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Vireo song repertoires and migratory distance: Three sexual selection hypotheses fail to explain the correlation

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Abstract

Previous studies have found a relationship between migration and the degree of elaboration of sexually selected traits, but investigators have differed in the mechanisms they proposed to account for this association. We examined the relationship between song repertoire size and distance migrated among birds in the genus *Vireo*. There is a strong positive relationship between migratory distance and repertoire size in this genus, but our data do not support the specific predictions of any of the three proposed mechanisms (the “rapid pairing,” “good migrations,” and “territory lottery” hypotheses). Migration distance is presumably correlated with other life-history characteristics that influence the development of sexually selected traits.

Keywords: bird song, migration, sexual selection, song repertoires, vireos.

In recent years a tremendous research effort documented that sexual selection is a widespread and influential force on the evolution of morphology and behavior, leading to a clearer understanding of its operation. One aspect that remains poorly understood is why there is tremendous variation in the development of sexually selected traits, even among closely related species with superficially similar life histories (Andersson, 1994).

Mating systems have long been considered to be a likely correlate of variation in sexually selected traits, as polygamous species are expected to show greater variation in mating success (Darwin, 1871; Kirkpatrick, 1987). The results of recent comparative studies of birds have been mixed, however; some studies have shown that particular traits are correlated strongly with polygyny (plumage conspicuousness: Baker and Parker, 1979; size dimorphism: Payne, 1984), and others have found weak correlations (tail dimorphism: Winquist and Lemon, 1994), or no significant correlation at all (size and plumage dimorphism: Møller, 1986; song repertoires: Read and Weary, 1992). Höglund (1989) found no significant association between size or plumage dimorphism and the occurrence of lekking, and Trail (1990) pointed out that about 25% of lek-breeding bird species were monomorphic in size and plumage, although lek breeding has traditionally been viewed as the most extreme form of polygyny. Oakes (1992) did find more frequent sexual size dimorphism among lekking species (with probability values ranging from 0.064 to 0.003) when the data were analyzed using Maddison’s concentrated changes test. Two studies have found that variation within the broader traditional categories of mating systems is important. Møller and Birkhead (1994) found that plumage brightness was more closely related to extra-pair paternity than to social mating system, although this correlation was still relatively weak ($r^2 = .109$). Scott and Clutton-Brock (1989) found that males were brighter in waterfowl species that paired frequently and suggested that such life-history variation among monogamous birds might be one factor obscuring the expected relationship between polygyny and exaggerated sexually selected traits.

Another suggested correlate of the development of sexually selected traits is migratory behavior. There are several

explanations for why migration should be correlated with sexual selection. Catchpole (1982) suggested that migratory species seem to have larger song repertoires than resident species (a relationship confirmed for within-genera comparisons by Read and Weary, 1992). Catchpole proposed that migratory species would have less time available for pairing and breeding and that this would favor rapid pairing and increase sexual selection pressure in the migratory species relative to residents. We refer to this idea as the “rapid pairing” hypothesis. Fitzpatrick’s (1994) “good migrations” hypothesis suggests that if the development of sexually selected traits is influenced by the suitability of the wintering grounds (through their effects on the condition of the birds), then females in migratory species might be able to choose mates with genes that would help guide their offspring to suitable wintering areas. A third hypothesis is based on the idea that resident and migratory species may use different strategies to acquire territories and breeding opportunities. Migratory species are likely to face a situation where all potential territories are available when the first individuals begin to return to the breeding grounds, and acquisition of territories may subject most individuals to intense competition, which will favor those sexually selected traits used in intrasexual competition. Resident species, in contrast, cannot rely on a large number of territories being vacant at any particular time, and success in acquiring a territory may depend primarily on being the first individual to detect a vacancy and to occupy the area. This “territory lottery” hypothesis suggests that chance is more important in acquiring a territory in resident species and that traits used in intrasexual competition will not be as strongly emphasized. Mate choice may also be restricted in resident species if year-round pair bonds are normally maintained and opportunities for pairing usually arise after a member of an established pair dies. In such systems there will be few potential mates available for comparison at any time and therefore less incentive to advertise individual quality. A concept similar to the territory lottery hypothesis is discussed by Fitzpatrick (1998) with respect to intrasexual selection alone.

