significantly higher spring *Zugunruhe* intensity than Austrian birds. These patterns are difficult to explain if *Zugunruhe* is expected to correspond closely to actual migration, and if partial migrant populations are expected to show greater dimorphism of migratory phenotypes (Berthold 1988a). They are more easily reconciled with regulation of migration where *Zugunruhe* may mark a window of opportunity during which environmental factors act to repress or activate actual migration (Helms 1963, Gwinner and Czeschlik 1978, Chan 2005, Helm 2006).

Austrian and Irish stonechats clearly differed from Siberian long-distance migrants. Both European populations showed significantly longer *Zugunruhe* periods during spring compared to autumn; this pattern was opposite to the one observed in Siberian stonechats. The long spring period of nocturnal restlessness is likely to represent *Zugunruhe*, rather than summer restlessness (Gwinner and Czeschlik 1978) because it ceased when the birds' reproductive organs matured (Helm and Gwinner 2005), just like migration of free-living stonechats (Raess and Gwinner 2005). Instead, the early, and long, spring restless periods of both European populations may reflect the readiness of these short-distance migrants to react to variation in local conditions that may allow for an early return to the breeding grounds, or, contrarily, for maximising arrival condition by pausing migration at favourable stop-over sites (Alerstam 2006, 2011). We have no convincing explanation for the short *Zugunruhe* window in autumn relative to Siberian stonechats, but speculate that it may reflect the shorter migration distance of the European populations.

The primary difference we detected between the two European populations related to the onset of *Zugunruhe* and matched our predictions. Irish stonechats showed by far the earliest spring migratory tendencies of all populations, regularly starting by late January. This early endogenous spring window fits well with field data, including those from ringing recoveries (Helm et al. 2006). Early spring arrival is expected both because of the more temperate environment of the British Isles, allowing for suitable environmental conditions earlier in the year, and because returning partial migrants will compete with resident conspecifics for territories upon arrival (Lack 1943, 1944). However, Irish birds also started *Zugunruhe* significantly earlier in autumn compared to their continental counterparts. This finding is more challenging to interpret in ecological terms. In terms of biological timekeeping mechanisms, it confirms a shift of the entire annual cycle of Irish compared to Austrian stonechats: annual cycle organisation and photoperiodic responses of both populations were identical, but migrations, reproduction and moult were all advanced by approximately one month in Irish stonechats (Helm 2003, 2009, and unpubl.).

Hybrid phenotypes

Our data show that hybrid stonechats express behavioural traits that are generally intermediate with respect to their parental groups. This is most obvious for the timing measures of Austrian × Siberian hybrids compared to Austrian or Siberian groups, and it indicates a strong genetic basis for both timing and intensity of migratory restlessness. These findings of intermediate phenotypes parallel data from other traits in stonechats, including timing of reproduction and moult, immune traits, metabolic measures, and life history traits (Gwinner et al. 1995, Helm et al. 2009, Versteegh et al. 2014, but see Tieleman et al. 2009). They also align with findings from other crossbreeding studies of migratory birds, including silvereyes *Zosterops lateralis* (Chan 2005) and Blackcaps (Berthold 1988a, Helbig 1996), although inheritance patterns in quail *Coturnix coturnix* appeared to be biased towards resident types (Deregnaucourt et al. 2005).

Sexes

In contrast to the extensive differences between populations, the sexes of stonechats exhibited similar endogenous migratory programmes, in line with their unusual behaviour of wintering in heterosexual pairs (Gwinner et al. 1994). We found no effect of sex on the frequency with which birds abstained from *Zugunruhe* or on the intensity or autumnal timing of *Zugunruhe*. However, males started spring *Zugunruhe* on average 4.6 d earlier than females. Protandry in spring migratory timing has been documented in the wild in many species, and it is seen as advantageous that males arrive to defend territories as early as possible (Kokko et al. 2006, Coppack and Pulido 2009, Alerstam 2011). Our findings add to the increasing evidence that such differences between the sexes can be hard-wired. Maggini and Bairlein (2012) have recently shown that in wheatears *Oenanthe oenanthe*, protandry of *Zugunruhe* persisted even in the absence of environmental cues such as photoperiod, and is therefore part of the birds' circannual programme (Gwinner 1986, 1996).

Age, season and individual activity levels

Development and age

In our study, juvenile stonechats showed strong nocturnal restlessness even before the beginning of postjuvenile moult. Likewise, hand-raised first year birds of other species also showed periods of elevated nocturnal activity after fledging, but prior to finishing postjuvenile moult (Gwinner 1990, Mukhin 1999). Wild birds are unlikely to commence migration during intense moult (Jenni and Winkler 1994), but postfledging movements have been associated with movements to moulting areas or explorative behaviours (Mukhin et al. 2005, Brown and Taylor 2015). Prospecting and training flights of young birds during the summer may be relevant for the development of celestial compass systems and establishment of navigational targets for return migration (Mukhin et al. 2005). Stonechats have been reported to move locally in juvenile flocks, for example to suitable moulting sites (Urquhart 2002), and ringing recoveries confirm such early-life movements (Helm et al. 2006). Juvenile restlessness in captivity could therefore represent a true urge to move, but one that differs from actual migration.

Subsequently, the expression of the stonechat endogenous migratory programme changed profoundly with age in ways that depended on season and population. Generally, occurrence and intensity decreased with age, and these decreases were most conspicuous in the more weakly migratory populations (Kenyan, Austrian, Irish, compared to Siberian) and in the lower-intensity migratory season, autumn. Across all populations, older stonechats were approximately twice as likely to abstain from *Zugunruhe* compared