

Review article

complicating interpretation of Read and Weary's (1992) findings. Irwin (2000) found that song complexity increased with latitude in Greenish Warblers (*Parus caeruleus*), 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-

- Botero, C.A., Boogert, N.J., Vehrencamp, S.L. & Lovette, I.J.** 2009. Climatic patterns predict the elaboration of song displays in mockingbirds. *Curr. Biol.* **19**: 1151–1155.
- Botero, C.A., Dor, R., McCain, C.M. & Safran, R.J.** 2014. Environmental harshness is positively correlated with intraspecific divergence in mammals and birds. *Mol. Ecol.* **23**: 259–268.
- Brainard, M.S. & Doupe, A.J.** 2002. What songbirds teach us about learning. *Nature* **417**: 351–358.
- Brumm, H. & Naguib, M.** 2009. Environmental acoustics and the evolution of bird song. *Adv. Study Behav.* **40**: 1–33.
- Byers, B.E.** 2011. Birdsong, migration and sexual selection: a skeptical view. *Anim. Behav.* **82**: e1–e3.
- Byers, B.E.** 2015. Migration and song elaboration in wood-warblers (*Geothlypis*). *Auk* **132**: 167–179.
- Cardoso, G., Hu, Y. & Mota, P.G.** 2012. Birdsong, sexual selection, and the flawed taxonomy of canaries, goldfinches, and allies. *Anim. Behav.* **84**: 111–119.
- Catchpole, C.K.** 1982. The evolution of bird sounds in relation to mating and spacing behavior. In Kroodsma, D. E. & Miller, E. H. (eds) *Acoustic Communication in Birds, Vol. I*: 297–319. New York: Academic Press.
- Catchpole, C.K. & Slater, P.J.** 2008. *Bird Song: Biological Themes and Variations*. Cambridge: Cambridge University Press.
- Collins, S.A., de Kort, S.R., Pérez-Tris, J. & Tellería, J.L.** 2009. Migration strategy and divergent sexual selection on bird song. *Proc. R. Soc. Lond. B* **276**: 585–590.
- Collins, S.A., de Kort, S.R., Pérez-Tris, J. & Tellería, J.L.** 2011. Divergent sexual selection on birdsong: a reply to Byers. *Anim. Behav.* **82**: e4–e7.
- Cramer, E.R.A., Hall, M.L., De Kort, S.R., Lovette, I.J. & Vehrencamp, S.L.** 2011. Infrequent extra-pair paternity in the Banded Wren, a synchronously breeding tropical passerine. *Condor* **113**: 637–645.
- Cuadrado, M.** 1994. Winter territoriality in migrant Black Redstarts *Phoenicurus ochrurus* in the Mediterranean area. *Bird Study* **42**: 232–239.
- Ewert, D.N. & Kroodsma, D.E.** 1994. Song sharing and repertoires among migratory and resident Rufous-sided Towhees. *Condor* **96**: 190–196.
- Ferretti, V., Liljesthrom, M., López, A.S., Lovette, I.J. & Winkler, D.** 2016. Extra-pair paternity in a population of Chilean swallows breeding at 54 degrees south. *J. Field Ornithol.* **87**: 155–161.
- Fitzpatrick, S.** 1994. Colourful migratory birds: evidence for a mechanism other than parasite resistance for the maintenance of 'good genes' sexual selection. *Proc. R. Soc. Lond. B* **257**: 155–160.
- Freeberg, T.M., Dunbar, R.I. & Ord, T.J.** 2012. Social complexity as a proximate and ultimate factor in communicative complexity. *Philos. Trans. R. Soc. B* **367**: 1785–1801.
- Gil, D. & Gahr, M.** 2002. The honesty of bird song: multiple constraints for multiple traits. *Trends Ecol. Evol.* **17**: 133–141.
- Gil, D., Slater, P.J. & Graves, J.A.** 2007. Extra-pair paternity and song characteristics in the Willow Warbler *Phylloscopus trochilus*. *J. Avian Biol.* **38**: 291–297.
- Greig, E.I., Price, J.J. & Pruett-Jones, S.** 2013. Song evolution in Maluridae: influence of natural and sexual selection on acoustic structure. *Emu* **113**: 270–281.
- Handley, H.G. & Nelson, D.A.** 2005. Ecological and phylogenetic effects on song sharing in songbirds. *Ethology* **111**: 221–238.
- Hedenström, A.**