This article examines the correlation between migratory behavior and song repertoire size among species of the genus *Vireo* and tests these three hypotheses. The vireos are an excellent group for such a study because there is a great deal of variation in song repertoire size and migratory behavior in what is in most respects a uniform genus. Repertoires range from 1 to at least 95 song types, and there are resident species in both tropical and temperate climates as well as short- and long-distance migrants. Vireos are small (8.5-20 g), primarily insectivorous passerines that live in forested or scrub habitats. Most species are rather drab in plumage and all are nominally monogamous, although an isolated case of polygyny and frequent extra-pair fertilizations are known to occur at least in the red-eyed vireo (*Vireo olivaceus*; Morton et al., 1998; Mountjoy, 1997). We tested the rapid pairing hypothesis by comparing sympatric pairs of vireo species to test the prediction that later-arriving species should possess larger repertoires. The good migrations and territory lottery hypotheses are similar in that both predict a dichotomy between resident species (with low levels of sexual selection and therefore small song repertoires) and migratory species (with more intense sexual selection and larger repertoires). We tested these hypotheses by asking whether migratory species, examined separately, still show a relationship between migration distance and song repertoire size. No such relationship is predicted by the good migrations or territory lottery hypotheses, so any correlation within the subset of migratory species would imply that alternative hypotheses are required to explain a link between migration and sexual selection.

Methods

Estimates of song repertoire size were obtained for 28 of the 31 species recognized by Sibley and Monroe (1990) in the genus *Vireo* (Table 1). We used published estimates where available, using the maximum values for individual repertoires when a range was given or when more than one estimate was available. Repertoire estimates for other species were based on analysis of commercially available recordings (Barlow, 1995). We prepared spectrograms for all songs analyzed using Canary software (Charif et al., 1995) and classified songs based on visual assessment. Two species were omitted from most analyses (*V. gilvus* and *V. swainsonii*) because no precise literature estimates of repertoire size were available, and the available recordings were too short to make an estimate of the repertoire sizes, which are apparently quite large (*V. gilvus*: Howes-Jones, 1985; the possibly conspecific *V. swainsonii* is probably similar). A minimum limit for the repertoire size of *V. gilvus* was obtained by analyzing a small sample of song from one individual. This recording was made at Burchard Lake, Pawnee County, Nebraska, USA, on 18 July 1996. We prepared spectrograms for 36 consecutive songs of *V. gilvus* using Canary software (Charif et al., 1995) and assigned them to song types based on visual inspection. The Noronha vireo (*Vireo gracilirostris*) was also omitted from all analyses because the published analysis of its song (Barlow and Bartolotti, 1988) is believed to be inaccurate (Olson, 1994).

We estimated migration distance for each species as the difference between the latitude of the northern edge of the breeding range and the northern edge of the wintering range, based on published maps and range descriptions (American Ornithologists' Union, 1983; Godfrey, 1986; Howell and Webb, 1995; Scott, 1987; Sibley and Monroe, 1990).

To control for the lack of independence of related species, we analyzed the data using the Comparative Analysis by Independent Contrasts (CAIC) package (Purvis and Rambaut, 1995). The CAIC software calculates standardized linear contrasts, which

Table 1. Migration distance and repertoire size estimates for vireos

Species	Distance migrated ^a	Repertoire estimate ^b	Repertoire source
<i>Vireo brevipennis</i>	0	1	This study
<i>Vireo bellii</i>	19.5	3	This study
<i>Vireo modestus</i>	0	2	This study
<i>Vireo nanus</i>	0	1	This study
<i>Vireo latimeri</i>	0	1	This study
<i>Vireo griseus</i>	9.5	17	Borror (1987)
<i>Vireo caribaeus</i>	0	2	This study
<i>Vireo pallens</i>	0	1	This study
<i>Vireo gundlachi</i>	0	2	This study
<i>Vireo crassirostris</i>	0	1	This study
<i>Vireo bairdii</i>	0	1	This study
<i>Vireo vicinior</i>	8	12	Borror (1972)
<i>Vireo atricapillus</i>	12	7	This study
<i>Vireo nelsoni</i>	0	10	This study
<i>Vireo flavifrons</i>	23.5	7	James (1984)
<i>Vireo cassinii</i>	24	14	James (1981)
<i>Vireo plumbeus</i>	18	12	James (1981)
<i>Vireo solitarius</i>	29	18	James (1981)
<i>Vireo osburni</i>	0	1	This study
<i>Vireo huttoni</i>	0	3	Davis (1995)
<i>Vireo carmioli</i>	0	10	This study
<i>Vireo hypochryseus</i>	0	1	This study
<i>Vireo leucophrys</i>	0	2	This study
<i>Vireo gilvus</i>	34.5	36 ^c	This study
<i>Vireo philadelphicus</i>	42	25	Borror (1972)
<i>Vireo olivaceus</i>	58.5	95	Godard (1993)
<i>Vireo flavoviridis</i>	26	21	Borror (1972)
<i>Vireo altiloquus</i>	17.5	9	Borror (1972)
<i>Vireo magister</i>	0	23	This study

a. Measured as degrees of latitude between northernmost wintering areas and northernmost breeding areas.

