ECOLOGICAL AND EVOLUTIONARY CHARACTERISTICS

OF FLIGHT-CALLS OF THE WOOD-WARBLERS (PARULIDAE)

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Andrew Farnsworth

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ECOLOGICAL AND EVOLUTIONARY CHARACTERISTICS
OF FLIGHT-CALLS OF THE WOOD-WARBLERS (PARULIDAE)

Andrew Farnsworth, Ph.D.

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Many songbirds produce simple, species-specific flight-calls. Some fundamental features of flight-calls remain poorly known, including their functions and variability. I reviewed available information on flight-calls and studied: 1) relationships between calling and weather; 2) seasonal flight-call use in warblers; 3) inter- and intraspecific variation in warbler flight-calls; 4) methods for analyzing flight-calls; and 5) relationships between warbler flight-calls and ecological and evolutionary characteristics.

I examined relationships among call counts, weather, and bird density. I studied flight-calling in warblers during migratory and non-migratory periods. I recorded flight-calls from captive warblers to evaluate inter- and intraspecific differences and quantify variance among species, individuals, and ages and between sexes. I compared three methods to assign calls to caller using discriminant analysis: 1) spectrographic cross-correlation (SPCC); 2) energy-distribution (ED) measurements; and 3) classification tree analysis (CTA) of ED measurements. I used a multi-locus phylogeny to quantify the extent of phylogenetic signal in flight-call spectrographic characteristics. I employed a quantile regression and null model approach to compare interspecific phylogenetic divergence with corresponding spectrographic differences.

I found that: 1) call counts correlated with bird density and weather, but not with weather alone after controlling for density; 2) warblers use flight-calls most extensively during migration, but not exclusively; 3) variation in flight-call properties is greatest among species, with subtle variation among individuals and ages and between sexes; 4) SPCC data yielded the lowest misclassification rates and may best represent individual differences; and 5) in phylogenetically controlled and uncontrolled analyses many energy distribution and syllable structure measurements associated with phylogeny, vegetation density and vegetation height but not with migration strategy, wintering distribution, or morphological characteristics.

Flight-calls are probably more functional as species identifiers than as individual identifiers, and such functions may extend beyond migratory periods. Additionally, phylogenetic and ecological effects occur in flight-calls, and evolutionary histories of structural and signal properties may differ. Species recognition may be important in the evolution of syllable structure, whereas adaptation to environment may be important in the evolution of spectral and temporal properties. Incorporating individual-specific information and meteorological data into acoustic monitoring protocols could increase dramatically the power of these methods.

BIOGRAPHICAL SKETCH

Andrew Farnsworth developed a keen interest in birds at a young age. By age five, he was birding around his home in Rye, New York. As his passion for birds grew, Andrew developed a particular interest in bird migration, fostered by many autumn days at local hawk watch sites. By age ten, Andrew was regularly leading bird walks at Westchester County parks, especially at Marshlands Conservancy in Rye. In May 1990, Andrew captained the first youth-birding team in the 24-hour World Series of Birding in New Jersey. Andrew attended Cornell University in August 1991, making the acquaintance of Bill Evans, flight-call research pioneer, and later receiving his B.S. in Natural Resources in May 1995. In August 1995, he co-led his first tour for Victor Emanuel Nature Tours in Peru and continues to lead tours until the present.

In 1998 and 1999, Andrew captained consecutive winning teams in the Great Texas Birding Classic. Although birds had always been his true passion, Andrew is also a performing musician; since July 1997, he has toured extensively with his band, Mectapus, which has released three CDs to date. However, Andrew realized that his true calling was in unraveling the remaining mysteries of nocturnal migration and flight-calling behavior, so he returned to academic pursuits, energized by meeting Dr. Sidney Gauthreaux at the American Ornithologists' Union meeting in St. Louis during April 1998. By the fall of 1999, Andrew had returned to school, beginning at Clemson University as a research assistant in Dr. Gauthreaux's radar ornithology laboratory. He received his M.S. in Zoology in August 2001, comparing nocturnal bird density measures from surveillance radar and nocturnal flight-call counts from acoustic sensors. It was during his research at Clemson that Andrew met his wife-to-be, Patricia Ryan. After graduation, Andrew moved to New York to join Patricia and to begin working for the National Audubon Society as the Ford Audubon Science

Fellow. He worked for a year analyzing bird distribution data and developing Internet technology to improve access to such data for the public.

Andrew returned to Cornell University in the fall of 2002 after completing his Audubon fellowship, beginning his doctoral research in the Department of Ecology and Evolutionary Biology under Dr. John Fitzpatrick. Upon returning to academic pursuits, Andrew combined his extensive field experience with explicit research goals focused on nocturnal bird migration, flight-calling behavior, and radar ornithology. He continued this trend at Cornell, conducting his fieldwork on flight-calls in numerous locations across the United States, Mexico, and the Greater and Lesser Antilles while pursuing a variety of other ornithological projects, including two Rapid Biological Inventories in Cuba, and the Ivory-billed Woodpecker Recovery Project in Arkansas, and co-authoring species' accounts for Handbook of the Birds of the World.

