

## Review article

# The relationship between latitude, migration and the evolution of bird song complexity

NADJE NAJAR\*  & LAURYN BENEDICT*School of Biological Sciences, University of Northern Colorado, Greeley, CO 80639, USA*

For the past several decades it has been proposed that birds show latitudinal variation in song complexity. How universal this variation may be and what factors generate it, however, are still largely unknown. Furthermore, while migration is confounded with latitude, migratory behaviour alone may also be associated with variation in song complexity. In this paper we review the literature to assess current ideas on how latitude and migratory behaviour may drive large-scale geographical patterns of song complexity. At least seven distinct hypotheses have been proposed in 29 studies of the topic. Four of these hypotheses posit that sexual selection pressures co-vary with latitude and/or migration, resulting in concordant changes in song. Other hypotheses suggest that mechanisms other than sexual selection, such as large-scale changes in environmental sound transmission properties, may be at play. Sixteen studies found support for increased song complexity with increased latitude and/or migration, whereas 13 did not. Relatively few studies exist on this topic, and methodological differences between them and variable definitions of ‘complexity’ make it difficult to determine whether results are comparable and concordant. At a minimum, it is possible to conclude there is no strong evidence that song complexity increases with latitude and/or migration in all birds. Future work should focus on examining multiple hypotheses at once to further advance our understanding of how latitude, migration and song complexity may or may not be related.

**Keywords:** acoustic adaptation, geographical variation, hypotheses, sexual selection.

Bird song has served as an excellent model for understanding how acoustic signal complexity evolves. There is copious research on the subject of what promotes and constrains song complexity in birds (Andersson 1994, Irwin 2000, Nowicki & Searcy 2004, Catchpole & Slater 2008, Freeberg *et al.* 2012). Across these studies and others, song ‘complexity’ is a variably defined concept which typically incorporates combinations of measurements of song repertoire size, acoustic frequency, timing and structure (Nowicki & Searcy 2004).

Several authors have suggested that large-scale patterns of bird song variation evolve in high-

latitude temperate regions because the conditions there are conducive to increases in song complexity. The idea that high-latitude breeding may relate to song complexity was first advanced when Catchpole (1982) noted that migratory *Acrocephalus* warblers have larger repertoires than sedentary congeners. He suggested that migrants have less time to pair and breed, increasing pre-breeding sexual selection pressures which promote vocal complexity. A subsequent comparative analysis by Read and Weary (1992) found the connection between song complexity and migratory behaviour may be widespread in passerines and may represent common selective pressures acting on migrants. Of course, the propensity to migrate is confounded by breeding latitude and all its associated environmental variables, potentially

\*Corresponding author.  
Email: [nadje.najar@unco.edu](mailto:nadje.najar@unco.edu)  
Twitter: @nadjenaar

complicating interpretation of Read and Weary's (1992) findings. Irwin (2000) found that song complexity increased with latitude in Greenish Warblers *Phylloscopus trochiloides*, a species with no sedentary populations, which suggested migration alone is not sufficient to explain an apparent propensity for signals to become more elaborate towards the poles. Since then, many studies have attempted to re-evaluate how latitude and/or migration may influence the evolution of song complexity. However, few studies explicitly test or consider more than a single hypothesis, and the field as a whole lacks cohesion.

Geographical variation in bird song has been well studied with regard to song learning, dialect formation and functions, variability in song form and frequencies, and patterns of song sharing among individuals (Podos & Warren 2007). Far fewer studies have compared song complexity among multiple latitudinally widespread conspecific populations or different species (Table 1). Nevertheless, this is an important topic if we wish to understand the processes that drive species-, family- and higher-level variation. The few geographically large-scale studies of this topic illustrate some interesting patterns and propose a multitude of ideas to explain them (Table 2). However, aside from an oft-cited emphasis on sexual selection, those patterns and ideas have not been discussed within a single theoretical framework. These studies cover a wide range of passerine diversity and nearly every author has their own definition of 'complexity', a problem in itself that makes collective discussion and analysis difficult at best for any studies of bird song. This paper will review the available evidence to address an open question: does song complexity vary consistently across avian groups in relation to latitude and migratory behaviour and, if it does, what processes drive that variation?

### Latitudinal effects

Several studies have found latitudinal variation in song complexity that is not necessarily related to migratory behaviour (e.g. Irwin 2000, Mahler & Gil 2009, Weir & Wheatcroft 2011, Cardoso *et al.* 2012; Table 1). Hypotheses proposed to explain this variation invoke both ecological selection (Weir *et al.* 2012) and sexual selection (Catchpole 1982) as the causes of these patterns (Table 2).