b. Repertoire estimates are of maximum individual repertoire size, except where noted.

c. Estimate for *V. gilvus* is a minimum estimate and was used only for arrival-date comparisons.

represent differences between two species or groups of species at each node in the phylogeny. The contrasts are standardized by dividing the raw contrasts by their expected standard deviation in order to eliminate heterogeneity of variance. The standardized contrasts were then analyzed using standard linear regression with the regression line forced through the origin. The phylogeny used in these analyses (Figure 1) was based on the single most parsimonious tree found by Murray et al. (1994) using cytochrome b sequence variation. Murray et al. analyzed only 11 species; the other species in the genus were added to this framework based on super-species groupings and traditional taxonomic views regarding relationships within the genus (American Ornithologists' Union, 1983; Sibley and Monroe, 1990) and some additional molecular evidence (Johnson, 1995). For the purpose of analysis in CAIC, we assumed equal branch lengths in the phylogeny (equivalent to assuming a punctuational model of evolution). Distance migrated and repertoire size are continuous variables, so we used the recommended algorithm in CAIC ("Crunch") for continuous variables.

Arrival dates on the breeding grounds for species which regularly nest north of Mexico were compared by identifying independent pairs of species within the phylogeny, with the constraint that both members of a pair had to breed within the same geographic region. Five pairs were identified for which arrival date information could be obtained from regional annotated checklists.

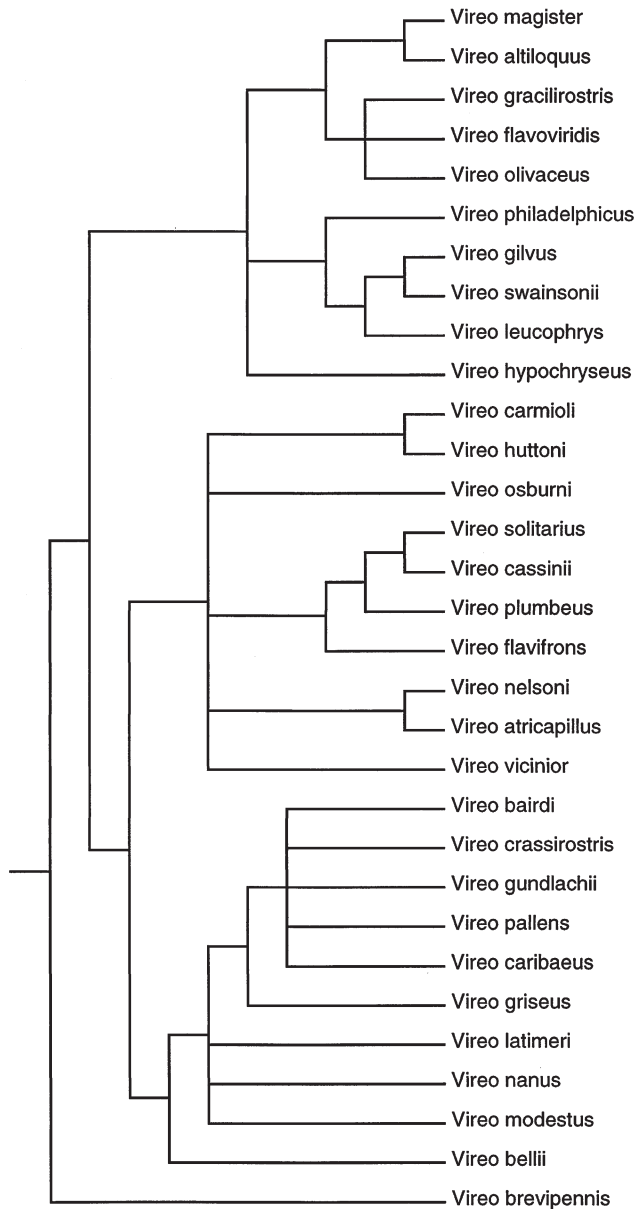


Figure 1 Hypothesized phylogeny of the vireos. Based on Murray et al. (1994) with additional species inserted to reflect traditional views on relationships in the genus.