At present, Andrew lives in New York, New York with his wife, Patricia Ryan. He plans to continue his research on flight-calls and bird migration and to begin applying his knowledge and experience to conservation goals.

ACKNOWLEDGMENTS

I deeply appreciate the support and inspiration from my committee, Drs. John W. Fitzpatrick, J. Irby Lovette, Jack W. Bradbury, and Chris W. Clark, without whom I would be lost in a sea of confusion. I would also like to thank some "ghost" committee members, Drs. Stephen Emlen and Kurt Fristrup, for advice during the earliest stages of the dissertation process and data collection as well as invaluable critical review and commentary during manuscript preparation. While each of their contributions is far greater than I could possibly hope to summarize in a few sentences, I will highlight a few specific instances of thanks for my special committee.

I thank Jack for agreeing to "co-advise" me, for offering honest opinions from the earliest stages of my research, and for schooling me in statistical arts, the likes of which I could only have dreamed (nightmare?). I thank Chris for his boundless energy and enthusiasm, in particular for guiding me toward the possibilities of conservation through acoustics. I thank Irby for wisdom and advice far beyond his years, for providing me with the insight and inspiration to pursue a direction I would likely not have otherwise traveled, and for providing the raw materials to make my visions of comparative analysis a reality. Finally, I thank Fitz for an idea jotted on a napkin in 1997 that began my graduate career, for providing a passionate and informed (as well as insane and highly mobile!) role model, and for leading (hurtling) me into a diversity and abundance of opportunities greater than I could possibly imagine (for example, Cuba, Handbook of the Birds of the World, Ivory-billed Woodpecker).

In addition, I must make it clear that without Dr. William Provine, I would not have continued my pursuit of higher education in graduate school. His tireless and dogged efforts on my behalf and his kind words opened the doors to Clemson and Cornell, and for all his support, I thank him dearly.

and flight-calling. I only wish I could have spent more time in his basement learning the wealth of knowledge lurking quietly therein.

My life has not been the same since I met Victor Emanuel in 1986, and this fact was never more apparent than it was during my dissertation. Whether the countless hours of discussing migration, the opportunities to travel anywhere and everywhere, or the connections to an incredibly talented and diverse network of first-rate ornithologists and birders, the wealth of experiences that Victor made possible has enriched my life beyond my capacities to explain.

In the fall of 1991 during my first semester as an undergraduate at Cornell University, I met Bill Evans. Little did I know that this meeting would change the course of my career in ways I could never have anticipated? By putting names to the sounds I had heard for years at night, Bill opened my eyes and ears to a world of migration I had never known (and that few truly understood!). Bill's knowledge and passion for migration, coupled with a fun-loving, thoughtful, reasonable, and competitive streak, set me ablaze on my path to studying flight-calls. My time with him in the field over the last 15 years has always been enlightening, inspiring, and often frightening!

For holding my hands through the thickest statistical analysis and battling the ugliness of imperfect data, I thank Leila Hatch, Kathryn Cortopassi, Wesley Hochachka, Kurt Fristrup, Harold Figueroa, Matt Robbins, Aisha Thorn, Tim Krein, Russ Charif, Stefan Hames, Daniel Fink, the BORG collective (David Winkler, James Mandel, David Cerasale, Gernot Huber), Karen Grace-Martin, Françoise Vermeylen, Dan Steinberg and Salford Systems, Chuck Jessop and the CIT staff, and Josh Donlan. Your direction has been invaluable, helping me attain a level of comfort with a subject that previously lacked all things comfortable.

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Nothing will ever be attempted, if all possible objections must first be overcome.

—Dr Samuel Johnson, 1759

CHAPTER ONE: FLIGHT-CALLS AND THEIR VALUE FOR FUTURE

ORNITHOLOGICAL STUDIES AND CONSERVATION PROJECTS*

Abstract

Many passerine birds and their relatives have flight-calls, species-specific

vocalizations given primarily during sustained flight (for example, migration). While

references to flight-calls appear in the ornithological literature as early as the 1890s,

some of their most basic features remain poorly known, including their functions,

origins, ontogeny, the distances over which they are used, and how much individual

variation exists in call characters and calling rates. With improved knowledge of these

vocalizations, flight-calls could be useful in a variety of applications. Identifying the

function of flight-calls could illuminate how birds refine migration strategies during

crucial decision-making periods. Because flight-calls are relatively simple

vocalizations, they could be useful characters for future evolutionary and comparative

analyses. Flight-call monitoring can be a powerful method for studying nocturnal

migration. However, all such applications require more detailed knowledge of

nocturnal calling behavior. This review article summarizes the available information

on flight-calls, and it highlights areas where future research could improve and expand

this knowledge. Much of the information on flight-calls is archived in personal field

notes and recordings. Hence, this review relies unusually heavily on unpublished

information provided by colleagues.

What is a flight-call and what species give flight-calls?

