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Whip it good! Geographic consistency in male songs and variability in female songs of the duetting eastern whipbird *Psophodes olivaceus*

Daniel J. Mennill and Amy C. Rogers

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Geographic variation in male bird songs has been studied extensively, but there have been few investigations of geographic variation in female songs or sex differences in patterns of geographic variation. We compared patterns of variation in male and female songs of eastern whipbirds *Psophodes olivaceus* by analyzing recordings from 16 populations across the species' geographic range in eastern Australia. We found remarkably different patterns of geographic variation between the sexes. Female eastern whipbird songs are easily categorized into discrete song types. Song types are shared between nearby females, but female songs show pronounced differences at a continental scale. In contrast, male eastern whipbird songs show high consistency throughout the species' geographic range. All recorded males share the ability to transpose the frequency of the introductory whistle and most recorded males share the ability to vary the direction of the slope of the terminal whip crack. For eight of nine measured variables, female songs show significantly higher levels of variation than male songs. We discuss whether sex differences in dispersal, song learning strategies, and song function may explain these sex differences in patterns of song variation. We suggest that eastern whipbirds have experienced a decoupling of male and female song learning strategies and that the songs of each sex have responded to different selective pressures in the context of countersinging interactions. We speculate that consistency in male songs throughout the geographic range of eastern whipbirds may arise through female preference for males that perform large bandwidth whip cracks.

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Geographic variation in bird songs has been the subject of many investigations over the last four decades (e.g. Marler and Tamura 1964, Baptista 1975, MacDougall-Shackleton and MacDougall-Schackleton 2001). Research has focused principally on the importance of environmental and genetic effects on signal variation in geographically separated populations of songbirds. Overwhelmingly, these studies have been conducted on species in which only males sing. However, in many species of birds both males and females sing, especially in the tropics (Langmore 1998, Slater and Mann 2004). An understanding of geographic variation in female song and sex differences in geographic variation can provide us with a better understanding of the function and evolution of bird song.

In over 220 bird species, males and females coordinate their songs to produce vocal duets (Hall 2004). Although the adaptive significance of vocal duetting remains a matter of intensive investigation, it is clear that duetting birds generally exhibit sex role convergence in vocal behaviour where both sexes participate in vocal defence of territories (Slater and Mann 2004). Geographic variation in the songs of duetting birds has been noted for several species (e.g. eastern whipbirds *Psophodes olivaceus*, Watson 1969; yellow-naped amazons *Amazona auropalliata*, Wright and Dorin 2001). However, a detailed comparison of geographic variation between male and female songs throughout a species' geographic range has not been conducted previously.

The eastern whipbird is an endemic Australian passerine in which males and females sing precise, antiphonal duets (Watson 1969, Rogers and Mulder 2004). Pairs form stable, long-term partnerships with low rates of divorce, defend year-round territories 0.7–3.8 ha in size, and produce multiple clutches across a breeding season (Rogers and Mulder 2004; reproductive analyses conducted at Mimosa Rocks National Park in New South Wales). Females are solely responsible for nest building and incubation, but both parents feed nestlings and fledglings (Rogers and Mulder 2004). The geographic range of eastern whipbirds stretches along the eastern coast of Australia from northeastern Queensland to eastern New South Wales and Victoria. Their range is comprised of two disjoint areas with race *lateralis* in the north and *olivaceus* in the south (Pizzey and Knight 1999).

In this study, we explore geographic variation in the songs of eastern whipbirds across their geographic range. We compare variation in male songs against variation in female songs to investigate whether there are sex differences in geographic variation in whipbird song structure.