### Ecological hypotheses

Bird vocalizations are signals adapted to propagate through an environment (Brumm & Naguib 2009) and as more 'sound space' becomes available over a latitudinal gradient, songs may become more complex (Weir *et al.* 2012). The availability of sound space is negatively influenced by the amount of background noise generated by other animals (especially insects), the closeness of habitat (i.e. forests vs. grasslands) and the sound-attenuating properties of the vegetation (Morton 1975). Overall, habitat does become more open as one moves away from the equator, with larger frequency windows and less sound attenuation in the predominantly evergreen forests of high latitudes and elevations (as compared with the tropical forests of lower latitudes and elevations) (Weir *et al.* 2012). There are both fewer bird species (Botero *et al.* 2014, Weir & Lawson 2015) and less background noise from insects (Weir *et al.* 2012) at higher latitudes, potentially freeing bird song to evolve more complex forms. Irwin (2000), Singh and Price (2015) and Wei *et al.* (2017) suggest latitudinal variation in sound space may explain some or most of the variation in song form detected in their respective studies.

### Sexual selection hypotheses

Catchpole (1982) theorized that short breeding seasons offer birds less time to pair and breed, so there may be greater selection on traits that quickly allow a bird to choose the best mate available. This 'rapid pairing' hypothesis was first suggested for migratory birds, but the effect is correlated with latitude and would hold true for non-migrants that do not retain their pair bond from year to year. Both migrant and non-migrant species breeding at high latitudes have shorter breeding seasons than most of their low-latitude counterparts, with this effect being more pronounced at the highest latitudes (Wyndham 1950). On the other hand, it is possible that the need to pair rapidly would result in birds making worse choices, on average, than those birds breeding at lower latitudes. It is not well known how long an individual bird spends assessing potential partners or what the consequences are of having more or less time to pair (but see Sullivan 1994).

### Migration effects

Although both non-migrant and migrant birds may breed in the same habitats at the same time,

**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: migratory or sedentary	More complexity: higher or lower latitude	Measure of complexity	Reference
M & L; W	Common Yellowthroat <i>Geothlypis trichas</i> – 9 subsp.	North temperate	Sedentary <sup>a</sup>	No pattern	No. of notes/phrase, No. of elements/note	Bolus (2014)
M & L; W	Marsh Wren <i>Cistothorus palustris</i> – 18 ind.	North temperate	No pattern <sup>a</sup>	No pattern	Song repertoire size	Kroodtsma and Verner (1987)
M & L; W	Marsh Grassbird <i>Locustella pyleri</i> – 7 pop.	North temperate	No pattern	Lower <sup>b</sup>	No. of element types, element rate, song length, 3 frequency traits	Xing <i>et al.</i> (2017)
M & L; B	'Fringillidae' <sup>c</sup> – 65 pop.	Worldwide	Sedentary	Lower	Song/syllable repertoire size (from Read & Weary 1992)	Handley and Nelson (2005)
M & L; B	Troglodytidae – 3 sp.	North temperate, neotropical	Migratory	Higher	Song repertoire size	Kroodtsma <i>et al.</i> (2001) <sup>d</sup>
M & L; B	Passeriformes – 44 sp.	North temperate	No pattern	No pattern	PCA: 3 element diversity traits and 1 frequency trait	Medina and Francis (2012)
M & L; B	<i>Vireo</i> – 18–28 sp.	North temperate, neotropical	Migratory	Higher	Repertoire size (from the literature)	Mounjoy and Leger (2001)
M & L; B	<i>Phylloscopus</i> – 80 sp.	Worldwide	No pattern	Lower <sup>e</sup>	Three traits derived from element, frequency, and tempo measures	Tietze <i>et al.</i> (2015)
M & L; B	Cettidae – 30 sp.	Worldwide	No pattern	Higher	No. of notes, strophe duration, longest note duration, 4 frequency traits	Wei <i>et al.</i> (2017)
M; W	Blackcap <i>Sylvia atricapilla</i> – 4 pop.	North temperate	Migratory	Not tested	Song length, No. of note types/No. of notes in song	Collins <i>et al.</i> (2009) <sup>f</sup>
M; W	Eastern Towhee <i>Pipilo erythrophthalmus</i> – 2 pop.	North temperate	Sedentary	Not tested	Song repertoire size	Ewert and Kroodtsma (1994)
M; W	Red-winged Blackbird <i>Agelaius phoeniceus</i> – 5 pop.	North temperate	Migratory	Not tested	Song repertoire size (from the literature)	Morton (1986) <sup>g</sup>
M; W	White-crowned Sparrow <i>Zonotrichia leucophrys</i> – 3 subsp.	North temperate	Migratory	Not tested	Repertoire size, No. of complex syllables	Nelson <i>et al.</i> (1996)
M; W	Song Sparrow <i>Melospiza melodia</i> – 5 pop.	North temperate	Sedentary	Not tested	Repertoire size, minimal units of production	Peters <i>et al.</i> (2000)
M; B	Mimidae – 29 sp.	North temperate, neotropical	Migratory	Not tested	Song duration, syllable duration, syllable types/song	Botero <i>et al.</i> (2009)
M; B	<i>Geothlypis</i> – 9 sp.	North temperate, neotropical	No pattern	Not tested	Song duration, No. of notes/song, No. of elements/note, No. of note types/song	Byers (2015)