Flight-calls of passerine and related birds (cuckoos and woodpeckers, among others)

are defined as species-specific notes, either frequency-modulated or pure, of up to

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several syllables, generally in the 1-9 kHz frequency band and 50-300 ms in duration. Spectrograms of a range of representative passerine flight-calls are depicted in Figure 1.1. These calls are the primary vocalizations given by many species of birds during long, sustained flights, particularly migratory flights (Evans and O'Brien 2002). Despite the name *flight-call*, birds may produce these calls in a variety of contexts other than migratory flight, including while perched (notably the cardueline finches, Mundinger 1970) and while interacting with fledged young (notably the parulid warblers; personal observations). Many species also use their flight-calls year-round (Evans and O'Brien 2002), and some species regularly give flight-calls while in diurnal flight (e.g. Yellow-rumped Warbler *Dendroica coronata*; Evans and O'Brien 2002). Flight-calls are distinct from songs, and more importantly they are distinct from other types of short calls, such as chip notes and alarm calls.

Nearctic and Neotropical species – Flight-calls have been studied most intensively in North America, and Evans and O'Brien (2002) compiled a guide to the flight-calls of migratory birds occurring in the eastern part of the continent (mostly east of the 100th meridian). This unique resource provides detailed information on flight-calls, including descriptions of the vocalizations and flight-calling behavior, spectrographic representations, examples, and identification tips. Not all of the species contained in the guide regularly give flight-calls, and not all of those that regularly give flight-calls give them at night. For example, cuckoos, woodpeckers, corvids, larks, swallows, thrushes, wood-warblers, tanagers and grosbeaks, emberizid sparrows, blackbirds, and finches (among other groups) give flight-calls regularly, but most woodpeckers, corvids, larks, swallows, and finches rarely use these calls at night (these are primarily diurnal migrants). Groups of species that do not regularly give flight-calls (during diurnal or nocturnal movements) include New World flycatchers (Tyrannidae), vireos (Vireonidae), and mimids (Mimidae).

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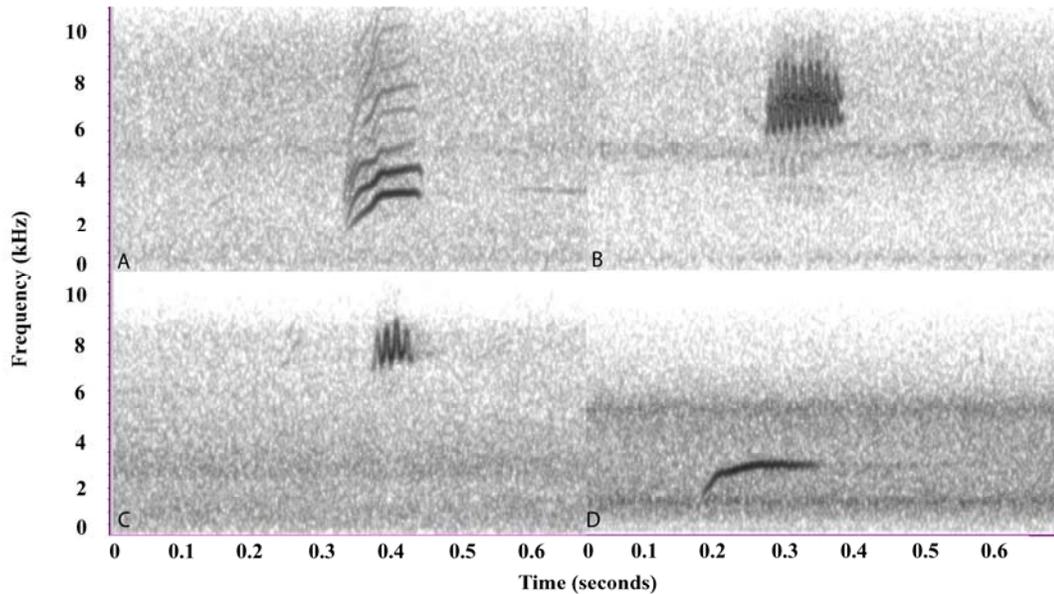
Figure 1.1. Examples of passerine flight-calls. A) Bobolink *Dolichonyx oryzivorus*. B) Indigo Bunting *Passerine cyanea*. C) Blackpoll Warbler *Dendroica striata*. D) Swainson's Thrush *Catharus ustulatus*. Note that these axes of these spectrograms have identical scales, facilitating comparison among the different species' calls. B and C depict modulated calls, while A and D depict flight-calls or parts of flight-calls with pure tones. These flight-calls come from Evans and O'Brien (2002).