Methods

Sound recordings

We measured eastern whipbird recordings from 16 different populations along the east coast of Australia: Kuranda (16°49'S, 145°38'E) and Atherton (17°17'S, 145°27'E) in northeastern Queensland, Nambour (26°37'S, 152°57'E), Toowoomba (27°33'S, 151°57'E), Mount Tamborine (27°58'S, 153°12'), and Lamington National Park (28°15'S, 153°8'E) in southeastern Queensland, and Sydney Royal National Park (33°50'S, 151°13'E), Eurobodalla National Park (36°47'S, 150°8'E), Bogola Head point (36°15'S, 150°9'E), Mystery Bay (36°18'S, 150°8'E), Wallaga Lake (36°22'S, 150°0'E), Middle Beach (36°38'S, 150°0'E), Mimosa Rocks National Park (36°41'S, 149°59'E), Tathra (36°43'S, 149°59'E), Wallagoot Lake (36°47'S, 149°56'E), and Bournda National Park (36°47'S, 149°52'E) in New South Wales (NSW). Birds in Atherton were recorded by DJM. Birds in NSW were recorded by ACR. Birds in Lamington National Park and Mount Tamborine were recorded by David Putland of the University of Queensland. Recordings from the remaining locations were obtained from the Macaulay Library at Cornell University.

In two populations, birds were uniquely colour-banded to facilitate individual recognition. In the remaining 14 populations, we distinguished between pairs by analyzing songs recorded from different areas of each population. Eastern whipbird pairs show long-term fidelity and pairs aggressively defend territories against their neighbours throughout the year (Rogers

and Mulder 2004). Therefore, we are confident that pairs sampled from different areas of each population do in fact represent different individuals. When there was ambiguity about whether multiple recording sessions might come from the same pair, we measured songs only from the longest continuous recording session and did not include the remaining sessions in our analyses.

Sound measurements

We digitized field recordings using Syrinx-PC (J. Burt, Seattle WA) and analyzed fine structural details of male and female songs using both Syrinx-PC and CoolEdit 2000 (Syntrillium, Phoenix AZ). To facilitate comparison between the sexes, we chose measurements that describe the temporal and frequency characteristics of songs that could be measured for both male and female songs (see Fig. 1). For each song we measured: (1) the number of syllables, (2) the length of the first syllable, (3) the frequency of maximum amplitude (FMA) for the first syllable, (4) the FMA for the terminal syllable, (5) the highest frequency of the terminal syllable, (6) the lowest frequency of the terminal syllable, (7) the time between the point of highest and lowest frequency of the terminal syllable, (8) whether the terminal syllable was primarily ascending or descending, and (9) the number of inflection points in the terminal syllable. Based on measurements 5–7, we calculated an additional measurement: (10) the rate of frequency change in the terminal syllable (calculated as the highest frequency minus lowest frequency divided by the time between the points of highest and lowest frequency). We used an effective frequency resolution of 1 Hz for all frequency measures and 1 ms for all temporal measures.

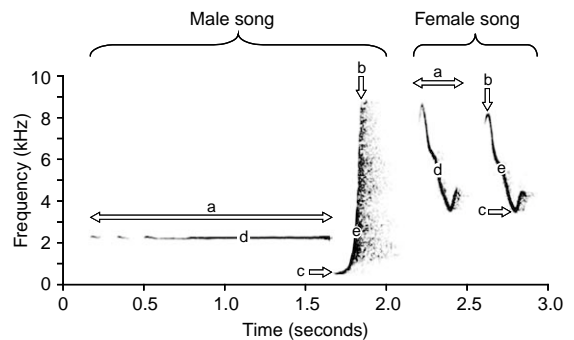


Fig. 1. Sound spectrogram of a typical eastern whipbird duet, comprised of a male song followed by a female song. The male initiates the duet with a long whistle followed by a frequency modulated whip crack. The female terminates the duet with a song that often consists of two repeated syllables (“chew chew”). We measured the same features of both the male song and the female song, including: (a) length of the first syllable, (b) highest frequency of the terminal syllable, (c) lowest frequency of the terminal syllable, (d) frequency of maximum amplitude (FMA) of the first syllable, and (e) FMA of the terminal syllable.