(continued)

Table 1. (continued)

Study design	Study system	Breeding range	More complexity: migratory or sedentary	More complexity: higher or lower latitude	Measure of complexity	Reference
M: B	<i>Acrocephalus</i> – 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, <i>Cisticola erythrops</i> - rangewide	Paleotropical	Not applicable <sup>b</sup>	No pattern	No. of unique syllables	Benedict and Bowie (2009)
L: W	Common Reed Bunting, <i>Emberiza schoeniclus</i> – 3 subsp.	North temperate	Not tested	Lower	No. of unique syllables/song	de Oliveira Gordinho <i>et al.</i> (2015)
L: W	Greenish Warbler, <i>Phylloscopus trochiloides</i> – 3 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 <i>Troglodytes aedon</i> –rangewide	North temperate, neotropical	Not tested	Higher	Five note traits, eight tempo traits, three frequency traits	Kaluthota <i>et al.</i> (2016)
L: W	Yellow Wagtail, <i>Motacilla flava</i> – 5 subsp.	North temperate	Not tested	Lower	No. of elements/syllable	Odeen and Björklund (2005)
L: W	Three subspecies of Yellow-eyed Junco, <i>Junco phaeonotus</i> – 3 subsp.	North temperate, paleotropical	Not applicable	Lower	No. of unique syllables, No. of unique notes/trill	Pieplow and Francis (2011)
L: B	<i>Serinus</i> and <i>Carduelis</i> – 44 sp.	North temperate, neotropical, paleotropical	Not tested	Higher	PCA: frequency range, two-voiced syllables, buzzy syllables, song duration, No. of syllables/song	Cardoso <i>et al.</i> (2012)
L: B	Maluridae – 16 sp.	Paleotropical	Not applicable	Higher	Song versatility, note variety	Greig <i>et al.</i> (2013)
L: B	<i>Phylloscopus</i> – 30 sp.	North temperate, paleotropical	Not tested	Higher	PCA: song duration, No. of song types, No. of syllable types, No. of element types, No. of elements/song, No. of syllables/song	Mahler and Gil (2009)
L: B	<i>Phylloscopus</i> – 2 sp.	North temperate	Not applicable	Higher	Song repertoire, song rate, repetition rate	Singh and Price (2015)
L: B	Passeriformes – 232 sp.	North temperate, neotropical	Not tested	Higher <sup>d</sup>	No. of syllable types/song	Weir and Wheatcroft (2011)

\*Heavily biased to temperate breeders. <sup>a</sup>Found pattern of complexity difference between eastern and western lineages. <sup>b</sup>Xing *et al.* (2017) note that, counter to their expectations, song duration decreased with latitude. <sup>c</sup>Major revisions have since been made to this group. <sup>d</sup>Song length, however, does increase with latitude, and this trait is associated with increased extra-pair paternity (Gil *et al.* 2007) (and may therefore be more informative than song 'complexity'). <sup>e</sup>This paper does not explicitly compare these three wren species in terms of migration, latitude and complexity, but it has been referred to in Byers (2015) as such an example. <sup>f</sup>See Byers (2011) and Collins *et al.* (2011) for further discussion of the limitations of this study. <sup>g</sup>Only one published study is referenced in this example (Yasukawa 1981), the rest are personal communications. <sup>h</sup>Refers to either completely migratory or completely sedentary species so differences among these classes cannot be compared. <sup>i</sup>Complexity increases for oscines but not for suboscines, which have no pattern.

