

Occurrence and life history correlates of vocal duetting in North American passerines

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Vocal duetting, where two birds produce temporally coordinated vocalizations, has been reported in a taxonomically and geographically diverse set of avian species. Researchers have suggested a number of potential correlates of duetting, including long term monogamy, year-round territory defense and sexual plumage monomorphism. Because the majority of duetting species are tropical, they have been the focus of the most comprehensive studies to date. There is, therefore, a real need for data regarding avian duets in temperate species. I used the recently completed Birds of North America species reports to examine the frequency, evolutionary origins and potential life history correlates of duetting behavior in North American passerines. “Duetting” behavior was reported in 7% of species from 12 avian families, likely representing 17 separate evolutionary origins. Duetting species showed apparent long term monogamy and year-round territoriality at frequencies more than double those of non-duetting passerines: 65% of duetting species were long term monogamous, compared to 27% of non-duetting species, and 50% of duetting species defended the same territory throughout the year, compared with only 11% of non-duetting species. Duetting and non-duetting species showed statistically indistinguishable frequencies of sexual plumage monomorphism. Comparative analyses of duetting species and their sister taxa revealed that the shift to duetting is accompanied by a gain of long term monogamy and year-round territoriality more often than it is associated with a loss of those traits. This study provides intriguing summary evidence that selective factors promoting duetting may be associated with a sedentary, monogamous lifestyle, and may operate similarly across taxonomic groups. Furthermore, vocal duetting may be considerably more common among temperate-zone species than previously recognized.

Vocal duetting occurs when two birds, generally a mated pair, produce temporally coordinated vocalizations in which “bouts of certain elements in the repertoire of one bird frequently overlap with bouts of certain elements in the repertoire of its mate” and “there is some organization of both participants’ elements within the region of overlap” (Farabaugh 1982). Over 220 avian species from at least 44 different families have been reported to duet (Thorpe 1972, Farabaugh 1982). A best-guess estimate is that 3–4% of species worldwide produce vocal duets, but it is unclear how often duetting species occur in different geographical regions, and whether or not selective pressures promoting duetting are similar across latitudinal gradients (Hall 2004).

Unlike the majority of research on bird song, in-depth studies of duetting behavior have generally focused on tropical or sub-tropical avian species, and duetting is thought to be rare among temperate-zone species (Kroodsma et al. 1996, Morton 1996, Langmore 1998). Temperate and tropical avian species experience different environmental pressures and life-history trajectories that may create a divergent set of behavioral needs. Temperate-zone species are often migratory, with short breeding seasons that create relatively brief periods of intense activity

and distinct sex roles that may include major asymmetries in song production, reproductive behavior, and territory defensive behavior. In contrast, many tropical species experience relatively little temporal environmental fluctuation, leading to sex role convergence which likely promotes behaviors including female song, monogamy, shared territory defense and duetting (Morton 1996).

Functional hypotheses for duetting postulate that duets may function in signaling location, reproductive status, individual quality, or motivation to a duetting partner (reviewed in Hall 2004). Duets may also function in cooperative resource defense by paired birds or mate-guarding by one member of a pair (reviewed in Hall 2004). Duets functioning in many of these contexts might be more valuable in a situation where duetting partners have similar sex-roles. For example, coordination of reproduction, resource defense, or other behaviors may be important in species where both partners contribute significantly to such tasks (Farabaugh 1982). Similarly, signaling quality or mated status via duets may be particularly valuable in species where sexes are similar, and general appearance or behavior may not be obvious indicators of sex. Thus, lifestyle may promote duetting behavior, and the occurrence

of duetting in species with particular life history traits may reflect the action of natural selection.

When Thorpe (1972) initiated investigation into the topic of vocal duetting, he postulated that most duetting species were tropical in distribution and were sexually monomorphic. Subsequent study supported the hypothesis that duetting is predominantly a tropical phenomenon and concluded that vocal duetting is associated with long term monogamy and year-round territoriality in a group of mostly tropical species (Farabaugh 1982). The same study found no evidence that duetting species in tropical Panama are more likely than non-duetting species to be monomorphic (Farabaugh 1982).