The introductory whistle of the male eastern whipbird song typically contains several short amplitude breaks at the beginning (e.g. in Fig. 1 the male song has two amplitude breaks). We did not count these amplitude breaks as separate syllables because the number of amplitude breaks detected depended on the distance between the recordist and the bird. Therefore, for males we calculated measurement 2 (above) as the length of the entire whistle, including these short breaks when they were present.

Geographic distance calculations

We estimated the geographic distances between the 16 recording sites using the Australian Government's Geoscience Australia "As the Cocky Flies" website (www.ga.gov.au). These distance estimates are accurate to hundreds of meters for sites that are hundreds of kilometers apart and to a few kilometers for sites that are thousands of kilometers apart.

Sample size and analytical methods

We sampled songs from 112 eastern whipbirds: 59 males and 53 females. For 52 pairs we sampled both the male and female, for seven pairs we sampled only the male, and for one pair we sampled only the female. We analyzed a total of 578 songs, with an average of 5.2 ± 0.3 songs per individual and 7.0 ± 0.5 individuals per population. We measured songs blind to the population origin of the singer. For each song, we calculated measurements 1–10 (above) and then computed an average value for each individual for each measurement.

We used two techniques to analyze variation in male and female songs. First, we visually inspected sound spectrograms to understand broad patterns of variation. Second, we compared variation in male versus female song attributes by calculating the coefficient of variation (standard deviation divided by the mean) for the song measurements described above. We use Levene's test of unequal variance to evaluate whether male and female songs showed different levels of variation. All analyses were conducted in JMP 5.0 (SAS Institute, Cary NC). All values are reported as mean \pm SE. All tests are two-tailed.

Results

Consistency in male songs

Male eastern whipbirds' songs show high acoustic similarity across their geographic range (Fig. 2). All recorded male songs have two sections: a long introductory whistle and an explosive whip crack. The male

whistle is a pure frequency tone 2.10 ± 0.04 seconds in length (average for $n = 59$ males). The frequency of the whistle is highly variable between individuals (range: 1139–5595 Hz). However, the frequency of the whistle is also highly variable between successive songs from a single individual (largest range detected for a single male: 1655–5595 Hz). One extensively recorded male sang 22 different whistle frequencies. Therefore male whistles are not easily categorized into discrete types but, instead, vary in frequency across a large frequency spectrum.

The male whip crack is a frequency modulated tone which rapidly ascends or descends across a broad frequency spectrum of 7632 ± 35 Hz in just 0.166 ± 0.002 seconds ($n = 59$ males). In all recordings from all populations, the whip crack was the loudest portion of the male song. For many males, we recorded both ascending whip cracks (e.g. song depicted for population 1 in Fig. 2) as well as descending whip cracks (e.g. song depicted for population 2 in Fig. 2). We detected both ascending and descending whip cracks in more than half of the populations we sampled (Fig. 3) despite a limited number of recordings in many populations. Similarly, males in two other populations have been observed to produce both types of whip cracks (Davidson and Langmore 1991, McGuire 2005). Although male whipbird songs show variation in the frequency of the whistle and the slope of the whip crack, both within and among individuals, they nevertheless show remarkable consistency throughout eastern Australia.

Males of race *lateralis* and race *olivaceus* showed no significant differences in song features (ANOVA: all $F_{1,58} < 3.7$, all $P > 0.06$) except for the lowest frequency of the terminal syllable, which was significantly lower in *lateralis* male songs (701 ± 15 Hz) than *olivaceus* male songs (751 ± 6 Hz; ANOVA: $F_{1,58} = 9.0$, $P < 0.01$).

Variability in female songs

Female eastern whipbirds' songs show pronounced variation across their geographic range (Fig. 2). Most female songs contain two syllables, although we found female songs containing as few as one or as many as three, while Watson (1969) reports as many as four syllables in songs of whipbirds from Sherbrooke Forest at Kallista, Victoria. Many female songs are composed of two or three repeated syllables while others contain two or three different syllables.