**Table 2.** Published hypotheses on how latitude and migration may drive song complexity.

Hypothesis	Reference	Synopsis	Predictions
Sound space	Weir <i>et al.</i> (2012)	Song becomes more complex with more available frequency windows	Background noise and habitat features vary with latitude. ↑Latitude → ↑Complexity
Rapid pairing	Catchpole (1982)	At high latitudes birds have less time to pair and breed. Increased sexual selection drives elaboration of signals	Elaboration varies with latitude and/or migratory distance ↑Latitude/↑Migration → ↑Complexity
Temporal isolation	Bolus (2014)	Migration isolates metapopulations both temporally and spatially, decreasing genetic/cultural transmission between them	Migrants have greater variability in song via isolation by distance ↑Migration → ↑Complexity
Panmictic migrants	Bolus (2014)	Migrants disperse farther than residents, leading to greater mixing	Migrants have less variation than residents ↑Migration → ↓Complexity
Good migrations	Fitzpatrick (1994)	Migrants are under strong selection to find good wintering grounds. Females will choose males whose genes can guide offspring to these places	Signal elaboration and genetic variation greater in migrants <sup>a</sup> Migration → ↑Complexity
Ranging	Morton (1986)	Dialects exist in sedentary birds to assess sound degradation and threat level, migrants have no dialects and larger repertoires to disrupt this process	Sedentary birds form small dialects, migrants have larger repertoires with no dialects Migration → ↑Complexity
Territory lottery	Mountjoy and Leger (2001)	Sedentary birds acquire territories by chance; selection is lower in these populations	Signal elaboration higher in migrants Migration → ↑Complexity

<sup>a</sup>Fitzpatrick (1994) is discussing plumage elaboration and moult as a mechanism for determining how well an individual did on their wintering grounds. Mountjoy and Leger (2001) argue this could also apply to song complexity.

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 migrants disperse farther than non-migrants, song variation in migrants is expected to be less than that of non-migrants. Bolus (2014) found support for this latter hypothesis in her study of Common Yellowthroats *Geothlypis trichas*.

#### Sexual selection hypotheses

Migrants must successfully navigate to their breeding and wintering grounds each year, a process thought to be largely under genetic control (Pulido 2007). The ‘good migrations’ hypothesis posits that moult taking place on the wintering grounds indicates the condition of the bird, and individuals with the genetic propensity to find the best wintering grounds will have the highest quality plumage for the following breeding season



(Fitzpatrick 1994). Mountjoy and Leger (2001) suggest this mechanism may extend to song complexity, although they do not propose a mechanism. Perhaps birds that migrate to the best wintering grounds have more time, energy and resources to devote to crystallizing a large song repertoire (Brainard & Doupe 2002), possibly by devoting more resources to growth of the song nuclei in the brain during their first winter. Females that then choose to mate with those males acquire 'good migration' genes for their offspring.

Sedentary species or populations are more likely to have dialects, which often include only a small number of song types (Podos & Warren 2007). The 'ranging' hypothesis (Morton 1986) posits that dialects evolved in sedentary birds to convey more accurately the location of the singer to its neighbours. Because birds within a dialect zone are all familiar with the common song type(s), they can compare songs that they hear with their own song in order to assess the amount of degradation and thus how far away the song originates and whether it constitutes a threat. Morton (1986) proposed that migratory species evolved repertoires to disrupt this ranging function of song. Unfamiliar, unrangeable songs could lead a neighbour to waste time and energy searching for a far-away signal or ignore a song that was actually a threat. This benefit would drive the evolution of constantly changing or larger repertoires in all individuals. There is evidence that birds are better able to range songs that are in their own repertoire (McGregor *et al.* 1983, Morton *et al.* 2006) and respond to unfamiliar song types from outside their territory more strongly than to familiar songs (Shy & Morton 1986). However, this hypothesis makes no inference as to whether the territory holder recognizes the song as coming from a new rival or a familiar neighbour, factors which are known to affect a bird's singing response (e.g. Stoddard *et al.* 1991, 1992). It is not clear what benefit neighbours gain from this disruption or how they avoid it, and the hypothesis does not satisfactorily explain the propensity for sedentary species to form dialects, as there is no reason why they should not also benefit from repertoire 'disruption'.

Regardless of how far migrants travel, the fact that they do not overwinter in their breeding territory obliges them to reacquire a territory the following year. The authors of the 'territory lottery'

hypothesis suggest this should manifest as greater elaboration of traits in migrants irrespective of migration distance (Mountjoy & Leger 2001). This ignores reports of winter territoriality in some migratory species (Marra *et al.* 1993, Cuadrado 1994, Stutchbury 1994). Then again, it is just as plausible to predict elaboration in the opposite direction: if sedentary birds must continuously defend their territories from intruders (e.g. Salomonson & Balda 1977, Kraaijeveld & Dickinson 2001), whereas migrants do not, sedentary birds could evolve more elaborate traits to advertise honestly their ability to defend that territory. Winter singing or territorial behaviour is poorly understood, and the relationship between either serial acquisition or continuous defence of a territory and song evolution even less so. These subjects present an interesting avenue for future research.