- Ödeen, A. & Björklund, M.** 2005. Dynamics in the evolution of sexual traits: losses and gains, radiation and convergence in Yellow Wagtails (*Motacilla flava*). *Mol. Ecol.* **12**: 2113–2130.
- de Oliveira Gordinho, L., Matheu, E., Hasselquist, D. & Neto, J.M.** 2015. Song divergence between subspecies of Reed Bunting is more pronounced in singing styles under sexual selection. *Anim. Behav.* **107**: 221–231.
- Peters, S., Searcy, W.A., Beecher, M.D. & Nowicki, S.** 2000. Variation in the organization of song sparrow repertoires. *Auk* **117**: 936–942.
- Pieplow, N.D. & Francis, C.D.** 2011. Song differences among subspecies of Yellow-Eyed Juncos (*Junco phaeonotus*). *Wilson. J. Ornithol.* **123**: 464–471.
- Podos, J. & Warren, P.S.** 2007. The evolution of geographic variation in birdsong. *Adv. Stud. Behav.* **37**: 403–458.
- Price, J. J.** 2015. Rethinking our assumptions about the evolution of bird song and other sexually dimorphic signals. *Front. Ecol. Evol.* **3**: 40. <https://doi.org/10.3389/fevo.2015.00040>.
- Pulido, F.** 2007. The genetics and evolution of avian migration. *Bioscience* **57**: 165–174.
- Read, A. F. & Weary, D. M.** 1992. The evolution of bird song: comparative analyses. *Philos. Trans. R. Soc. B* **338**: 165–187.
- Salomonson, M.G. & Balda, R.P.** 1977. Winter territoriality of Townsend's Solitaires (*Myadestes townsendii*) in a Piñon-Juniper-Ponderosa pine ecotone. *Condor* **79**: 148–161.
- Selvin, H.C.** 1958. Durkheim's Suicide and problems of empirical research. *Am. J. Sociol.* **63**: 607–619.
- Shy, E. & Morton, E.S.** 1986. The role of distance, familiarity, and time of day in Carolina wrens responses to conspecific songs. *Beh. Eco. Soc.* **19**: 393–400.
- Simpson, E.H.** 1951. The interpretation of interaction in contingency tables. *J. R. Stat. Soc.* **13**: 238–241.
- Singh, P. & Price, T.D.** 2015. Causes of the latitudinal gradient in birdsong complexity assessed from geographical variation within two Himalayan warbler species. *Ibis* **157**: 511–527.
- Stoddard, P.K., Beecher, M.D., Horning, C.L. & Campbell, S.E.** 1991. Recognition of individual neighbours by song in the song sparrow, a species with song repertoires. *Behav. Ecol. Sociobiol.* **29**: 211–215.
- Stoddard, P.K., Beecher, M.D., Campbell, S.E. & Horning, C.L.** 1992. Song-type matching in the song sparrow. *Can. J. Zool.* **70**: 1440–1444.
- Stutchbury, B.** 1994. Competition for winter territories in a Neotropical migrant: the role of age, sex and color. *Auk* **111**: 63–69.
- Sullivan, M.S.** 1994. Mate choice as an information gathering process under time constraint: implications for behaviour and signal design. *Anim. Behav.* **47**: 141–151.
- Tietze, D.T., Martens, J., Fischer, B.S., Sun, Y., Klusman-Kolb, A. & Päckert, M.** 2015. Evolution of leaf warbler songs (Aves: Phylloscopidae). *Ecol. Evol.* **5**: 781–798.
- Wei, C., Price, T.D., Liu, J., Alström, P. & Zhang, Y.** 2017. The evolutionary origin of variation in song length and frequency in the avian family Cettiidae. *J. Avian Biol.* **48**: 1295–1300.
- Weir, J.T. & Lawson, A.** 2015. Evolutionary rates across gradients. *Methods Ecol. Evol.* **6**: 1278–1286.
- Weir, J.T. & Wheatcroft, D.J.** 2011. A latitudinal gradient in rates of evolution of avian syllable diversity and song length. *Proc. R. Soc. Lond. B* **278**