

Review article

complicating interpretation of Read and Weary's (1992) findings. Irwin (2000) found that song complexity increased with latitude in Greenish Warblers (*Phylloscopus collybitz*), a species with no sedentary populations, which suggested migration alone is not sufficient to explain an apparent propensity for signals to become more elaborate

Table 1. Summary of studies examining variation in bird song complexity in relation to latitude and migratory behaviour. The 'measure of complexity' is reported as the authors themselves report it in their respective studies. Unless otherwise noted, song measurements were made by the authors. B, between species; ind., individuals; L, latitudinal comparison; M, migration comparison; M & L, both migration and latitude considered; pop., populations; sp., species; subsp., subspecies; W, within species; #, no. of.

Study design	Study system	Breeding range	More complexity:
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Study design	Study system	Breeding range	More complexity: migratory or sedentary	More complexity: higher or lower latitude	Measure of complexity	Reference
M: B	Acrocephalus – 6 sp.	North temperate	Migratory	Not tested	(full) syllable repertoire	Catchpole (1982)
M: B	Passeriformes – 165 sp.	Worldwide*	Migratory	Not tested	Song/syllable repertoire size, versatility (from the literature)	Read and Weary (1992)
L: W	Red-faced Cisticola, Cisticola erythrops - rangewide	Paleotropical	Not applicable ^h	No pattern	No. of unique syllables	Benedict and Bowie (2009)
L: W	Common Reed Bunting, Emberiza schoeniclus – 3 subsp.	North temperate	Not tested	Lower	No. of unique syllables/song	de Oliveira Gordinho et al. (2015)
L: W	Greenish Warbler, Phylloscopus trochiloides – 5 subsp.	North temperate	Not applicable	Higher	PCA: song length, No. of units/song, No. of unit types/song, bandwidth, No. of units/unit song length	Irwin (2000)
L: W	House Wrens Troglodytes aedon –rangewide	North temperate, neotropical	Not tested	Higher	Five note traits, eight tempo traits, three frequency traits	Kaluthota et al. (2016)
L: W	Yellow Wagtail, Motacilla flava – 5 subsp.	North temperate	Not tested	Lower	No. of elements/syllable	Odeen and Björklund (2005)
L: W	Three subspecies of Yellow-eyed Junco, Junco phaeonotus – 3 subsp.	North temperate, paleotropical	Not applicable	Lower	No. of unique syllables, No. of unique notes/trill	Pieplow and Francis (2011)
L: B	Serinus and Carduelis – 44 sp.	North temperate, neotropical, paleotropical	Not tested	Higher	PCA: frequency range, two-voiced syllables, buzzy syllables, song duration, No. of syllables/song	Cardoso et al. (2012)
L: B	Maluridae – 16 sp.	Paleotropical	Not applicable	Higher	Song versatility, note variety	Greig et al.

migrants face unique challenges. For clarity, we refer to 'migratory species' as any birds that make seasonal movements such that there is a distinct and different breeding and non-breeding location for a particular individual tens to thousands of kilometres apart, even if not all members of the species make such a movement (Newton 2010). The ability to migrate requires physiological and navigational adaptations that may be absent in non-migrants (Hedenström 2008). The potentially long distance travelled and the fact that migrants reside in at least two often dramatically different locations lays different selective pressures on them irrespective of breeding latitude. A number of hypotheses have been advanced to explain how these pressures might affect song complexity.

Ecological hypotheses

Bolus (2014) recently proposed two hypotheses to explain how migrant dispersal patterns may influence song evolution in migrants compared with non-migrants. Because they move away from their breeding grounds each year, migrants are likely to vary more in both the timing and the location of their subsequent nesting than non-migrants. The 'temporal isolation' hypothesis posits that if

individuals return to a particular location on different schedules, the staggering of their arrivals could isolate sub-populations breeding in the same place (e.g. Bearhop *et al.* 2005). Migrants would exhibit greater song variation through a mechanism similar to the one that drives sedentary populations to form local dialects, and this variation would be generated mainly via drift rather than as a result of selection for variability per se. The 'panmictic migrants' hypothesis suggests the opposite: if

studies, which are more equivocal in their results (Table 2). This could be a telling symptom of an ecological fallacy, where this apparent 'effect of scale' could be due to one or several causal variables going unmeasured (Simpson 1951, Selvin 1958). It is also possible that this is an illustration of the comparability problem (Read & Weary 1992), whereby studies between distantly related species must necessarily use fewer metrics to compare them, although many within-species studies also use only one or a few metrics. Alternatively, multiple metrics may evolve along different trajec-

data to conclude this confidently (e.g. Macedo 2008, Cramer 2011, Ferretti 2016). More study is needed to assess the ecological correlates of sexual selection in tropical regions, and more studies of tropical species are needed to characterize patterns of song complexity at all latitudes.

Both ecology and sexual selection are often cited as factors driving geographical patterns of song complexity, but it is rare for researchers to measure their effects in this context. While many studies do attempt to take the environment into account in some way (such as by classifying them as 'boreal' vs. 'tropical' forest or 'open' vs. 'closed' species), only two studies included here actually measured the habitat and acoustic features at their study sites (Irwin 2000, Singh & Price 2015), and another three used mean climate measures (Botero 2009, Medina & Francis 2012, Xing 2017). Fully to test the ecological hypotheses included in this review the field requires more studies that explicitly quantify the sound space available at varying latitudes and to determine whether more complex songs fill a wider swathe of that space.

The underlying assumption of sexual selection hypotheses is that song complexity or song reper-

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