## METHODS

We used Google Scholar, Semantic Scholar and Web of Science to search for combinations of variations of key terms: migration (e.g. migrate, migratory, migrating), latitude (latitudinal), geographical variation (variability), (bird) song complexity, repertoire and song evolution (elaboration). At a minimum we read the first 200 hits for each combination of terms. We also searched through all the citations of the papers found studying this topic and papers that present relevant hypotheses. Our goal was not to conduct a meta-analytic review of all studies of the song characteristics of a species or group to search for geographical patterns, but to review studies where bird song complexity was explicitly considered in relation to latitude and/or migration. We did not consider studies featuring relatively short migratory distances (i.e. overall geographical extent <500 km).

## RESULTS

Our search of the literature discovered 29 papers that report the presence or absence of a latitudinal trend or a difference between migrants and non-migrants in some measure of song complexity. Measures of complexity were defined by the authors in most studies. Several studies of repertoire size were included because, despite the authors of these studies not characterizing this metric as 'complexity', repertoire size is often used as a complexity metric.

Of the 29 papers, 15 are comparisons between species and 14 are comparisons among subspecies or populations within one species. All of the studies are of passerines, only one of which considers suboscines. Nine studies looked for differences between migrants and non-migrants, 11 studies looked for latitudinal patterns, and nine studies considered both latitude and migratory strategy. Song complexity was assessed in many ways, mostly by measuring song repertoire size, counting and/or measuring the number and duration of elements, notes, syllables or phrases per unit, estimating song versatility or variety, or consulting previously published metrics (summarized in Table 1).

Increased song complexity was associated with migratory behaviour in eight studies and decreased song complexity in four studies; there was no pattern in six studies (Table 1). When considering potential effects of latitude, the outcomes are similarly variable: song complexity increased towards the poles in 10 studies but decreased in six, and four studies found no pattern (Table 1). Overall, more studies found a relationship between migration and/or latitude and increased song complexity (16) than with decreased song complexity (9), but this is not significantly different from an expected proportion of 0.50 (two-tailed binomial test  $P = 0.59$ ). Most studies do, however, find an effect of latitude and/or migration (25) rather than no pattern at all (4) (expected proportion 0.50, two-tailed binomial test  $P < 0.001$ ). Because patterns may vary with taxonomic level, we also asked how studies comparing populations of a single species differed from studies comparing multiple species. Of the within-species studies, five found support for complexity increasing with latitude (2) or migratory behaviour (3), seven found support for complexity decreasing with latitude (4) or migratory behaviour (3), and two studies found no pattern (Table 1). Of the between-species studies, 11 found support for complexity increasing with latitude (6) or migratory behaviour (5), two found support for complexity decreasing with migratory behaviour, and two studies reported no pattern (Table 1).

## DISCUSSION

Seven of the hypotheses discussed here predict and 16 studies found positive correlations between avian song complexity and latitude and/or

migration, whereas only one hypothesis predicts and nine studies found negative correlations. Four studies reported no pattern. This may be an underestimate due to publication bias or may signal that in most species, latitude and migration influence song complexity but do so variably.

With only 29 studies considering such a broad topic it is difficult to reach general conclusions. Nevertheless, it is clear that not all existing studies draw similar conclusions (Table 1). Additionally, the many hypotheses imply that the field is nowhere near consensus on how latitude and migratory behaviour might affect song complexity. Six different hypotheses are similar in that they broadly associate complexity with increases in migration or movement towards the poles, but the existing research does not overwhelmingly support this predicted pattern. Moreover, the studies reviewed here suggest (and some support) five fairly distinct biological drivers of any proposed patterns: acoustic adaptation, rapid mate choice, cultural drift vs. mixing, navigational abilities and resource defence (Table 2). The authors of these hypotheses discuss these drivers as either ecological or sexual, but at least two (territory lottery and ranging) may be better characterized as socially selected, as they describe competition for territories, not mates (West-Eberhard 1983). Considering the results of published studies, it seems highly unlikely that only one mechanism is at play or that all species would exhibit similar patterns in geographical variation in song complexity. Different selection pressures may result in similarly increased or decreased song complexity in different species, further complicating our understanding of causes. This should be evident simply by noting that not all species are suitable for studying all hypotheses (e.g. species that are entirely sedentary or migratory) but the effects of latitude or migration are still apparent. Additionally, different methodological approaches may be appropriate for different species, and comparisons between studies that use these different measures may not always be valid (see below).