Results

The repertoire size of vireos is well correlated with the distance migrated by the species ($r = .741$, $n = 18$ contrasts, $p = .0003$; Figure 2). This correlation is not a result of any assumptions in the traditional classification incorporated in the phylogeny used here; the correlation remains highly significant when the analysis is restricted to the species represented in a phylogeny based on molecular data only ($r = .842$, $n = 8$ contrasts, $p = .0044$). The correlation also does not depend on the repertoire estimates derived from commercial recordings; the correlation is still significant if the analysis is restricted to species for which repertoire estimates are available in the literature ($r = .852$, $n = 9$ contrasts, $p = .0017$).

The correlation between repertoire size and migration distance does not appear to be due to correlations between repertoire size and either the northernmost breeding latitude or the northernmost wintering latitude. Repertoire size and northern-

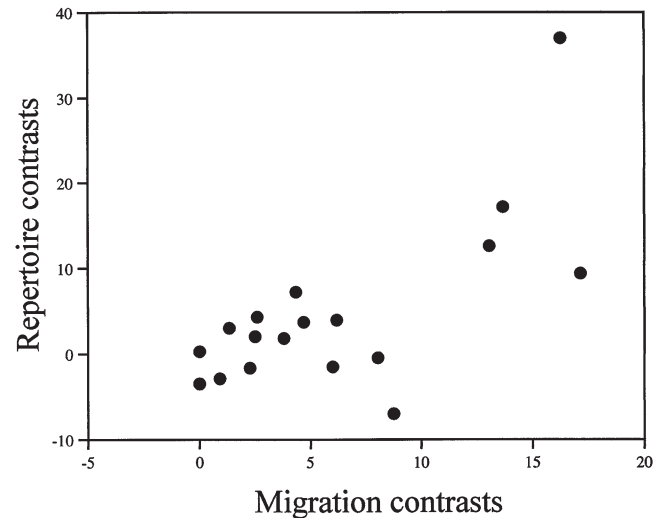


Figure 2. Relationship between migration contrasts and song repertoire contrasts for species in the genus *Vireo* ($r = .741$, $n = 18$ contrasts, $p = .0003$).

most wintering latitude are uncorrelated ($r = -.028$, $n = 18$ contrasts, $p = .908$), and although the correlation between repertoire size and northernmost breeding latitude is significant ($r = .598$, $n = 18$ contrasts, $p = .0069$) it is not as strong as the correlation with migration distance.

Catchpole's (1982) rapid pairing hypothesis predicts that species that return to the breeding grounds later should have larger repertoires. We compared the arrival dates and repertoire sizes in five species pairs. Data were available from more than one geographic area for four of these pairs. *V. gilvus* is included in this analysis based on a lower limit for its repertoire obtained from a Nebraska bird that sang 36 song types in 36 consecutive songs. The prediction that later-arriving species should have larger repertoires is not supported among the five species pairs analyzed; in only one pair does the later-arriving species have the larger repertoire, while in the other four pairs the earlier-arriving species has the larger repertoire (sign test: $p > .8$; Table 2).

Fitzpatrick's (1994) good migrations hypothesis and the territory lottery hypothesis both predict that sexual selection should be more intense in migratory species compared to resident species, but they predict that all migratory species should experience similar sexual selection pressure regardless of the distance migrated. To test this prediction we restricted the analysis to those species that migrate. Even among all species that migrate, there is a significant correlation between song repertoire size and the distance migrated ($r = .812$, $n = 10$ contrasts, $p < .005$).

Recently, concerns have been expressed about problems in the reconstruction of ancestral characters (Cunningham et al., 1998) and other problems that may affect comparative analyses that use independent contrasts. It has been suggested that species-level analyses may, in some cases, be as appropriate a method for analysis of comparative data as is the use of independent contrasts (Losos, 1999; Ricklefs and Starck, 1996). Although we believe that the use of independent contrasts or other methods to control for phylogenetic effects is important, it is worth noting that our results do not depend on the use of such analyses. The correlation between migration and repertoire size is significant when analyzed as a simple linear regression using species-level data ($r = .589$, $n = 31$ species, $p = .0005$). Similarly, the correlation remains significant when only migratory species are considered ($r = .580$, $n = 14$ species, $p = .030$).