Female songs were easily categorized into discrete song types. In all populations, females sang with eventual variety, repeating one song type several times before switching to a new song type. Most females sang at least two different song types. The largest number of song types recorded from a single female

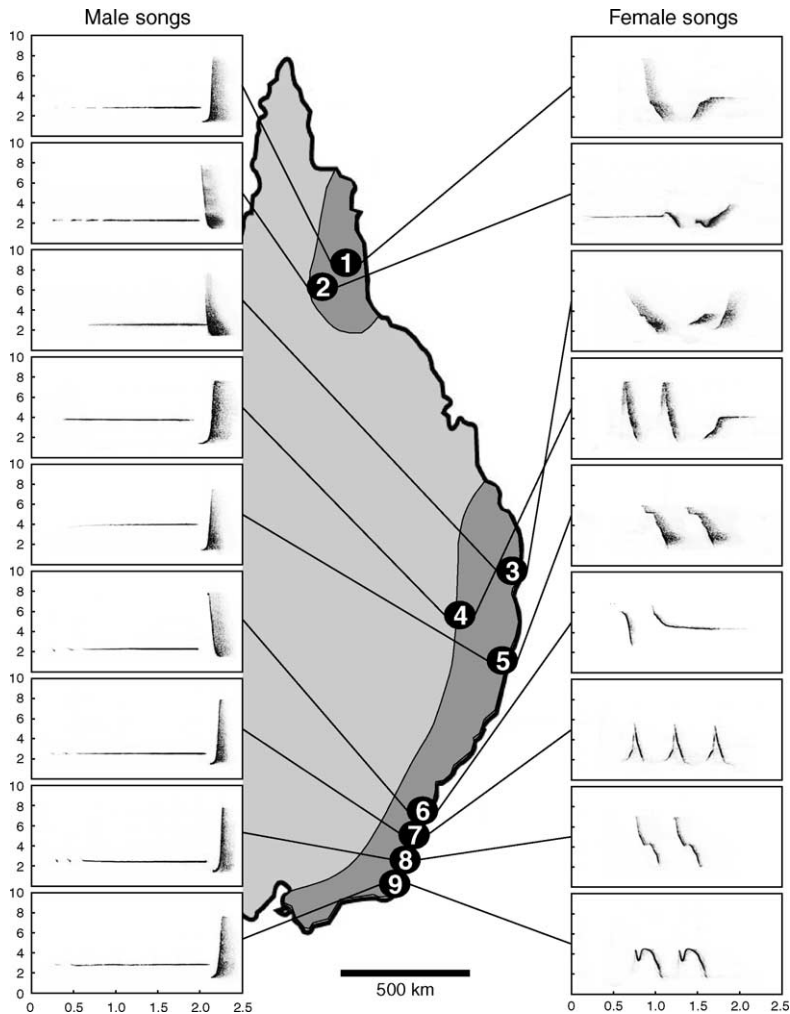


Fig. 2. Example male songs (left) and female songs (right) from nine populations of eastern whipbirds in Australia. Dark grey regions show the entire range of race *lateralis* in the north and race *olivaceus* in the south. Male songs share a highly similar structure across their geographic range, with the principal variation occurring in the frequency of the introductory whistle and bimodal variation in the slope of the whip crack. Female songs show highly variable structure. Populations depicted are: (1) Kuranda, (2) Atherton, (3) Nambour, (4) Toowoomba, (5) Lamington, (6) Bogola Head, (7) Wallaga Lake, (8) Mimosa Rocks, and (9) Bournda. Spectrograms show frequency (in kHz) on the vertical axes and time (in seconds) on the horizontal axes.

was three, but repertoire sampling was not exhaustive. Within populations, females commonly shared song types; for all 11 populations where we sampled multiple females, we found song types shared between two or more females. Between populations, we found song type sharing between females when those populations were in relatively close proximity (Fig. 3). On average, the maximum distance between populations where females shared a particular song type was 141 ± 122 km (range: 9.4–994 km; $n = 8$ song types which were shared between two or more populations).