## Song complexity

Thus far, in our discussions of song 'complexity', we have neglected to define the term. We are not alone in this: many authors do not precisely define (if at all) what constitutes complexity or may use statistical analysis to define complexity *post hoc*. It

is generally agreed that increases in song and syllable repertoire size as well as increases in note variability represent complexity (Catchpole & Slater 2008), but each study may define complexity in different ways. For example, Irwin (2000) states: 'Females... prefer greater song complexity and repertoire size...', implying complexity and repertoire size are conceptually different (albeit both influenced by sexual selection), whereas Peters *et al.* (2000) note: 'Song complexity is most often measured as song repertoire size...' This difference often stems from the different samples available to researchers and song differences between species. Studies that measure sound files obtained from sound libraries or using published estimates are limited in how many songs from a single individual they can acquire, and cannot measure repertoires or structural elements in the same way that studies which collect their own recordings can. Similarly, studies examining species that sing only a single song type might measure complexity in terms of the structure of the song, making those studies difficult to compare with studies of species whose complexity is largely characterized by having a song or syllable repertoire. Multi-species studies face additional challenges in choosing song complexity metrics. The more divergent the species are taxonomically, the fewer homologous measures are available for comparison. Studies that examine one species or genus often include many taxonomically specific measurements (such as whether a syllable uses two voices or the length of an introductory phrase common to the study species).

Of the studies in Table 1, four do not offer any definition of complexity or describe their measurements as reflecting song elaboration. Instead they are focused on the functions of repertoire size specifically, irrespective of the identity or features of the song types. Thirteen publications do offer an explicit definition, ranging from general (e.g. 'Complexity... generally includes a measure of note, syllable or song variety...' (Singh & Price 2015)) to more specific (e.g. '... and complexity (note variety and song versatility)' (Greig *et al.* 2013)). Twelve studies mention complexity but do not offer explicit definitions or are vague in their use of the term; complexity is instead defined implicitly using statistics (e.g. Cardoso *et al.* 2012) or in the text (e.g. 'complex syllables' in Nelson *et al.* 1996). Despite this lack of consensus, there is a general pattern of agreement in what an author measures as 'complexity'. All of the listed

studies include some count of unique elements per unit song length or among different songs as their key metric for complexity, suggesting that diversity in element structure is fundamental to defining 'complex' songs among song researchers.

If hypotheses that sexual selection pressure increases with latitude or migratory behaviour are largely correct, then we might also expect performance (the ability to sing physically challenging songs) to vary with these factors (Gil & Gahr 2002). Complexity may even be traded off for performance; in cases where complexity does not seem to vary geographically, it may be that performance does. Performance is not commonly discussed specifically in the reviewed studies, and the one study that refers to it explicitly lumps it together with complexity (Kaluthota *et al.* 2016). This suggests that researchers either do not generally consider performance to be directly related to complexity, or think it is perfectly correlated and complexity is simply easier to measure (although this is unlikely given the lack of supporting evidence). Performance in bird song is a comparatively new idea and there simply may not be enough research yet to draw conclusions one way or the other. It may be interesting to consider performance in future studies to help determine whether and how estimates of performance covary with song complexity and geography overall.

### Study system and data

The studies referenced in this review considered their questions in many ways: they may have studied populations of one species or compared multiple species, they used variable numbers of populations or species, and they may or may not have corrected for phylogeny. Song complexity analyses varied from comparisons of one or a few song measurements using *t*-tests and correlations, to principal coordinate analysis and model-based analyses of many song measurements. All of these studies were designed and analysed in different ways and are taxonomically diverse, making comparisons imperfect (Table 1). Although there is no way to circumvent this comparability problem completely, it is important to note these methodological differences so they can be considered in comparisons.

Studies conducted between species seem to find support for increased complexity with latitude or migration more frequently than within-species



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 trajectories, following different hypotheses. Of the 11 studies that examined repertoire size, seven find complexity to be correlated with latitude or migration, but four do not. Of the eight studies that use only song or syllable repertoire size, or both, as their metrics of complexity, four find increases, three find decreases, and one finds no pattern of song complexity related to latitude or migration. Collectively, these studies use 10 different bird 'groups' (e.g. Old World warblers, New World sparrows), making it difficult to assign differences in results to differences in life history. Thus, although most studies do find an effect of latitude or migration, either positive or negative, there is no clear indication that certain methods of comparison or measures of complexity show a greater or smaller tendency to vary with latitude.

Data sources for song features also varied widely for these studies; some gleaned song measurements from the literature, and others measured them from sound recordings. Those studies using sound recordings varied in the number and geographical distribution of recordings available to them depending on whether they used archived recordings from sound libraries or made their own field recordings. Some studies generated new measurement practices and others relied on applying approaches or reanalysing data previously described in the literature. Using previously published descriptions is not a bad practice, but care must be taken in their use. This is particularly true when discussing variation in structural elements because different people may have different tolerances as to when to call something the same or not. A good example of this was discussed in Ewert and Kroodsmas's (1994) study of Eastern Towhee *Pipilo erythrophthalmus* song. They found that their method of classifying Towhee song types differed significantly from a previous author's classification scheme, and identified fewer song types.

Clear description of methods for defining structural elements is vitally important to facilitate comparisons.