Palearctic and Paleotropical species – Although less intensively studied than Nearctic species, numerous Palearctic and Paleotropical species also give flight-calls (Chappuis 1989, van den Berg et al. 2003). Some of these are closely related to vocal New World species, such as *Turdus* thrushes (e.g. Fieldfare *Turdus pilaris* and Redwing *Turdus iliacus*), cardueline finches, pipits, and *Regulus* crests; others species are more typically Old World, like bee-eaters (Meropidae), *Emberiza* buntings (such as Rustic Bunting *Emberiza rustica* and Ortolan Bunting *Emberiza hortluna*), many wagtails (Motacillidae) and larks (Alaudidae), and fringillid finches. Like some Nearctic birds, not all of these species regularly give these vocalizations at night. In fact, it is primarily European *Turdus* thrushes (Siivonen 1936, Browne 1953, Vleugel 1954, 1960, Chappuis 1989, van den Berg 2003) and some *Emberiza* buntings and *Regulus*

crests (Magnus Robb, personal communication) that regularly give flight-calls during nocturnal migration. Other Palearctic-Paleotropical species also give flight-calls at night, including several species of pitta (Fairy Pitta, SRS Lin, personal communication; Blue-winged Pitta, Phillip Round, personal communication), some Asian and Australo-Papuan cuckoos such as Long-tailed Koel *Eudynamys taitensis* and Pied Cuckoo *Clamator jacobinus* (Narena Olliver, personal communication), and Woodland Kingfisher *Halcyon senegalensis* (Dalena Mostert, personal communication). Future field work in Africa, Asia, and Australia will probably highlight numerous additional species that also give flight-calls at night.

Like New World exceptions that rarely give flight-calls, there are also Palearctic birds that rarely give flight-calls: Old World flycatchers (Muscicapidae) and Old World warblers (Sylviidae) are generally silent during migration. However, some species, such as Pied *Ficedula hypoleuca* and Spotted Flycatcher *Muscicapa striata*, not normally heard during nocturnal movements apparently vocalize under poor visibility conditions (Bruderer, personal communication; also Herremans 1993), and some sylviid warblers infrequently use vocalizations (similar to fledgling calls) during diurnal movements (Blackcap *Sylvia atricapilla*, Chiffchaff *Phylloscopus collybita*; Marc Herremans personal communication; African River Warbler; JM Kriek personal communication).

Identification – A frequently asked question is, how does one know the identity of a calling bird when it is migrating at night and is not visible? Identification of some calls is simple because the nocturnal vocalizations are the same as the diurnal vocalizations (*Catharus*; Howes 1912, Evans 1994). However, the identification of many species is often more complicated and requires deeper investigation and additional information. This information generally comes from two distinct sources (Evans and Mellinger 1999, Evans and Rosenberg 2000):

1) Comparisons of the spectrograms of diurnal flight-calls of known species and unknown nocturnal flight-calls – Many birds observed in visible morning flights often give flight-calls (Evans and Rosenberg 2000, Evans and O'Brien 2002; see Gauthreaux 1978, Hall and Bell 1981, Weidner et al. 1992 for a description of the morning flight phenomenon); also, direct comparison of unknown nocturnal vocalizations and flight-calls recorded from birds in captivity or from birds with attached miniature microphones, is possible (Hamilton 1962, Farnsworth and Lanzone unpublished data, Cochran unpublished data). See Figure 1.2 for an example of these types of comparisons.

2) Correlating the seasonal timing and geographic range of nocturnal calls with known timing and migration ranges for each species. Species-specific migration calendars are available for many species and locations in North America, often generated from accounts of the species killed during nocturnal migration and collected at tall structures (colliding with television towers, lighthouses or buildings) and historical arrival and departure dates (see Evans 1994, Evans and Rosenberg 2000; also Hedges 2001).
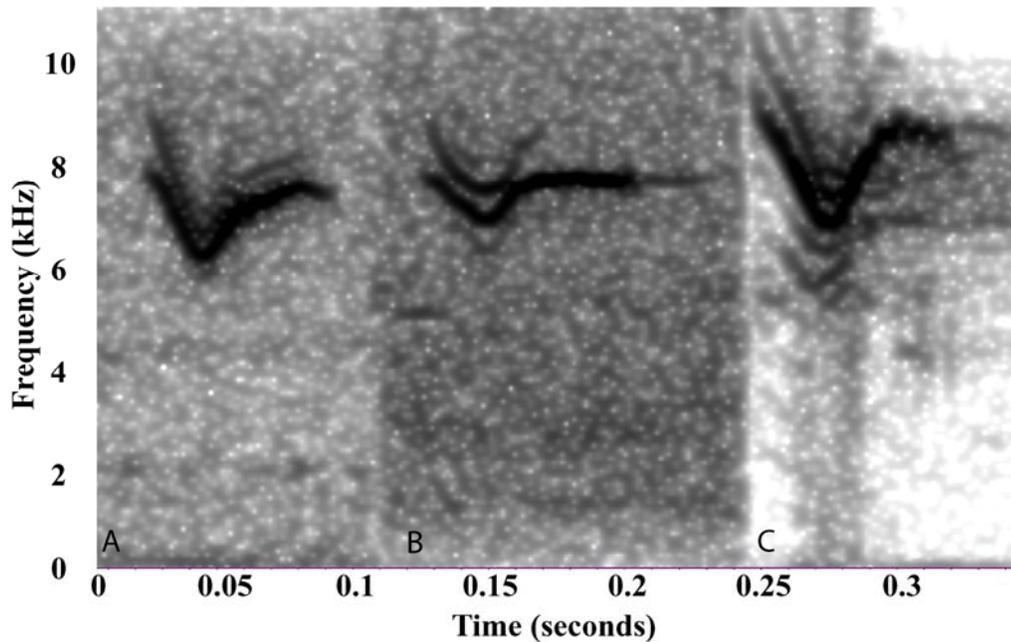
Figure 1.2. Flight-calls of American Redstart *Setophaga ruticilla.* A) Diurnal flight-call. B) Nocturnal flight-call. C) Flight-call recorded in captivity.