The song types recorded from females of race *lateralis* and race *olivaceus* showed no significant differences in song features (ANOVA: all $F_{1,18} < 1.5$, all $P > 0.23$, $n = 19$ female song types) except that *lateralis* female song types had fewer inflection points in the terminal syllable (0.2 ± 0.6) than *olivaceus* female song types (1.7 ± 0.4 ; ANOVA: $F_{1,18} = 4.4$, $P = 0.05$). No female song types were shared between *lateralis* and *olivaceus* females.

Male versus female variation

Female eastern whipbird songs show significantly higher variation than male songs for eight of the nine variables we measured (Table 1; sign test: $P = 0.04$, $n = 9$ comparisons). The only acoustic feature which showed higher variation in male songs than female songs was the frequency of the introductory syllable (i.e. the male whistle frequency). In accordance with previous findings (Watson 1969), we found very low levels of variation in the terminal syllable's highest frequency and lowest frequency; that is, male whip cracks show a remarkably similar bandwidth throughout Australia.

Discussion

Songbird vocalizations show tremendously different patterns of geographic variation, ranging from extreme geographic constancy in some species to extreme

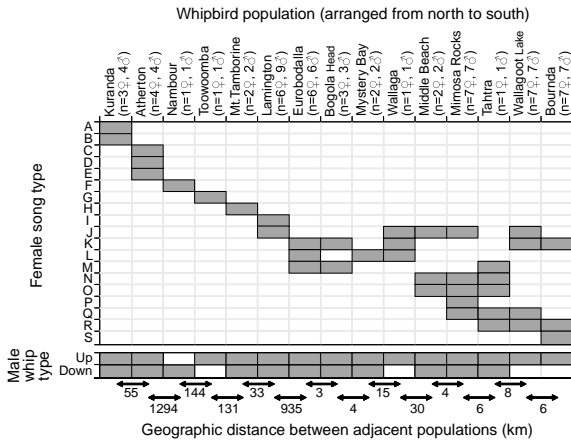


Fig. 3. Presence of female song types (top) and male whip types (bottom) across 15 eastern whipbird populations where both sexes were sampled. Shaded boxes show song types that were detected in each population. Female song types A thru I, P, and S were found in only one population each, whereas the remaining song types were found in multiple populations. Male ascending whip types and descending whip types were both found in most populations. Populations are arranged from north (at left) to south (at right) and distances between adjacent populations are shown at the bottom.

geographic variation in others (Martens 1996). We observed each of these extremes in the songs of male and female eastern whipbirds up and down the east coast of Australia. Male eastern whipbird songs show variation in the frequency of the whistle syllable and in the slope of the whip crack syllable, but nevertheless show high acoustic consistency throughout the species' geographic range. In contrast, female eastern whipbird songs are organized into discrete song types that are shared by females within populations and between females in nearby populations but exhibit extensive variability at a continental scale. Watson (1969) analyzed recordings of a very small number of eastern whipbirds and found constancy in male songs and variability in female songs. Our analyses of male and female songs from 16 populations across the species' geographic range confirm that eastern whipbirds provide a striking example of sex differences in patterns of geographic variation.

The two syllables of male eastern whipbird songs vary in different ways, yet variation in both syllables appears to play an important role in intrasexual communication. Males transpose their whistle syllable across a frequency range of approximately 4000 Hz. During countersinging interactions between territorial birds, males often match the frequency of their opponent's whistle, both in race *lateralis* in the north and race *olivaceus* in the south (pers. obs. McGuire 2005). Variation in note frequency is also heard in other songbirds, including the territorial songs of male black-capped chickadees *Poecile atricapillus* (Kroodsma et al. 1999) and male stripe-breasted wrens *Thryothorus thoracicus* (D. J. Mennill per. obs.).

