the factors associated with variation in *Zugunruhe* within and between populations. Here, we investigate a long-term nocturnal activity dataset from several taxa of the stonechat complex (genus *Saxicola*), providing new insight into the variation and regulation of this migratory trait. Furthermore, comparison of *Zugunruhe* across studies and taxa has been hampered by heterogeneous and sometimes subjective quantifications. To address this issue, we propose a single quantitative approach to analyse nocturnal activity data in the phenotypically diverse stonechat system.

Stonechats are a well-studied taxon in avian biology (Gwinner et al. 1983, Wikelski et al. 2003, Illera et al. 2008, Helm 2009, Zink et al. 2009, Versteegh et al. 2014). These widespread songbirds breed across an unusually extensive latitudinal range, from ca 70°N in Siberia to 30°S in South Africa (Fig. 1A, Urquhart 2002). Within this range, they show large variation in morphology, physiology, and life history, including a broad spectrum of migratory behaviours from resident to long-distance migrant. Therefore, studies on stonechats offer opportunities to examine variation in these traits within a single species complex, with the benefit of reduced cross-species comparative noise. Extensive studies in the field and laboratory have compared stonechats from various environments with different migratory phenotypes. The least migratory population in our dataset comprises residents from east Africa (Kenya), followed by partial migrants from the British Isles (Ireland), obligate short-distance migrants from central Europe (Austria), and the most migratory population, long-distance migrants from west Siberia (Kazakhstan) (Helm 2009).

Stonechats included in this study were raised under common garden conditions in decades-long captive breeding studies, which collected data on a broad range of traits. To examine patterns of inheritance, birds were selectively bred within and crossbred between populations (Helm et al. 2005, Helm 2009). Key findings demonstrated a high degree of inheritance of annual cycle organization and physiological traits (Wikelski et al. 2003, Helm 2009, Tieleman et al. 2009, Versteegh et al. 2014). Stonechats generally displayed distinct population-specific phenotypes, even under common-garden conditions, and F1 hybrids mostly exhibited intermediate trait values (Gwinner 1996, Helm et al. 2009, Tieleman et al. 2009, Versteegh et al. 2014). Variation in many traits was associated with migratoriness, including dimensions of wing (Baldwin et al. 2010) and brain (Fuchs et al. 2014).

Nonetheless, the strengths of the stonechat system for advancing migration research have hardly been fully played out (Zink 2011, Ketterson et al. 2015), and analyses of nocturnal activity profiles collected within the experimental breeding scheme have only been touched upon (Helm and Gwinner 2005, 2006, Helm et al. 2005, Helm 2006). One striking finding was that resident Kenyan stonechats display *Zugunruhe*: lower in intensity compared to short-distance migrants from Austria, but with similar timing

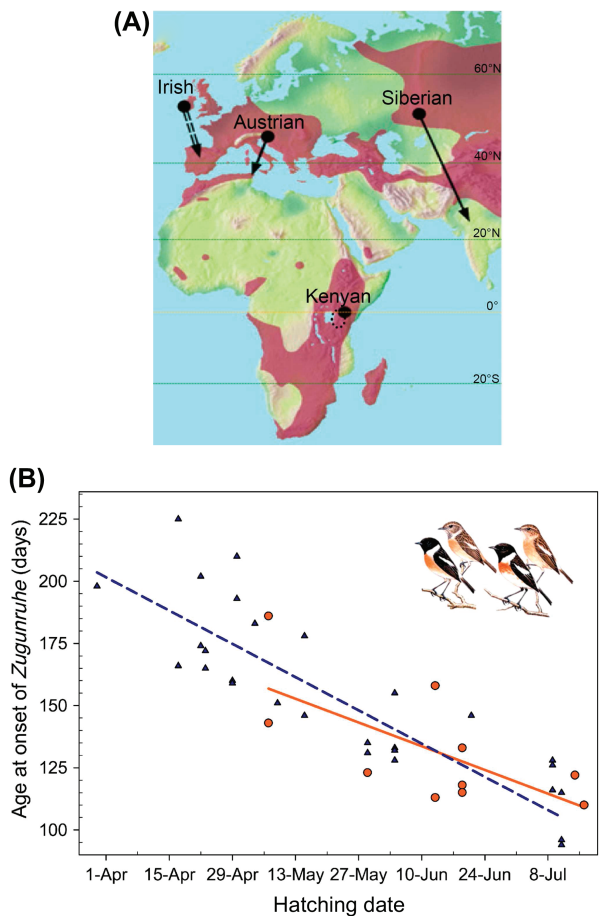


Figure 1. (A) Stonechat range map highlighting the locations and migratory phenotypes of the four populations: partially migratory Irish stonechats *Saxicola rubicola hibernans*, medium distance migrants *S. rubicola rubicola* from Austria, resident *S. torquatus axillaris* from Kenya, and long-distance migrants *S. maurus* from Siberia (Kazakhstan). Arrows indicate migratory routes between breeding and wintering grounds. We further included the following two hybrid groups: Austrian \times Siberian and Austrian \times Kenya. (B) Adjustment of the timing of *Zugunruhe* in response to the day lengths experienced over a bird's posthatching period, for captive Austrian and Kenyan stonechats. The onset ages of *Zugunruhe* for Austrian stonechats are shown as blue triangles (dashed blue line); the onset ages for Kenyan stonechats are shown as orange dots (solid orange line). Stonechats hatching later in the breeding season compensated for this by commencing *Zugunruhe* at earlier ages. Inlay: pairs of Austrian (left) and Kenyan (right) stonechats. Modified after Helm and Gwinner (2006).

characteristics (Fig. 1B, Helm and Gwinner 2006). Here, we present a more complete analysis of *Zugunruhe* in stonechats. Our long-term data, which for many birds started soon after fledging, enable us to compare population-specific programmes and address open questions in *Zugunruhe* research: do *Zugunruhe* patterns remain consistent as birds age? Are differences between spring and autumn migration seasons consistent among migratory species (e.g. *Zugunruhe* timing and intensity, and effects of age and sex)? Are birds that display high *Zugunruhe* generally more active birds, or is migratory activity a completely independent activity trait?

In our efforts to answer these questions, our first objective is to develop robust analysis methods for *Zugunruhe*