Early flight-call research (pre-1959): evidence of nocturnal migration and patterns

Although ornithologists debated certain aspects of bird migration strategies and patterns into the late 19th and early 20th centuries (for example, do birds migrate across the Gulf of Mexico? Frazar 1881, Cooke 1904, Lowery 1945, 1946, Williams 1945, 1947), most accepted that many species of birds migrate at night (Chapman 1888, Cooke 1904, 1915, Lowery 1946). It was largely the flight-calls of migrating birds that authors cited as direct evidence of such nocturnal movements, using the calls to identify species, to assess the magnitude of migration, and as a quaint reminder of the wonders of bird migration. Libby (1899) tallied 3600 calls during the course of five hours of passive listening near Madison, Wisconsin on 14 September 1896, the first published attempt to quantify nocturnal migration using flight-calls. Kopman (1904) and Carpenter (1906) referenced thrush vocalizations heard during nocturnal migration

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(especially Veery *Catharus fuscescens* and Gray-cheeked Thrush *Catharus minimus*). Howes (1912) detailed the nocturnal vocalizations of Swainson's Thrush (*Catharus ustulatus*) in terms of the location and timing of this species' migratory routes during fall in northeastern United States. Tyler (1916) highlighted the diversity of flight-calls and also noted that flight-calls appear in a species' vocal repertoire during periods of migration.

Studies through the 1950s illuminated the temporal pattern of nocturnal calling (*Turdus* in Finland and Ireland, Siivonen 1936 and Browne 1953, respectively; *Catharus* in Gaspé, Ball 1952). Ball (1952) produced one of the most comprehensive studies on the timing of migration of a particular species through a region using flight-calls (autumn migration of *Catharus* thrushes in the Gaspé Peninsula). Popular accounts of nocturnal call counts from eastern North America also appeared regularly, usually as call totals or interpreted numbers of *Catharus* thrushes passing over during a portion of an evening (Audubon Field Notes; see brief summary in Evans and O'Brien 2002).

Toward the end of the 1950s, interest in quantifying nocturnal migration sparked a new debate about the relationship between the timing of peak bird density aloft and the timing of peak flight-call counts. The relationship between flight-call counts and direct visual observations of migratory birds passing in front of the full moon (Lowery and Newman 1955, Newman 1956) suggested that calling peaks at a different time than the actual density of birds in the atmosphere: bird density peaked 2-3 hours after sunset (Lowery and Newman 1955, Newman 1956) while vocalization peaked in the hours just before dawn (Ball 1952). Also, direct visual data indicated that the distribution of nocturnal migrants in the air was relatively even, in contrast to flight-call data that suggested a clumped distribution (Ball 1952). To some, the record of nocturnal calling exaggerated the impression of large-scale migration detected by

moon-watching (Vleugel 1960); and to further confound the situation, European call count data indicated *Turdus* calling activity peaked close to local midnight with another spike in activity just before dawn (Vleugel 1954, summarized 1960). The interpretation of the acoustic record, especially in relation to actual numbers of birds aloft at night, was not at all clear.

Modern flight-call research (post 1959): automation, recognition, and identification

Although the limits and variability of human hearing largely prevented objective comparisons among earlier studies of migration, technological developments of the 1940s and 1950s enabled researchers to make audio recordings of nocturnal bird migration useful for more efficient and objective data collection, analysis, and comparisons (see Evans and O'Brien 2002). The invention of the sound spectrograph made visual comparisons of similar sounds possible (Koenig et al. 1946), and the perfection of magnetic tape and tape recording devices made archiving sounds a reality. Graber and Cochran (1959) sampled nocturnal flight-calls using a microphone and a parabolic antenna, automatically recording calls to magnetic tape at 10-minute intervals during entire nights of migration. Such techniques provided the foundation for future, in-depth examination of the aural records of nocturnal migration. Graber (1968) further advanced these techniques by comparing the acoustic record of nocturnal migration with radar and diurnal field census data. However, the meaning of the acoustic record of nocturnal migration remained equivocal (Graber 1968), although Graber and Cochran (1959, 1960) suggested that qualitative data from acoustic monitoring complemented quantitative data from visual methods. Additionally, the function of flight-calls was still unknown, although Hamilton (1962) presented evidence from birds recorded in captivity that suggested that calls functioned as a means of communication among individuals in flocks.

