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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).

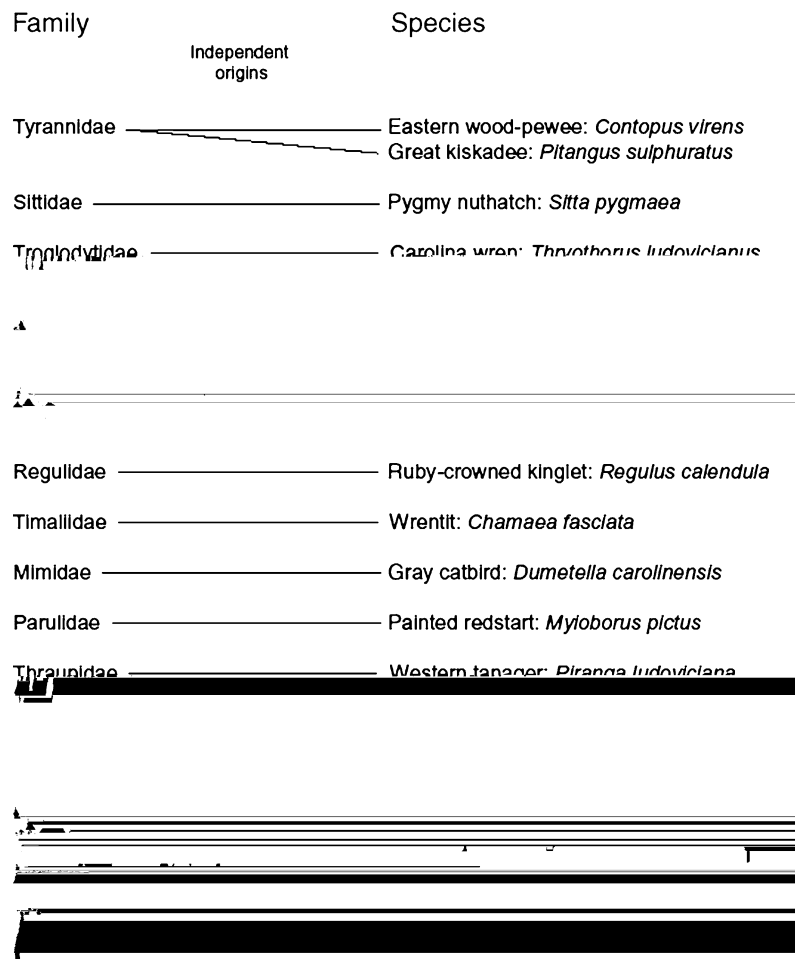
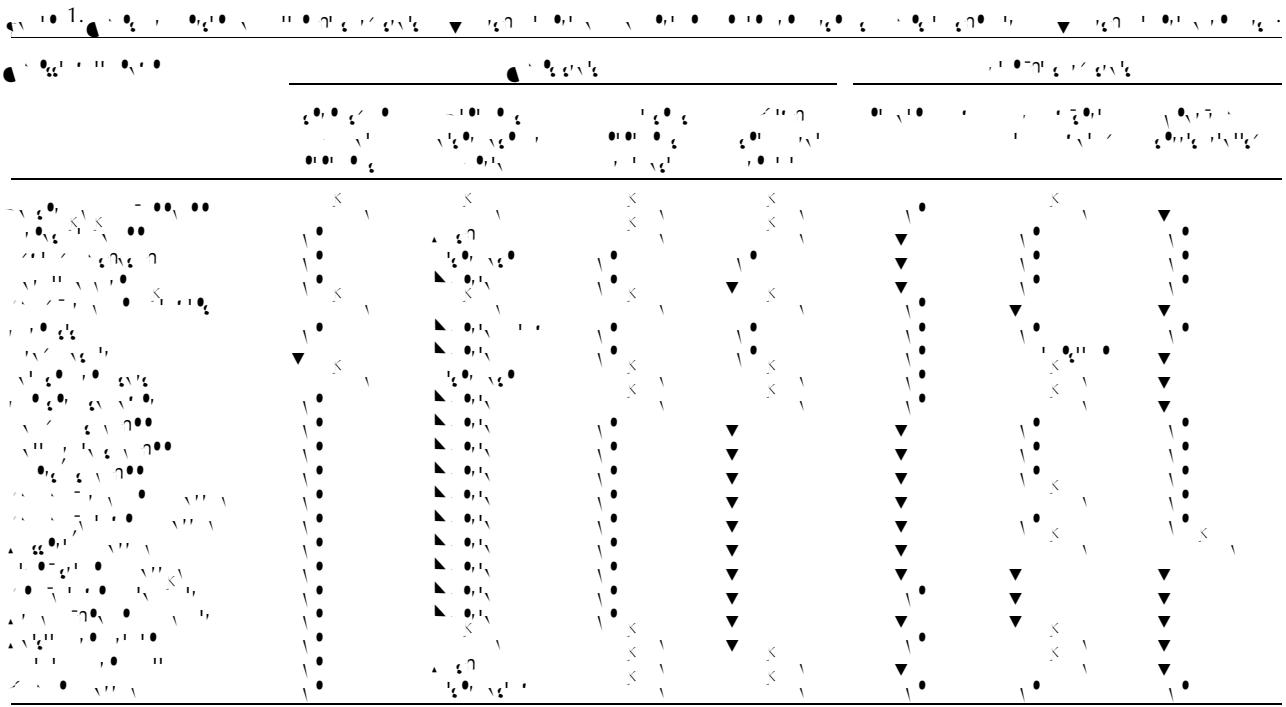


Fig. 1. Species names, familial affiliations and independent origins of passerine species reported to duet in the birds of North America reports. Lines linking family and species names represent independent evolutionary origins of duetting as determined from published phylogenies and character states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



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.

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 wrenit, the gray catbird, and all seven Emberizids.

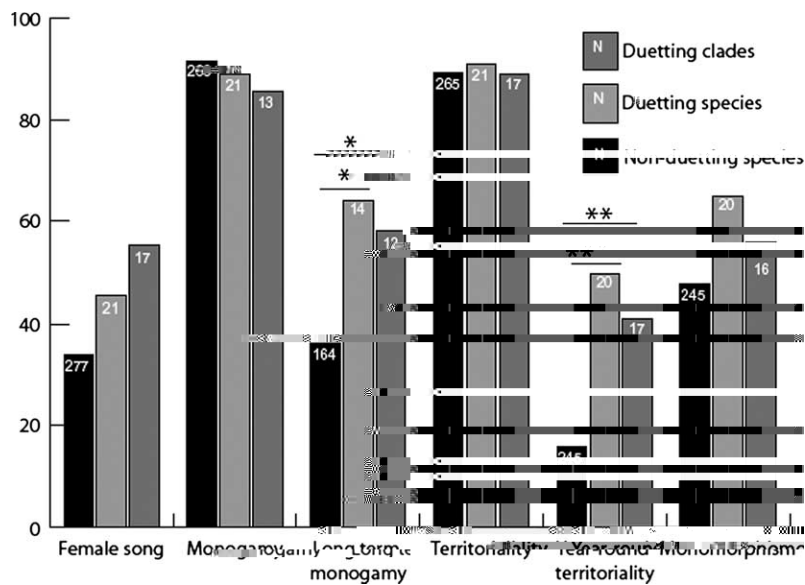


Fig. 2. Percentage of North American passerine non-duetting species, duetting species and duetting clades exhibiting six life-history traits according to the Birds of North America reports. Stars indicate significant differences between groups according to Fisher's exact tests:  $* = P < 0.05$ ,  $**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

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

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

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

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