Table 1. Comparison of variation in the acoustic features of male and female eastern whipbird songs. Female songs show significantly higher variation than male songs for all measurements except the frequency of maximum amplitude (FMA) of the first syllable.

Song feature	Males			Females			Which sex is more variable?	Levene test of unequal variance	
	Mean	SE	CV*	Mean	SE	CV*		F _{1,110}	P
Number of syllables	2.00	0.00	0%	2.06	0.03	16%	Females	21	0.0001
Length of first syllable (s)	2.10	0.03	15%	0.23	0.03	44%	Females	39	0.0001
FMA of first syllable (Hz)	2715	107	38%	2976	113	17%	Males	23	0.0001
FMA of terminal syllable (Hz)	2263	80	19%	3220	85	24%	Females	9	0.003
Highest frequency of terminal syllable (Hz)	8376	125	3%	6330	132	22%	Females	64	0.0001
Lowest frequency of terminal syllable (Hz)	744	83	6%	1901	88	49%	Females	145	0.0001
Terminal syllable number of inflections	0	0.1	0%	1.6	0.1	84%	Females	210	0.0001
Highest-to-lowest frequency of terminal syllable (s)	0.17	0.01	10%	0.17	0.01	36%	Females	38	0.0001
Rate of frequency change in terminal syllable (Hz/s)	43.2	1.7	27%	23.0	1.8	60%	Females	11	0.001

* Coefficient of variation.

In black-capped chickadees, frequency-matching plays an important role during male-male territorial encounters (Mennill and Ratcliffe 2004). Future playback studies will evaluate the behavioural consequences of whistle frequency matching in eastern whipbirds. Future research will also evaluate whether males have many discrete whistle frequencies versus continuous variation in whistle frequency, and whether certain whistle frequencies may be associated with ascending versus descending whip cracks.

Male whip crack syllables show bimodal variation, either ascending or descending very rapidly across a bandwidth of almost 8000 Hz. During countersinging contests, males often match the slope of their opponent's whip crack and produce whip cracks in an overlapping or nearly-overlapping fashion (pers. obs.). Although the nature of matching is different for the continuously variable whistle syllable (i.e. frequency matching) versus the bimodally variable whip crack syllable (i.e. type matching), matching appears to play an important behavioural function during countersinging interactions for both song components.

The songs of female eastern whipbirds comprise vocal dialects in which distinct song types are shared locally between individuals but vary dramatically at a continental scale. Females engage in territorial countersinging interactions with neighbouring females, often in concert with their partners (i.e. counterduetting). During these interactions, females often match the song type of their female opponent (pers. obs.). In this regard, the song system of female eastern whipbirds resembles the song system of many bird species in which males are the primary singers. For example, in song sparrows (Burt et al. 2001) and banded wrens (Molles and Vehrencamp 2001) the repertoires of males are organized into discrete song types that are shared locally between individuals; in both species, song type matching is an aggressive signal during male-male song contests. Repertoires of shared song types in female whipbirds may similarly allow individuals to exchange aggressive signals by matching song types during female-female encounters.

What can explain the dramatic sex differences in patterns of geographic variation we observed in eastern whipbird songs? Males and females may follow different patterns of dispersal. If males disperse farther than females, this could contribute to greater homogeneity in male songs relative to female songs. Little is known about dispersal patterns for Australian birds in general and eastern whipbirds in particular, although female-biased dispersal is common in birds (Greenwood 1980). We have observed the dispersal of two males and two females in the colour-banded population of whipbirds at Mimosa Rocks National Park; all four birds were observed as yearlings within 2.0 km of their natal site (A. C. Rogers unpubl. data). The longest eastern whipbird dispersal record, for a bird of unknown sex, is 4 km

(ABBBS bird banding record; $n = 348$ recaptured eastern whipbirds). Given that the birds we recorded are separated by thousands of kilometers and that the sexes appear to disperse similarly short distances, it seems unlikely that male-biased dispersal could account for the patterns we observed here.

