

data. When looking at nocturnal activity data, researchers are often faced with noisy time series that contain putative migration-related signals whose clarity varies among species and individuals. In particular, it has been challenging for existing methods to simultaneously.

a) Determine the presence or absence of *Zugunruhe* in the nocturnal activity profile of a bird. In many studies, some proportion of birds may show very little or inconsistent bouts of nocturnal activity. Depending on study-specific criteria, records of these birds could get dropped completely from the study, remain included in population measures of 'migratoriness' (e.g. for average *Zugunruhe* profiles; Berthold 1988a), or be assigned the status of 'non-migrants' (e.g. in studies of partial migrant populations).

b) Define the onset, completion and duration of the *Zugunruhe* period. Nocturnal activity frequently also occurs outside of the migration period of wild conspecifics. *Zugunruhe* has often been distinguished from other nocturnal activity by thresholds and cut-off practices based on informed guesses or varying subsidiary criteria (e.g. occurrence of moult) that are not always comprehensively reported.

c) Assess the consistency of *Zugunruhe* estimates when measured over more than one migration period. Data from individuals are often presented only for a single migration period, leaving open whether the behaviour is a stable, age-independent trait – expected, for example, for some genetic studies (Berthold 1988a).

d) Distinguish inter-individual differences in *Zugunruhe* from differences in activity that may be unrelated to migration. Many studies have quantified activity only for seasonal time windows designated as migration periods, and during the night but not the day. While it is likely that inter-individual variation in nocturnal activity during the migration season correlates with variation in migratory disposition, alternative explanations are possible and should be accounted for. For example, such variation may be explained by individual differences in overall activity levels, which have been reported across animal species (van Oers and Naguib 2013).

Although most studies address a subset of these issues in some manner, analytic processes have often lacked robust, objectively defined, and thus transferrable criteria (Pulido et al. 1996, Helm and Gwinner 2006). Considerations of how to process the data substantially influence the outcome of a study. For example, the results of studies using *Zugunruhe* to classify captive birds as putative migrants or residents will vary depending on the choice of time windows, threshold levels, and processing of noisy *Zugunruhe* profiles.

We address these analytical issues by presenting an automated procedure based on changepoint analysis. Using a single algorithm for birds of all migratory phenotypes, we determine presence, timing and intensity of *Zugunruhe* on an individual level. Specifically, we assign presence or absence of *Zugunruhe* to all individuals, thereby deriving proportions of putative migrants based on *Zugunruhe* for all populations, and we use activity data from the full annual cycle of individuals to obtain robust estimates of the timing of *Zugunruhe*.

Using these quantifications, we then analyse activity data of the stonechat populations and their hybrids with the following objectives.

1) Examine population-level variation in the occurrence, timing and intensity of *Zugunruhe*. Based on field-derived

differences in migratoriness, we test the prediction that birds originating from resident and partially migratory populations (Kenyan and Irish) are more likely to refrain from engaging in *Zugunruhe*; if they do show *Zugunruhe*, we expect intensities to be lower than in obligate short- and long-distance migrants (Austrian and Siberian). We therefore anticipate that intensity and duration will increase in the following sequence: Kenyan < Irish < Austrian < Siberian. We expect this pattern to hold for both spring and autumn seasons. Likewise, we test the prediction that timing of *Zugunruhe* relates to reported population differences in annual cycles, phenology, and migratory strategy (Helm 2009). In spring, we expect partially migratory populations to engage in *Zugunruhe* earlier than obligate short- and long-distance migrants. Conversely, for autumn we expect that long distance migrants will be the first, and partial migrants the last, to leave the breeding grounds.

2) Examine hybrid phenotypes. We investigate whether timing, prevalence, and intensity of *Zugunruhe* in hybrids are intermediate relative to parental phenotypes.

3) Identify differences between autumn and spring migration periods. Based on field evidence that migration is often more compressed and intense in spring than autumn (Alerstam 2011), we predict that *Zugunruhe* profiles are also more intense in spring than in autumn. We expect this pattern to be consistent among the three migratory populations, and possibly also in residents.

4) Examine the consistency of activity with age. Based on the premise that *Zugunruhe* reflects genetically programmed migratory traits, we test the prediction that *Zugunruhe* is consistently displayed over the lifetime of a bird. Because in weakly migratory species patterns may be flexible (Schwabl and Silverin 1990, Hegemann et al. 2015), we also test the prediction that *Zugunruhe* traits should have lower consistency in partial and short-distance migrants compared to the most migratory population. We first examine nocturnal restlessness during the postfledging phase, before the end of postjuvenile moult (referred to as 'juvenile restlessness'). Then, we focus on *Zugunruhe* and test for changes in timing, intensity, and frequency of occurrence with age, whether such changes differ among populations, and whether they also apply to year-round diurnal and nocturnal activity.

5) Compare analyses based on assignment of individuals as either migrants or residents to population-wide analyses. Classification of birds as either showing *Zugunruhe* (i.e. putative migrants) or not showing *Zugunruhe* (i.e. putative residents) filters nocturnal restlessness data prior to further analysis. *Zugunruhe* studies differ in whether or not individuals are divided by behaviour in this manner. To assess the effects of this classification on conclusions about *Zugunruhe* in stonechats, we compare outcomes of our analyses of birds identified as showing *Zugunruhe* to overall population-wide analyses of diurnal and nocturnal activity.

6) Examine the relationship between *Zugunruhe* and daytime activity. The few studies that have investigated how daytime activity changes during *Zugunruhe* suggest that birds compensate for sleepless nights by slight increases in daytime rest (Rattenborg et al. 2004, Fuchs et al. 2006). We therefore quantify the extent to which increased nocturnal