### Future directions

Comparative analyses by Read and Weary (1992), and later Weir and Wheatcroft (2011), seem largely responsible for popularizing the idea that migration and latitude may play a role in the evolution of complex bird song, specifically that song complexity increases with being migratory and with increasing latitude of breeding. However, not all studies agree with this assessment, and even those that do are difficult to compare in order to determine the underlying mechanism(s) at play. Although the idea that there is an 'expected outcome' of increasing complexity towards the poles has become common, the present review of the empirical literature finds that there is no broad consensus and no expectation to be violated. Rather, more research is needed to better demonstrate whether patterns exist and, if so, what the possible mechanisms generating them are.

Future studies of a variety of species that measure song complexity in conjunction with relevant ecological or sexual selection variables will go a long way towards advancing our understanding of the relationships between latitude, migration and song elaboration. Table 1 is dominated by Old World warblers, New World sparrows and New World wrens. More diversity of study species would indicate whether these hypotheses hold up for other groups of birds. For example, broadly distributed non-passerines with vocalizations much like passerine song, such as members of the Columbidae, Trochilidae or Cuculidae, may prove to be interesting groups for study. Noticeably missing from these studies are suboscines. Studying species that do not learn their songs would be informative both as controls for hypotheses where song learning is part of the proposed mechanism and as parallel comparisons for hypotheses where song learning is inconsequential.

Most hypotheses included here made (or implied) predictions about the breeding biology of tropical and temperate-zone species but few quantified traits of tropical breeders. Although theory predicts certain characteristics of tropical species, such as low rates of extra-pair paternity and long breeding seasons, there is not enough

data to conclude this confidently (e.g. Macedo *et al.* 2008, Cramer *et al.* 2011, Ferretti *et al.* 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 *et al.* 2009, Medina & Francis 2012, Xing *et al.* 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 repertoire size is a good proxy for the strength of sexual selection and that, given a choice, birds will choose to mate with individuals that have a more elaborate or complex song. However, this is often not explicitly tested and there is debate in the literature about how such testing should be done (Wilkins *et al.* 2013, Byers 2015, Price 2015). None of the studies included here measured proxies of sexual selection, such as time to pairing, reproductive success, or level of parasite or disease infection, leaving room for improvement in future studies. Researchers positing connections between song complexity and female choice should test whether females actually prefer the 'complex' traits in question. Additionally, several hypotheses mention resource defence in the context of sexual selection, but this could be more accurately described as being mediated by social selection. None of the studies reviewed here invoke social selection (i.e. selection for competition for resources other than mates, such as nesting sites, food or space, West-Eberhard 1983) as a force driving changes in song complexity. Future studies considering both social and sexual selection would be valuable.

## CONCLUSIONS

The studies reviewed here attempted to document latitudinal patterns of avian song complexity. Despite a variety of hypotheses mostly rooted in sexual selection theory, it is still unclear whether and to what extent song complexity may be influenced by latitude and its correlate, migration. Certainly there is no overarching theory on the topic beyond the observation that vegetation is different at high latitudes or a weak appeal to 'higher sexual selection pressures' assumed to exist in these places. What we can clearly conclude is that latitude and migration do not universally affect song complexity in the same way among birds and that increased latitude or migratory behaviour is not always associated with increased complexity. This is perhaps an unsurprising result but an important one to acknowledge, given the overwhelming bias in the theoretical literature towards predicting a universal directional trend. High latitudes and migration affect birds in a multitude of ways, and it is unrealistic to expect one hypothesis to explain all or even most of the variation observed in bird song features. Many of the studies discussed here are observational and correlational, an excellent approach for initial studies, but none go any further. That being said, many studies cited in this review do find an effect of latitude or migration in their study system and future studies should explicitly test the hypotheses that offer the most potential to explain these outcomes.

We thank TJ Hathcock, Stephanie Pitt and four anonymous reviewers for providing useful comments and criticisms that helped to improve the manuscript. A University of Northern Colorado graduate student assistantship funded this research.

## REFERENCES

- Andersson, M.B. 1994. *Sexual Selection*. Princeton: Princeton University Press.
- Bearhop, S., Fiedler, W., Furness, R.W., Votier, S.C., Waldron, S., Newton, J., Bowen, G.J., Berthold, P. & Farnsworth, K. 2005. Assortative mating as a mechanism for rapid evolution of a migratory divide. *Science* **310**: 502–504.
- Benedict, L. & Bowie, R.C.K. 2009. Macrogeographical variation in the song of a widely distributed African warbler. *Biol. Lett.* **5**: 484–487.
- Bolus, R.T. 2014. Geographic variation in songs of the Common Yellowthroat. *Auk* **131**: 175–185.

