



Programmed and flexible: long-term *Zugunruhe* data highlight the many axes of variation in avian migratory behaviour

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Studies of *Zugunruhe* – the ‘migratory restlessness’ behaviour of captive birds – have been integral to our understanding of animal migration, revealing an inherited propensity to migrate and an endogenous timing and navigation system. However, differences between *Zugunruhe* in captivity and migration in the wild call for more data, in particular on variation within and among taxa with diverse migration strategies. Here, we characterise *Zugunruhe* in a long-term dataset of activity profiles from stonechats (genus *Saxicola*) with diverse migratory phenotypes (976 migration periods from 414 birds), using a flexible and consistent quantitative approach based on changepoint analysis. For east African, Austrian, Irish, and Siberian stonechats and hybrids, we report key inter-population differences in the occurrence, timing, and intensity of *Zugunruhe*. In line with expectations, we found the highest *Zugunruhe* intensity in the longest-distance migrants, more variable patterns in short-distance migrants, and intermediate characteristics of hybrids relative to their parental groups. Inter-population differences imply high evolutionary lability of *Zugunruhe* timing within a robustly structured annual cycle. However, counter to theory, Irish partial migrants showed no segregation between migrant and resident individuals, and previously reported nocturnal restlessness was confirmed for resident African stonechats. Further features of nocturnal restlessness that did not align with migratory behaviour of stonechats were juvenile nocturnal restlessness even prior to postjuvenile moult, and protandry in spring, although stonechats winter in heterosexual pairs. Importantly, *Zugunruhe* of all populations declined with age, and the intensity of an individual bird’s *Zugunruhe* was correlated with activity levels during other parts of the annual cycle. Our results confirm endogenous, population-specific migration programmes but also reveal apparent discrepancies between *Zugunruhe* and migration in the wild. We thus highlight both the continued potential of *Zugunruhe* study and the need for circumspect interpretation when using migratory restlessness to make inferences about migration in the wild.

The phenomenon of bird migration, particularly regular biannual movements, has captured human interest throughout recorded history (Alerstam 1990, 2011). How do birds know when to depart, which direction to fly, when to stop, and when to return? Given that migration takes place in mid-air and often spans continents, answering these questions based solely on observations of free-living birds has been intrinsically difficult (Birkhead 2008). Although new tracking technologies are beginning to overcome this challenge, they are limited in their potential to answer fundamental questions because each bird’s journey is a unique experience under a particular suite of environmental conditions (Delmore and Irwin 2014, Bäckman et al. 2016). Much of our understanding of the regulation of migration therefore continues to be based on studies of songbirds in captivity. These studies leverage the fact that many nocturnally migrating species spontaneously modify their activity patterns during the migration seasons of wild conspecifics, even when kept under constant conditions in captivity. Instead of their usual rest at night, captive migratory birds extend their activities after sunset, flying, hopping and whirring their wings

often until the morning (Berthold 2001, Birkhead 2008). This behaviour, called migratory restlessness, or *Zugunruhe*, has been extensively used as a proxy for studying migration. In general, intensity and/or duration of *Zugunruhe* increases with the ‘migratoriness’ of a population, measured for example by the distance covered by wild migrants or by the proportion of individuals that migrate. The behavioural phenomenon of migratory restlessness is not restricted to birds and has also been characterised in, for example, fish and insects (Leverson 1997, Mouritsen and Frost 2002, Sudo and Tsukamoto 2015).

However, the comparability between *Zugunruhe* and actual migration in the wild is not always clear (Farner 1955, Helms 1963, Berthold 1988a, b, Newton 2008). For example, resident populations of otherwise migratory species can show apparent *Zugunruhe* (Chan 2005, Helm and Gwinner 2006), and juvenile birds of some migratory species display nocturnal restlessness well in advance of actual migration (Mukhin 1999). Migratory songbirds in captivity often extend *Zugunruhe* far beyond the seasonally appropriate migration time window (e.g. summer restlessness, Gwinner