Evidence suggests that temperate zone duetting species may share life-history characteristics with tropical duetting species, but this idea has not been extensively tested (Farabaugh 1982). An analysis of vocal and visual duetting behavior in Western Palearctic non-passerine birds named 46 duetting species, and found an association between monogamous pair-bonds, breeding season territoriality, monomorphism and duetting (Malacarne et al. 1991). The criteria for defining a duet and the number of species surveyed were not well described but, even so, results lend support to established hypotheses. Life history traits in Western palearctic non-passerine duetters are similar to those found in the tropics, except for the association between duetting and monomorphism. Malacarne et al. (1991) suggest that monogamy and territoriality, regardless of duration, occur at higher frequencies in duetting than non-duetting Western Palearctic non-passerine species. These results fit with general predictions made by other researchers, but would be more informative if long term and short-term monogamy and territoriality were assessed separately.

Results suggesting that vocal duets exist in a variety of temperate zone non-passerines inspire questions about the prevalence and life history correlates of duetting in temperate zone passerine species. North American bird species tend to be well studied, and the wealth of information available for this group makes possible a thorough, quantitative review of duetting behavior and life-history correlates. This study summarizes data on North American passerine duetting species. Specifically, I examine duet occurrence to assess the prevalence and taxonomic diversity of duetting species, describe the variety of duet structures exhibited by North American passerines, and survey life history traits to look for correlations between monogamy, territoriality, monomorphism and duetting. I also assess female song, which is generally thought to be rare among temperate zone species but which may be a signal of sex role convergence and may be closely linked with duetting (Morton 1996).

Methods

I used the recently completed Birds of North America (BNA) species reports to examine the frequency, evolutionary origins and potential life history correlates of duetting behavior in North American passerines (Poole 2006). Data retrieved from the online reports provide the most comprehensive descriptions of species-specific

attributes currently available for birds that breed in the USA and Canada. I surveyed reports for the 300 passerine species found on the North American continent, and scored the following traits as either present, absent, or unreported: vocal “duets”, seasonal monogamy, long term monogamy, seasonal territoriality, year-round territoriality, and sexual plumage monomorphism. Long term monogamy was defined as monogamy with the same partner across multiple breeding seasons, and year-round territoriality required that individuals defend a single territory of some kind throughout the year. Additionally I scored female “song” present in a species if reported present and absent if reported absent or if unreported. Thus, for the purposes of this review, duets and female song are both identified and defined by the authors of the relevant BNA reports, all of whom are expert authorities regarding the species in question. General definitions state that duets occur when two birds produce coordinated vocalizations structured to include stereotyped vocal elements, with some degree of temporal coordination (Farabaugh 1982, Hall 2004). Female songs may be generally described as relatively long, complex vocalizations that can be distinguished from calls which tend to be of short temporal duration and composed of only one or two syllables (Langmore 1998).

To assess taxonomic breadth of duetting behavior, I used the familial designations contained in the BNA Reports. I considered the appearance of duetting behavior as an independent evolutionary origin if it occurred in a single species within a large family, or if a literature search revealed that sister taxa to the duetting species do not duet and parsimony indicated a shift to duetting in the focal species. When duetting species were closely related to each other, I used published phylogenies to determine relationships and to determine the origin of duetting behavior in the relevant clade(s).

Excluding female song, frequencies of behavioral and life history traits for each behavioral group were calculated as the number of species in that group exhibiting the behavior divided by the number of species in that group for which the behavior was reported present or absent. Species for which life history traits were reported to vary, such as those species that are polygynous in some populations and monogamous in other populations, were left out of all calculations. For each group, the frequency of female song was calculated as the number of species in which song was present over all species surveyed. Female song was treated separately on the premise that song may be considered a male trait by some authors, and its absence in females may go unreported.

Frequencies of life history traits were assessed for three groups: 1) all non-duetting species, 2) all duetting species, and 3) each separate origin of duetting behavior. When multiple species appeared to share a single evolutionary origin of duetting behavior, the presence or absence of each life history trait for that lineage was determined based on trait presence or absence in the majority of species for which it was reported. Character states never showed conflicting presence/absence patterns in species within the same group, so this rule merely allowed me to assign character states to groups in which some species had unreported data. Fisher's exact tests were used to compare the frequencies of life history trait occurrences in the duetting versus non-duetting

species and in duetting clades versus non-duetting species. Duetting clades were included as a group in an effort to control for shared ancestry among duetting species. Unfortunately, the lack of a complete phylogeny for all North American passerine species precludes the use of independent contrasts techniques (Felsenstein 1985). Grouping duetting species into clades that each represent a single evolutionary origin of duetting removed some, but not all of the phylogenetic non-independence from the duetting group. Non-duetting species were not manipulated to control for evolutionary history. The proportions of each life history trait in these groups, therefore, do not perfectly represent the frequency of appearance of that trait in evolutionary time.