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Whereas electronic technologies made possible acoustic sampling across increasingly large temporal and spatial scales of migration, labor-intensive data collection and analysis, expensive and bulky recording media, and unwieldy and often unreliable recording devices effectively limited the scope of acoustic studies. However, by the late 1980s and early 1990s technological advances (for example, increased computer processor speed, detection algorithms; see www.oldbird.org for details) allowed researchers to resolve many technical issues that hindered previous attempts using acoustics to study nocturnal migration. Dierschke (1989) recorded nocturnal flight-calls automatically at Helgoland, Germany using a device activated by signals of specific duration, loudness and frequency. This method conserved audio tape and saved analysis time, bypassing portions of night when no calling occurred. Improved detection and classification algorithms (Mills 1995, Taylor 1995) provided the means to extract flight-calls automatically from either previously made recordings or real-time data from an active microphone. Such software generally detects nocturnal flight-calls by locating isolated temporal energy peaks in a specified frequency range and classifies calls by tracking frequencies over time with an artificial neural network. Simultaneous advances in spectrographic analysis methods (Clark et al. 1987) and computer software and programs (Canary, Charif et al. 1995) made more rapid examination and discrimination of similar calls a reality.

Inexpensive portable and durable microphone designs, pioneered by Evans (1994, 2000, Evans and Mellinger 1999), provided the means to collect flight-call data across larger geographic and temporal scales (Evans and Rosenberg 2000, Mills 2000). Improved radar technologies and coverage afforded the opportunity to compare measures of nocturnal migration at much greater scales (after Graber 1968; Larkin et al. 2002, Farnsworth et al. 2004). Flight-call identification also progressed, culminating in the production of the first electronic identification guide (Evans and

O'Brien 2002). With increasing knowledge of the identity of nocturnal vocalizations, research and conservation efforts could use acoustic methods to examine species-specific patterns (Evans 1994, Millikin 1998, Evans and Mellinger 1999, Evans and Rosenberg 2000, Evans 2000).

Patterns of flight-calling behavior

Effects of atmospheric conditions – Several relationships between call counts and atmospheric conditions are apparent from the literature and to observers in the field during a migration season. Call counts increase with increasing cloud cover and decreasing cloud ceiling, especially in the presence of artificial lighting (Cochran and Graber 1958, Graber and Cochran 1960, Ogden 1960, Graber 1968, Clemens 1978, Dorka 1966, Thake 1983, Evans and Mellinger 1999). Call counts also increase as birds approach frontal boundaries, the transition between air masses of different density (Peterssen 1956), where conditions unfavorable for migration such precipitation, high winds, and poor visibility force birds to pile up or descend (Graber and Cochran 1960). Calling usually occurs during periods of seasonally appropriate wind directions (Graber and Cochran 1960). Vleugel (1960) found that call counts of *Turdus* thrushes in Holland during autumn increased with the passage of cold fronts and decreasing temperature. Call counts are also positively correlated with 24-hour trends of falling temperatures in autumn, and the converse is true in the spring (Graber and Cochran 1960). There are two potential caveats to extrapolating from the results of these studies: the studies represent site-specific results; and there is a lack of information about rates of calling and their relationship to independent measure of bird numbers.

Effects of altitude and topography – The effects of flight altitudes on calling rates are not well known. Evans (2000) recorded many vocalizations in the lowest 500m above

the ground during autumn migration (see also Black 1997). Evans and Rosenberg (2000) and Evans (2000) indicated that flight altitudes of calling warblers was lower (less than 200-300 m) than the flight altitudes of calling thrushes (up to 450-500 m). There is also temporal variation in the flight altitudes of calling birds, and average altitudes can be substantially lower or higher on different nights (Black 1997, Evans personal communication). Whether calling is primarily a boundary layer phenomenon, occurring only in the atmospheric strata close to the ground, is not known.

Although migration occurs across broad spatial scales (Lowery and Newman 1955, Parslow 1969, Gauthreaux et al. 2003), there is evidence suggesting that topographic features such as mountains or hilly terrain and coastlines concentrate birds (Eastwood 1967, Bruderer 1978, Richardson 1978, 1990, Åkesson 1993, Williams et al. 2001); these features also appear to concentrate flight-calls. Evans and Mellinger (1999) found that changing wind conditions resulted in larger numbers of calls counted on the coast of Texas; southwesterly winds for bird migrating inland toward the coast, and to avoid drifting over the Gulf of Mexico birds piled up on the coast and then moved north along it. Additionally, Evans (2005) reported that during low cloud ceiling conditions, altitudinal variations of terrain disrupt the flight of calling migrant passerines, effectively concentrating calling birds in areas with lower altitudes.

Temporal patterns – Despite the variability in all of these relationships, patterns of call counts across seasons and years are often consistent and probably represent some true behavioral and biological patterns (for example, the migration timing of different species). Conversely, nightly temporal patterns of calling exhibit much greater variability. These patterns could represent site-specific differences and additional unknown behavioral and biological patterns. Ball (1952) recorded approximately 90% of thrush vocalizations in the hours just before dawn with a ratio of 27 calls after

midnight to 1 call before midnight (from a total of 33921 calls). Graber and Cochran (1960) supported this conditionally: although they detected migration consistently at any hour of the night, there was a marked peak in calling in the hours just before dawn if migration occurred all night. Farnsworth and Russell (2005) reported a similar pattern in an acoustic study of migration over the Gulf of Mexico (south of Alabama), finding that the nightly peak of call counts occurred in the 2 hours just before dawn. In contrast, call counts of *Turdus* thrushes in Europe usually peaked in the hours closest to local midnight, with deviations from this pattern usually associated with a frontal passage (Siivonen 1936, Browne 1953, Vleugel 1954, 1960). Furthermore, recent studies found that flight-call counts varied extensively throughout the night, though many nights showed peaks in the hours close to local midnight (Ross et al. 1995, Farnsworth et al. 2004).