Table 2. Comparison of repertoire sizes with respect to relative arrival dates in vireo species breeding in the same geographic area

Species compared	Area (reference) ^a	Relative repertoire size of later-arriving species
<i>Vireo bellii</i>	North-central Texas (1)	Smaller
<i>Vireo griseus</i>	Oklahoma (2)	Smaller
	Wisconsin (3)	Smaller
	Missouri (4)	Smaller
<i>Vireo vicinior</i>	California (5)	Larger
<i>Vireo huttoni</i>	Big Bend, TX (6)	Larger
	Arizona (7)	Larger
<i>Vireo flavifrons</i>	Wisconsin (3)	Smaller
<i>Vireo solitarius</i>	Minnesota (8)	Smaller
	Ontario (9)	Smaller
	Connecticut (10)	Smaller
	Ligonier Valley, PA (11)	Smaller
	Tennessee (12)	Smaller
	South Carolina (13)	Smaller
<i>Vireo gilvus</i>	Minnesota (8)	Smaller
<i>Vireo philadelphicus</i>	Ontario (9)	Smaller
<i>Vireo olivaceus</i>	Florida (14)	Smaller
<i>Vireo altiloquus</i>		

Catchpole's (1982) rapid pairing hypothesis predicts that later-arriving species should have larger repertoires.

a. References: (1) Pulich, 1988; (2) Sutton, 1967; (3) Robbins, 1991; (4) Robbins and Easterla, 1992; (5) Grinnell and Miller, 1944; (6) Wauer, 1973; (7) Brandt, 1951; (8) Janssen, 1987; (9) James, 1991; (10) Zeran-ski and Baptist, 1990; (11) Leberman, 1976; (12) Robinson, 1990; (13) Wayne, 1910; (14) Stevenson and Anderson, 1994.

Discussion

There is a robust correlation between repertoire size and distance migrated in vireos. This correlation explains almost 55% of the substantial variation in repertoire size in this genus, which seems to be a higher proportion of variation accounted for by a single variable than has been found in any other comparative study of a sexually selected trait. However, none of the three proposed hypotheses that might explain this correlation appears to be supported by the data.

Catchpole's (1982) rapid pairing hypothesis is the only one of the three hypotheses considered here to have been previously applied to interspecific variation in song repertoires. Read and Weary (1992) suggested that their finding of larger repertoires in migratory species than in residents supported the rapid pairing hypothesis, but they did not consider any alternative explanations for an association between migration and repertoire size. Although only five pairs of species were tested, the fact that the large repertoire species returned earlier in four of the five pairs, counter to the prediction of the hypothesis, seems to argue strongly against this hypothesis.

Fitzpatrick's (1994) good migrations hypothesis was originally proposed to explain variation in plumage brightness, but it would seem to apply as well to other sexually selected traits such as bird song that may be affected by the condition of individuals as a result of the suitability of their wintering grounds. Although there is some evidence that condition affects the repertoire size of individual birds (Mountjoy and Lemon, 1996), there is no information on whether song repertoires are particularly sensitive to condition in winter or any other season. Fitzpatrick (1994) did use comparisons between more and less migratory species when testing the good migrations hypothesis, but it

would seem that this hypothesis does not make any predictions regarding the strength of selection between short- and long-distance migrants. Females in all migratory species would benefit from having a mechanism to assess the suitability of a male's wintering grounds, if obtaining good migratory genes is an important fitness benefit as the hypothesis suggests. The strong correlation between migration distance and repertoire size when only migrants are considered is thus not predicted by the good migrations hypothesis and suggests that some other explanation is required.

The territory lottery hypothesis is, to our knowledge, a novel hypothesis for explaining interspecific variation in the elaboration of sexually selected traits. Like the good migrations hypothesis, it predicts a dichotomy between resident and migratory species and does not predict any difference between short- and long-distance migrants. It is therefore also rejected on the basis of the correlation between migratory distance and repertoire size among migratory species.

Having rejected all three of the hypotheses available that predict an association between migration and sexual selection, there is a need to generate additional hypotheses that can provide an explanation for these data. It would also be worth-while to test whether current hypotheses can explain the results of previous studies (Fitzpatrick, 1994; Read and Weary, 1992) that have claimed to find an association between migration and sexual selection. It is unlikely that migration distance itself is in any sense a causative factor. Rather, it seems that there must be some other life-history correlates of migration that promote or allow the exaggeration of sexually selected traits.

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