As an alternative attempt to control for the effects of shared ancestry in non-duetting species, I identified transitions in life history traits between each duetting lineage and its most closely related North American outgroup. This comparison examined potential trait transitions for all scored vocal and life-history traits at the location where each duetting clade acquired duetting behavior. Thus, the comparison allowed me to examine how often during speciation life-history traits shift in conjunction with duetting behavior. Related lineages were identified based on information contained in the BNA reports or published

phylogenies whenever possible, and on taxonomic classifications from the BNA reports when necessary. Outgroups are not all true sister taxa because some species relationships are unresolved, and some species have sister taxa with geographical distributions outside of North America. When a single North American sister species could not be identified, duetting species were compared with the ancestral traits present across the majority of species in the appropriate clade. All comparisons were made using information from the BNA reports in an attempt to standardize data across species. Unless citations indicate otherwise, all species information was derived from the appropriate BNA report, each cited only once upon first appearance. All statistical analyses were performed using JMP, Version 5 (SAS Institute 2004).

Results

Occurrence

Duetting behavior was reported in 21 of 300 (7%) North American species from 12 of 31 (39%) surveyed passerine families (Fig. 1).

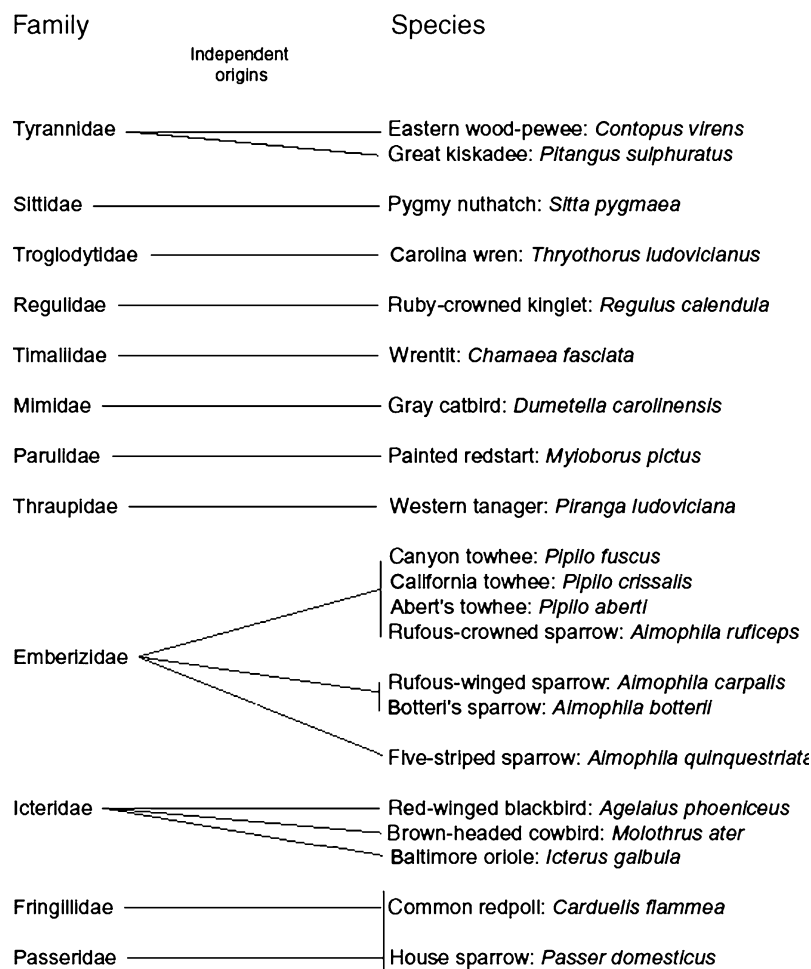


Fig. 1. Species names, familial affiliations and independent origins of passerine species reported to duet in the birds of North America reports. Lines linking family and species names represent independent evolutionary origins of duetting as determined from published phylogenies and character states in related species.