The factors responsible for the variability in nightly patterns of peak call counts are not known; these might include meteorological phenomena (patterns of local weather variations; Graber and Cochran 1960, Graber 1968, Evans and Mellinger 1999, Evans and Rosenberg 2000, Evans 2000) and variation in flock sizes and species composition (Miller 1921, Marler 1956, Hamilton 1962, Thake 1981, 1983, Farnsworth et al 2004). Some variability might be a function of different species descending at different times of night and calling at different rates during descent (Graber 1968). Furthermore, high individual variation in the rate of calling rate could be a major factor. Cochran (personal communication) placed small microphones on migrating Swainson's Thrushes. He found that mean call rates of migrating Swainson's Thrushes "ranged from 0 to 37 calls hour^{-1}, including one individual vocalizing 16 times minute^{-1} and one individual that did not call for 3 hours."

Hemispheric patterns – Another intriguing (and as yet unexplained) pattern is that, by nearly all accounts, vocalization by nocturnally migrating birds in the Palearctic seems

to exhibit a different pattern than vocalization in the Nearctic migration system. Calls occur with greater frequency, greater magnitude, and greater species diversity in the New World. Whether this is a function of small sample sizes of European studies, fundamental behavioral differences between the migration systems, phylogenetic effects, or some combination thereof, the explanation for this pattern is unknown. Anecdotal accounts from numerous European researchers suggest that flight-calling is limited even in the species that regularly vocalize at night (see Vleugel 1960 nightly call counts relative to Ball 1952).

Function of flight-calls

Previous workers have suggested that birds give flight-calls in response to fear (Hudson 1923), loneliness (Drost 1963), hunger or the light of approaching dawn (Ball 1952). In some species the use of flight-calls might signify the presence of a transient individual in a resident individual's territory (Blackbird *Turdus merula*; Magnus Robb personal communication). Further anecdotal information indicates that some parulid warblers might use flight-calls in aggressive interactions, though this behavioral association is apparently rare (Farnsworth personal observations). Some monomorphic, non-passerine birds (Swinhoe's Storm-Petrel *Oceanodroma monorhis*) use flight-calls for sex-specific discrimination in situations with limited visual information (for example, at night; James and Robertson 1985, Taoka and Nakamura 1990), though it is not known whether this is true for passerines. The consensus from the recent literature, together with anecdotal evidence, suggests that flight-calls function to maintain groups and to stimulate *zugunruhe* (migratory restlessness or activity) in conspecifics, perhaps especially in inexperienced birds (Tyler 1916, Ball 1952, Hamilton 1962, Drost 1963, Graber 1968, Thake 1981, 1983). Hamilton (1962) presented supporting evidence for these functions of flight-calls from his studies of captive Bobolinks: calling triggered mutual responses from birds in close proximity

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and was associated with migratory periods, nightly unrest and increased fluttering, and calling.

Flight-calls also highlight differences among geographically separated populations and, at least in some species, allow recognition of individuals (Mundinger 1970, Marler and Mundinger 1975, Mundinger 1979, Adkisson 1981, Groth 1993b, Hahn et al. 2001, Sewall et al. 2004). Whether the flight-calls of nocturnally migrating birds perform the same function is not known. Furthermore, whether birds use flight-calls in a way that is similar to use of contact calls and alarm calls, for group cohesion and social affiliation, is not known (Mammen and Nowicki 1981, Nowicki 1983, Groth 1993b, Marzlu and Balda 1992, Dufty and Hanson 1999, Baker 2000, Hahn et al. 2001, Sewall et al. 2004, Baker 2004). Nocturnal groupings might be social, maintained by flight-calls functioning to communicate such information (Lowery and Newman 1955, Graber and Cochran 1960, Hamilton 1962, 1967, Gauthreaux 1972, Balcomb 1977). Interspecific grouping does occur during nocturnal migration (Graber and Cochran 1960, Hamilton 1962, Evans and Mellinger 1999, Evans and Rosenberg 2000). However, concentrations could also be random groupings or the results of small-scale atmospheric motion that could generate such structure (Larkin 1982).