- 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. 1: 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., Liljeström, 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.** 2008. Adaptations to migration in birds: behavioural strategies, morphology and scaling effects. *Philos. Trans. R. Soc. B* **363**: 287–299.
- Irwin, D.E.** 2000. Song variation in an avian ring species. *Evolution* **54**: 998–1010.
- Kaluthota, C., Brinkman, B.E., dos Santos, E.B. & Rendall, D.** 2016. Transcontinental latitudinal variation in song performance and complexity in House Wrens (*Troglodytes aedon*). *Proc. R. Soc. Lond. B* **283**: 20152765.
- Kraaijeveld, K. & Dickinson, J.L.** 2001. Family-based winter territoriality in Western Bluebirds, *Sialia mexicana*: the structure and dynamics of winter groups. *Ann. Behav.* **61**: 109–117.
- Kroodsma, D.E. & Verner, J.** 1987. Use of song repertoires among Marsh Wren populations. *Auk* **104**: 63–72.
- Kroodsma, D.E., Wilda, K., Salas, V. & Muradian, R.** 2001. Song variation among *Cistothorus* wrens, with a focus on the Mérida Wren. *Condor* **103**: 855–861.
- Macedo, R.H., Karubian, J. & Webster, M.S.** 2008. Extra-pair paternity and sexual selection in socially monogamous birds: are tropical birds different? *Auk* **125**: 769–777.
- Mahler, B. & Gil, D.** 2009. The evolution of song in the *Phylloscopus* leaf warblers (aves: Sylviidae): a tale of sexual selection, habitat adaptation, and morphological constraints. *Adv. Stud. Behav.* **40**: 35–66.
- Marra, P.P., Sherry, T.W. & Holmes, R.T.** 1993. Territorial exclusion by a long-distance migrant warbler in Jamaica: a removal experiment with American Redstarts (*Setophaga ruticilla*). *Auk* **110**: 565–572.
- McGregor, P.K., Krebs, J.R. & Ratcliffe, L.M.** 1983. The reaction of Great Tits (*Parus major*) to playback of degraded and undegraded songs: the effect of familiarity with the stimulus song type. *Auk* **100**: 898–906.
- Medina, I. & Francis, C.D.** 2012. Environmental variability and acoustic signals: a multi-level approach in songbirds. *Biol. Lett.* **8**: 928–931.
- Morton, E.S.** 1975. Ecological sources of selection on avian sounds. *Am. Nat.* **109**: 17–34.
- Morton, E.S.** 1986. Predictions from the ranging hypothesis for the evolution of long distance signals in birds. *Behaviour* **99**: 65–86.
- Morton, E.S., Howlett, J., Kopysh, N.C. & Chiver, I.** 2006. Song ranging by incubating male Blue-headed Vireos: the importance of song representation in repertoires and implications for song delivery patterns and local/foreign dialect discrimination. *J. Field Ornithol.* **77**: 291–301.
- Mountjoy, D.J. & Leger, D.W.** 2001. Vireo song repertoires and migratory distance: three sexual selection hypotheses fail to explain the correlation. *Behav. Ecol.* **12**: 98–102.
- Nelson, D.A., Marler, P. & Morton, M.L.** 1996. Overproduction in song development: an evolutionary correlate with migration. *Anim. Behav.* **51**: 1127–1140.
- Newton, I.** 2010. *The Migration Ecology of Birds*. London: Academic Press.
- Nowicki, S. & Searcy, W.A.** 2004. Song function and the evolution of female preferences: why birds sing, why brains matter. *Ann. N.Y. Acad. Sci.* **1016**: 704–723.

- 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**: 1713–1720.
- Weir, J.T., Wheatcroft, D.J. & Price, T.D. 2012. The role of ecological constraint in driving the evolution of avian song frequency across a latitudinal gradient. *Evolution* **66**: 2773–2783.
- West-Eberhard, M.J. 1983. Sexual selection, social competition, and speciation. *Q. Rev. Biol.* **58**: 155–183.
- Wilkins, M.R., Seddon, N. & Safran, R.J. 2013. Evolutionary divergence in acoustic signals: causes and consequences. *Trends Ecol. Evol.* **28**: 156–166.
- Wyndham, E. 1950. Length of birds' breeding seasons. *Am. Nat.* **128**: 155–164.
- Xing, X., Slabbekoorn, H., Campbell, J., Li, F. & Ma, J. 2017. Distinct song parts of the endemic marsh grassbird of China vary with latitude and climate among migratory and sedentary populations. *Evol. Ecol.* **31**: 63–76.
- Yasukawa, K. 1981. Song repertoires in the Red-winged Blackbird (*Agelaius phoeniceus*): a test of the Beau Geste hypothesis. *Anim. Behav.* **29**: 114–125.

Received 24 May 2017;

revision accepted 28 June 2018.

Associate Editor: Andrew Farnsworth.