Duet descriptions

Reports of duetting behavior varied widely. Great kiskadees *Pitangus sulphuratus*, brown-headed cowbirds *Molothrus ater* and house sparrows *Passer domesticus* were reported to produce vocalizations that “resemble” duets, and which I treated as duets in this analysis (Lowther and Cink 1992, Lowther 1993, Brush and Fitzpatrick 2002). Some authors reported “apparent” duets, or merely that previous researchers had termed specific vocal behaviors “duets”. One species, the ruby-crowned kinglet *Regulus calendula*, is only known to duet in captivity (Ingold and Wallace 1994). In some reports, authors describe duetting behavior, while in others they merely mention that it exists. For example, McCarty (1996) states the following about eastern woodpeewees *Contopus virens*: “occasional duetting between mated pairs reported, but no details provided.” At the other end of the spectrum, Collins (1999) provides a thorough, 117-word description of duetting in rufous-crowned sparrows *Aimophila ruficeps*.

All authors reported duetting between mated (or presumed mated) pairs, using a variety of different vocalizations. Duets differed among species and, as described below, variable duet characteristics included: 1) the type of male and female duet contributions, 2) the sex of the duet initiator, 3) the overlap between male and female duet contributions, and 4) the timing of male and female duet contributions. General duet properties and life history traits of each species are summarized in Table 1.

Males and females of several North American duetting species, including gray catbirds *Dumetella carolinensis* and Baltimore orioles *Icterus galbula* use similarly constructed complex songs in duets (Whittle 1923, Beletsky 1982). Other species, such as Carolina wrens *Thryothorus ludovicianus* and brown-headed cowbirds, form duets that include male song and a female “chatter” vocalization (Shuler 1965). Species including great kiskadees and common redpolls *Carduelis flammea* produce duets composed of similar brief call notes from pair members of both sexes, while pygmy nuthatches *Sitta pygmaea* and house sparrows duet using sex-specific call notes (Brokaw 1893, Norris 1958, Knox and Lowther 2000).

Among well described duets there was variation in duet structure both across and within species. Pygmy nuthatch and common redpoll mates form duets both by alternating vocalizations and by vocalizing simultaneously (Brokaw 1893, Norris 1958). Among great kiskadees, red-winged blackbirds *Agelaius phoeniceus*, Baltimore orioles and house sparrows, mates alternate vocal phrases during duets (Beletsky 1982, Beletsky 1985). Carolina wrens, wrentits *Chamaea fasciata*, gray catbirds, the three *Pipilo* species and the four *Aimophila* species all construct duets by overlapping male and female vocalizations (Grinnell 1913, Whittle 1923, Marshall 1964, Shuler 1965, Wolf 1977). Among Carolina wrens, red-winged blackbirds and brown-headed cowbirds, females create duets by responding to vocalizations produced by their mates (Haggerty and Morton 1995, Yasukawa and Searcy 1995). In species including house sparrows and California towhees *Pipilo Crissalis*, either sex may initiate duetting.

In several species, including pygmy nuthatches, wrentits, and gray catbirds, male and female duet contributions are very precisely timed (Brokaw 1893, Grinnell 1913, Whittle 1923, Norris 1958). Other species, such as the Carolina wren, do not produce highly temporally precise duets, but do always time vocalizations with a low degree of temporal precision, such that they overlap. The majority of remaining species necessarily fall somewhere within this continuum, and it is likely that most do not show high levels of coordination. California towhees, for example, always time duets so that certain syllabic elements overlap, but their duets do not have a rigid temporal structure (LB unpubl. data).

Independent origins

Duetting behavior appears to have evolved at least 17 different times among North American passerines (Fig. 1). The pygmy nuthatch, Carolina wren, ruby-crowned kinglet, wrentit, gray catbird, painted redstart *Myioborus pictus*, western tanager *Piranga ludoviciana*, common redpoll and house sparrow all belong to families that include no other North American duetting species (Cimprich and Moore 1995, Hudon 1999, Barber et al. 2000, Kingery and Ghalambor 2001, Geupel and Ballard 2002). Additionally, there is no evidence that the ancestral condition in these 10 families included duetting behavior. The eastern woodpeewee and great kiskadee are both members of the family Tyrannidae but the eastern wood-pewee is nested within a clade of non-duetting peewees and flycatchers while the great kiskadee is allied with a group of non-duetting kingbirds (Zink and Johnson 1984). Within the Icteridae, blackbirds, cowbirds and orioles form distinct evolutionary lineages (Lanyon and Omland 1999) and parsimony suggests the independent evolution of duetting in the three duetting icterids. Red-winged blackbirds fall within a clade of non-duetting blackbirds, brown-headed cowbirds are the only duetting cowbirds, and Baltimore orioles are the only oriole species reported to duet (Rising and Flood 1998.).