Alternatively, patterns of variation in male and female songs may represent responses to different selection pressures. Variation in both male and female songs appears to be shaped by intrasexual selection through matched countersinging during territorial encounters (above), however male songs may be disproportionately shaped by intersexual selection. Abundant evidence suggests that male song plays an important role in mate attraction in a wide variety of species (Searcy and Yasukawa 1996), but there is very little evidence that female song plays a role in mate attraction (but see Langmore 1996). This asymmetry may account for the low levels of variation we observed in male whipbird song. Male songs may be under selective pressure to transmit information over longer distances and consequently increase opportunities for attracting females. The narrow spectral bandwidth of male whistles may allow them to transmit without spectral degradation over greater distances and may function especially well in long-range signaling (Wiley and Richards 1978). The male whip crack, which was consistently the highest amplitude syllable we recorded from male or female whipbirds, may also be adjusted to maximize long distance transmission (Watson 1969).

Males may benefit by singing songs with specific features that are preferred by females. For example, in swamp sparrows *Melospiza georgiana* females prefer males who sing songs that are technically challenging to perform (Ballentine et al. 2004). The male whip crack syllable has a higher bandwidth than any other tonal bird song syllable known to the authors, yet it is one of the least variant components of male whipbird song. We suggest that female preference for large bandwidth syllables may drive the convergence of male whip crack syllables across the eastern whipbird's geographic range, where an upper limit to syllable bandwidth is set by physiological limitations of the syrinx. That is, females may prefer males who "whip it good" and this preference may be responsible for the observed similarity of male songs up and down Australia's east coast.

Differences in male and female song learning strategies may provide a proximate basis for the observed differences in geographic variation in the songs of the two sexes. In some duetting species, including some *Laniarius* bush shrikes (e.g. Grafe et al. 2004), some *Thryothorus* wrens (e.g. Mennill and Vehrencamp 2005), and northern cardinals *Cardinalis cardinalis* (Lemon 1965), song elements of males and females are very similar, and in these species young birds may be able to learn songs from parents of either sex. Song learning has

not been investigated in whipbirds, however we assume that daughters must learn songs from adult females while sons must learn songs from adult males. The decoupling of male and female song learning systems probably provides the basis for divergence in patterns of variation in the sexes' song systems. Culturally transmitted within each sex, eastern whipbird songs may respond to different selection pressures on males and females.

Among these explanations, sex differences in dispersal distances are unlikely to play a major role in large-scale patterns of geographic variation between males and females, but the remaining explanations may each contribute to sex differences in song variation. Future research should evaluate male and female playback responses to local versus foreign song. In eastern whipbirds, we predict males will respond aggressively to both local and foreign stimuli but that females will respond more aggressively to local stimuli. Future research should also investigate sex differences in song learning strategies, sex differences in song matching behaviour during countersinging interactions, and whether females show strong preferences for high-bandwidth whip crack syllables.

Sex differences in patterns of geographic variation in song structure have been identified as an important avenue for avian research (Kroodsma et al. 1996) yet remain poorly explored or undocumented in most species. Female white-breasted wood-wrens *Henicorhina leucosticta* share their entire vocal repertoire with neighbouring females, whereas males sing song types which are individually unique (Stutchbury and Morton 2001). Female bay wrens *Thryothorus nigricapillus* share 100% of their vocal repertoire with other females, whereas 20% of each male's repertoire is individually unique (Levin 1996). The pattern of song sharing is similar between these female wrens and female eastern whipbirds, where song types are shared between neighbouring individuals. Among males, however, whipbirds show a high degree of similarity across their geographic range whereas both species of wren appear to show a high degree of differentiation, even at a local scale. Future research on other species where both sexes sing will help us to understand the adaptive significance of geographic variation in male and female song.

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