The seven North American emberizid species included in Fig. 1 apparently represent three duetting lineages (Groschupf 1992, Tweit and Finch 1994, Johnson and Haight 1996, Webb and Bock 1996, Lowther et al. 1999, Kunzmann et al. 2002, C. Cicero and J. D. Rising, unpub. data). Phylogenies indicate that the canyon *Pipilo fuscus*, California and Abert's *Pipilo aberti* towhees likely fall within a monophyletic group with the rufous-crowned sparrow. The rufous-winged *Aimophila carpalis*, and Botteri's *Aimophila botterii* sparrows are members of a second duetting clade, and the five-striped sparrow *Aimophila Quinquestriata* represents a third independent origin of duetting within this family (Patten and Fugate 1998, Carson and Spicer 2003, C. Cicero and J.D. Rising unpubl. data).

Life-history trait frequencies

Female song

High frequencies of female song may correlate with duetting because female duet contributions can be constructed of song, and because it may signal a general

Table 1. Duet properties and life history traits of North American passerine species reported to duet in the birds of North America reports.

Duetting lineage	Duet traits				Life-history traits		
	Stereotyped vocal elements?	Elements alternate or overlap?	Consistent element coordination?	High temporal precision?	Female song?	Long-term monogamy?	Year-round territoriality?
Eastern wood-peewee	Unknown	Unknown	Unknown	Unknown	Yes	Unknown	No
Great kiskadee	Yes	Both	Unknown	Unknown	No	Yes	Yes
Pygmy nuthatch	Yes	Alternate	Yes	Yes	No	Yes	Yes
Carolina wren	Yes	Overlap	Yes	No	No	Yes	Yes
Ruby-crowned kinglet	Unknown	Unknown	Unknown	Unknown	Yes	No	No
Wrentit	Yes	Overlapping	Yes	Yes	Yes	Yes	Yes
Gray catbird	No	Overlap	Yes	Yes	Yes	Sometimes	No
Painted redstart	Unknown	Alternate	Unknown	Unknown	Yes	Unknown	No
Western tanager	Yes	Overlap	Unknown	Unknown	Yes	Unknown	No
Canyon towhee	Yes	Overlap	Yes	No	No	Yes	Yes
California towhee	Yes	Overlap	Yes	No	No	Yes	Yes
Abert's towhee	Yes	Overlap	Yes	No	No	Yes	Yes
Rufous-crowned sparrow	Yes	Overlap	Yes	No	No	Unknown	Yes
Rufous-winged sparrow	Yes	Overlap	Yes	No	No	Yes	Yes
Botteri's sparrow	Yes	Overlap	Yes	No	No	Unknown	Unknown
Five-striped sparrow	Yes	Overlap	Yes	No	No	No	No
Red-winged blackbird	Yes	Overlap	Yes	No	Yes	No	No
Brown-headed cowbird	Yes	Overlap	Yes	No	No	No	No
Baltimore oriole	Yes	Unknown	Unknown	No	Yes	Unknown	No
Common redpoll	Yes	Both	Unknown	Unknown	No	Unknown	No
House sparrow	Yes	Alternating	Unknown	Unknown	Yes	Yes	Yes

tendency for females to be highly vocal. Among North American passerines, females were reported to sing in 43% of duetting species, 53% of duetting clades and 34% of non-duetting species (Fig. 2). Duetting species and clades show a greater tendency than non-duetting species to exhibit female song, but even in comparisons of all non-duetting species versus duetting clades the trend is non-significant (Fisher's exact test, $n = 294$, $P = 0.119$). Duetting species without female song included the great kiskadee, pygmy nuthatch, Carolina wren, all seven Emberizid species, the brown-headed cowbird and the common redpoll.

Monomorphism

Thorpe (1972) and Malacarne et al. (1991) concluded that duetting species have a tendency to be monomorphic, but Farabaugh (1982) found no support for this hypothesis in tropical species. In the temperate zone passerine species examined here, levels of monomorphism were very similar between duetting clades (56%) and non duetting species (48%), and only slightly higher in duetting species (65%) (Fig. 2). These differences were non-significant. Monomorphic duetters included the Eastern wood-pewee, the great kiskadee, the pygmy nuthatch, the Carolina wren, the wrentit, the gray catbird, and all seven Emberizids.

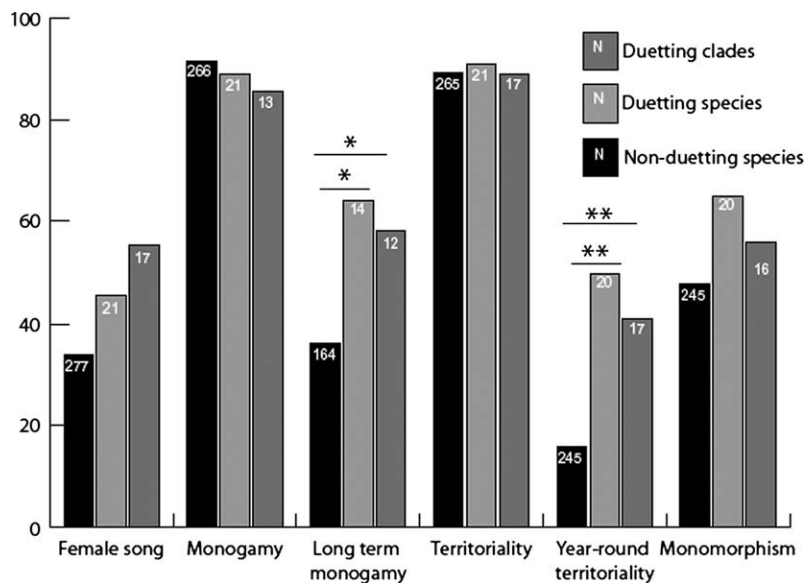


Fig. 2. Percentage of North American passerine non-duetting species, duetting species and duetting clades exhibiting six life-history traits according to the Birds of North America reports. Stars indicate significant differences between groups according to Fisher's exact tests: * = $P < 0.05$, ** = $P < 0.005$. Numbers in each bar represent sample sizes.

Monogamy

Authors generally agree that monogamy, and particularly long term monogamy, where pair bonds persist over many mating attempts, may be associated with duetting (Thorpe 1972, Farabaugh 1982, Malacarne et al. 1991). Frequencies of seasonal monogamy among North American passerines are similar for all groups. Among both non-duetting and duetting species, 90% are monogamous (Fig. 2). Non-monogamous North American passerine duetters include the polygamous red-winged blackbird and the brood parasitic brown-headed cowbird. Of seasonally monogamous duetting species, only the ruby-crowned kinglet and five-striped sparrow were reported not to maintain long term pair-bonds. Nine species have prolonged monogamous pair bonds, while no information or equivocal information was provided for an additional 8 species. Thus, 65% of duetting species and 58% of duetting clades show long term monogamy. These frequencies are significantly higher than frequencies among non-duetting species, of which only 33% are long term monogamous (Fisher's exact test: for duetting species vs. non-duetting species $n = 178$, $P < 0.05$; for duetting clades vs. non-duetting species $n = 176$, $P < 0.05$).

Territoriality

Like monogamy, territoriality, and the long term aspects in particular, are thought to correlate with vocal duetting (Farabaugh 1982, Malacarne et al. 1991). Roughly 88% of all North American passerine species surveyed for this review defended some type of territory during the breeding season (Fig. 2), with the only non-territorial duetting species being the brown-headed cowbird and the common redpoll. Of the 19 territorial duetting species, 10 maintain territories throughout the year. All of these species have long-term pair bonds, so mates are mutually defending territories. Five species migrate from breeding territories completely, and an additional four species that don't maintain year-round territories are partial migrants. Frequencies of seasonal territoriality do not differ between duetters (90%) and non-duetters (88%). Year-round territoriality is, however, significantly more common in duetting (50%) than in non-duetting (11%) species (Fisher's exact test: $n = 256$, $P < 0.001$) and there is a

similar difference between duetting clades (41%) and non-duetting species (Fisher's exact test: $n = 262$, $P < 0.001$).

Life-history trait transitions

Trait transitions were determined based on pairs of taxa shown in Table 2. Compared with non-duetting relatives, duetting taxa gained female song eight times, lost it twice (Table 3), and retained the ancestral state seven times. The shift to duetting is accompanied by a gain of long term monogamy three times, no losses of that trait (Table 3), and no change in four lineages. Similarly, the transition to duetting is accompanied by a gain of year-round territoriality five times, a loss once (Table 3), and no change in six lineages.

Discussion

The BNA reports differ in several ways when discussing duetting in North American passerine species. First of all, different authors may have had different tendencies to label a vocalization a duet. This type of discrepancy clearly occurred, and a review of the duetting literature indicates that some BNA authors failed to report duetting in species well-acknowledged to duet. For example, Farabaugh's (1982) list of North American duetting species includes the common crow, the northern cardinal, and the sulphur-bellied flycatcher – all species not described as duetters in the BNA reports, and therefore not included as duetters in my analyses. Discrepancies likely go in the other direction as well, such that the vocalizations of some species included in this review may not qualify as duets under further examination according to current duet definitions (Farabaugh 1982, Hall 2004). Overall, the data may contain some uncertainty, but results of this study support existing predictions, and provide a compelling quantitative overview of duetting in North American passerines.

A second major source of variation among BNA reports comes from the quantity and quality of information provided. Duet descriptions varied widely, from some that just stated "species \times duets" to others that described

Table 2. Duetting lineages and their most closely related North American sibling taxa, as determined from referenced publications.

Duetting lineage	Related taxon	Reference
Eastern wood-peewee	Western wood-peewee	BNA – McCarty 1996
Great kiskadee	<i>Tyrannus</i> spp.	BNA – Brush and Fitzpatrick 2002
Pygmy nuthatch	Brown-headed nuthatch	BNA – Kingery and Ghalambor 2001
Carolina wren	Bewick's wren	Barker 2004
Ruby-crowned kinglet	Arctic warbler	BNA – Ingold and Wallace 1994
Wrentit	Red-billed leiothrix	Familial affiliation
Gray catbird	other mimids	BNA – Cimprich and Moore 1995
Painted redstart	other parulids	BNA – Barber et al. 2000
Western tanager	Hepatic tanager	BNA – Hudon 1999
<i>Pipilo</i> spp. and rufous-crowned sparrow	Spotted towhee	Cicero and Rising, unpubl. data
Rufous-winged and Botteri's sparrows	Grasshopper sparrow	Cicero and Rising, unpubl. data
Five-striped sparrow	Black-throated sparrow	Cicero and Rising, unpubl. data
Red-winged blackbird	Tricolored blackbird	BNA – Yasukawa and Searcy 1995
Brown-headed cowbird	Shiny cowbird	Lanyon 1992
Baltimore oriole	Altamira oriole	BNA – Rising and Flood 1998
Common redpoll	Hoary redpoll	BNA – Knox and Lowther 2000
House sparrow	Eurasian tree sparrow	Familial affiliation

Table 3. Duetting clades that have either gained or lost three life history traits in conjunction with the gain of duetting. Gain or loss of each trait represents a transition from the trait possessed by each clade's most closely related North American sibling clade.

Gained	Lost
Female song	
Ruby-crowned kinglet	Pygmy nuthatch
Wrentit	Rufous-winged and Botteri's sparrows
Gray catbird	
Painted redstart	
Western tanager	
Red-winged blackbird	
Baltimore oriole	
House sparrow	
Long term monogamy	
Great kiskadee	
Carolina wren	
Rufous-winged	
Botteri's sparrows	
Year-round territoriality	
Great kiskadee	Gray catbird
Pygmy nuthatch	
Wrentit	
Towhee spp.	
Rufous-crowned sparrow	
House sparrow	

the duet vocalization in detail. In many cases, original sources provide more information about duet structure and context, but even some of the original sources are lacking in detail. Where descriptive information was available, species reported to duet did show typical duet characteristics, including stereotyped vocal element use and coordination. Other duet characteristics, including the degree of temporal coordination, sex of the initiator, and type of vocalization used to construct duets, were variable. Thus, duets from different species were all coordinated vocalizations, but differed a great deal in structure and usage. Given that the species represent 17 different origins of the behavior, such variation is probably to be expected and is potentially a very interesting topic for investigation. Furthermore, such diversity fits with currently recognized patterns. Among well studied duetting species, all of the duet characteristics mentioned above vary widely, and researchers are constantly documenting a variety of duet forms and functions (Hall 2004). More thorough duet descriptions for all species would contribute to our understanding of the many ways that vocal duets can be generated and employed.

Vocal duetting appears to be considerably more common among temperate-zone species than previously recognized. Seven percent of North American passerine species duet, roughly double the number that would be predicted from current worldwide estimates of duetting, and far more than might have been expected in a temperate geographic region. The 21 duetting North American passerine species are notably diverse, representing 17 independent evolutionary origins of the behavior in 12 passerine families. While encompassing fewer species, these numbers represent more familial diversity than Farabaugh (1982) reported among passerine duetters in Panama (64 species from 10 families). This wide familial diversity exists because 9 of 12 families include a single duetting species. Six of the 11 remaining duetting species also represent separate

evolutionary origins of duetting, and only twice have duetting clades diversified to include multiple duetting species. Thus, duetting behavior can be conserved across species within a clade, but also appears relatively frequently in clades with no history of the trait. Duetting may be a highly plastic behavior, making it more likely to arise in a large variety of unrelated groups. I expect that future studies will document duetting behavior in an increasing number of geographically and taxonomically diverse avian species. Additionally, our understanding of avian vocal duets would benefit greatly from phylogenetically-based studies of duet occurrence to assess both patterns of evolutionary origins and taxonomic diversity.

North American passerine duetting species showed a trend towards elevated frequencies of female song relative to non-duetting species. This pattern may simply represent a tendency for researchers to call female duet contributions songs, or it may reflect a real tendency for species with female song to develop duets. The existence of female song may signal a decrease in vocal asymmetry between the sexes, a condition that likely favors duetting. The existence of female song may also promote duet development if it implies increased levels of female vocalization in general. Female song, however, is not necessary for duetting – many of the duets described in North American species include female contributions that are not true song – and the absence of female song in so many duetting species is perhaps more surprising than its presence in others.

Vocal duetting in North American passerine species correlates with life history traits as predicted by previous studies. Among North American passerines, frequencies of sexual plumage monomorphism, seasonal monogamy, and seasonal territoriality were statistically indistinguishable between duetting and non-duetting species and lineages. Results of this study do not support claims that duetting species are more likely than non-duetting species to be monomorphic. Duetters did, however, show elevated frequencies of long term monogamy and year-round territoriality compared with non-duetters. Interestingly, it is the long term aspects of these two life history traits that appear to be associated with duetting. All passerines showed similar frequencies of monogamy and territoriality within the breeding season, but duetting species and lineages showed long term monogamy and year-round territoriality at frequencies more than double the background frequency for non-duetting passerines. Additionally, although the numbers are small, these two life history traits transition most often in the predicted direction in conjunction with duetting behavior. Compared with sister taxa, lineages that duet are more likely to exhibit long term monogamy and year-round territoriality.

Surveys of duetting behavior in Panamanian bird species, western Palearctic non-passerine species, and North American passerine species all conclude that duetting may be associated with certain life-history traits (Farabaugh 1982, Malacarne et al. 1991). These traits, long term monogamy and year-round territoriality in particular, are less common in temperate zone than tropical bird species, perhaps leading to the prevalence of duetting behavior in tropical areas (Morton 1996). Nevertheless, data reported here provide intriguing evidence that similar lifestyles may lead to similar methods of communication. If duets function to

coordinate behaviors between members of a pair, then long term residence on a single territory by a single pair might increase the benefits of coordinated signaling via duets. In such a situation, correlations between duetting, long term monogamy and year-round territoriality may exist because the sedentary monogamous lifestyle creates a situation in which the action of natural selection promotes the development and maintenance of vocal duets. If they depend on life history traits, selective factors promoting duetting should operate identically on all species, regardless of geographic and taxonomic boundaries, and would produce a pattern of duet occurrence like the one observed and described by decades of interested researchers like Thorpe (1972), Farabaugh (1982), and Malacarne et al. (1991). In the future, researchers looking to document duetting may do well to study vocal behavior among long-term monogamous species with year-round territoriality.

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