Although Balcomb (1977) argued against the benefits of coordinated migrant groups for nocturnal orientation, migrating birds could use flight-calls to obtain orientation information, to reduce dispersion of headings, and to determine changing wind direction by echolocation and monitoring Doppler shifts (Lowery and Newman 1955, Griffin 1969, Griffin and Buchler 1978, Thake 1981, 1983); such functions could be especially useful in reduced visibility, increasing the likelihood of being heard, hearing others, and avoiding collisions (Graber 1968, D'Arms and Griffin 1972, Thake 1983, Larom et al. 1997). Such a function could also have particular

importance for inexperienced migrants, and there is some evidence to suggest that young birds vocalize more frequently than adults (Cochran personal communication). Many flight-calls exhibit a pattern of rapid frequency sweeps that might be advantageous for birds deriving information (*contra* Thake 1983), with some frequencies encountering complex and favorable interference patterns for sound reflection or retransmission (Griffin and Buchler 1978). The ability to locate calls of other individuals improves as a function of abrupt beginnings and endings, discontinuities and repetition (Hamilton 1962), that are also characteristic of many flight-calls. Birds possess the ability to resolve small changes in frequency (Rock Pigeon *Columba livia*: Price et al. 1967; Budgerigar *Melopsittacus undulatus*: Dooling and Saunders 1973, Park and Dooling 1985, 1986; Brown et al.. 1988; Ali et al.. 1993; Barn Owl *Tyto alba*, Quine and Konishi 1974).

Future directions

As is clear from the review above, major gaps exist in our understanding of flight-calling behavior. Exploring the immediate causation, the ontogenetic aspects of the behavior, the behavior's evolutionary history and the patterns of change over time are all critical for understanding the functional significance of the behavior (Tinbergen 1963).

Are flight-calls learned? – Although flight-calls are one of the earliest call types to appear in the repertoire of juvenile cardueline finches (Mundinger 1979), these species learn and change flight-calls by imitation throughout life (Mundinger 1970). Is this pattern true for other passerines? Hamilton (1962) suggested that the calls were innate. Comparing the flight-calls of captive-bred birds with diurnal and nocturnal vocalizations of wild birds could provide some answers. No detailed seasonal usage pattern of flight-call vocalizations is available, and developing a time table for many

species will probably be informative. Understanding the ontogeny of flight-calls is crucial for future attempts to classify these calls, and it has important implications for determining flight-call functions. Furthermore, if flight-calls are learned behaviors in a diverse array of passerines, the influence of vegetation structure and ambient noise spectra could play an important role in the development of flight-calls (Hansen 1979, Nottebohm 1985).

What factors constrain flight-calls? – Recent studies show that different species of birds have different detection thresholds for signals in ambient noise (Klump 1996, Langemann et al. 1998), as well as different hearing thresholds (Dooling 1982, Dooling and Saunders 1975, Okanoya and Dooling 1987). Differences in the perceptual abilities of species could play important roles in determining variation in flight-call frequencies. Flight-calls may also experience different selection pressures related to encoding information (relative to selective pressure on songs). Reverberation, amplitude modulation rate, consistency of transmission and spectral distribution of ambient noise are important sonic properties defining song vocalizations, and these properties vary with selection pressures among habitats (Marler 1955, Morton 1975, Wiley 1991, Ryan and Brenowitz 1985). How these properties relate to the use and the function of flight-calls is not known. Additionally, although Hamilton (1962) did not believe that predators play a major role in shaping flight-calls, Gill and Sealy (2003, 2004) found evidence that high frequency "seet" calls alert individuals to brood parasites. Is it possible that flight-calls, similarly high in frequency and short in duration, could be used to communicate information above the frequency thresholds of predators (Langemann et al. 1998)? If flight-calls do have some explicit relationship to fledgling vocalizations (flight-calls originated from such vocalizations; Tyler 1916), is there a direct relationship between such anti-predatory behaviors and flight-calls?

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Over what distances are flight-calls used? – No studies have examined the range of distances over which birds use flight-calls for communication. Because signals indicative of longer range communication are lower in frequency (Larom 2002, Larom et al. 1997, Marten and Marler 1977), the pattern of high frequencies in flight-calls suggests that flight-calls might be used primarily for short distance communication. However, the constraints associated with sound production during flight are not known, but they have implications for nocturnal communication and the architecture of nocturnal groupings. Furthermore, optimal in-flight communication using certain frequencies could shape flight-call vocalizations that either travel best in specific atmospheric and microclimatic strata or avoid specific ambient noise spectra (Larom 2002, Rundus and Hart 2002, Slabbekoorn et al. 2002, Slabbekoorn and Peet 2003).

How variable are flight-call characters – Intraspecific variation in flight-calls is not a recent discovery (*Catharus*, Ball 1952), but the extent of this intraspecific variation in flight-call characters such as frequency has only recently received greater attention (Hahn et al. 2001, Evans and O'Brien 2002, Sewall et al. 2004). Some evidence suggests that certain species, notably thrushes, larks, pipits, and finches, have substantial variation in flight-call characters (Evans and O'Brien 2002, Magnus Robb personal communication; Cochran unpublished data, Farnsworth and Lanzone in preparation). The importance of such variation is also unknown, although Mundinger (1977) suggested that call-matching and imitation could be important factors. Furthermore, while a few studies have explored the extent of phylogenetic signal in songs (e.g. kinglets; Packert et al. 2003) and calls (e.g. herons; McCracken and Sheldon 1997), a limited number of species are represented and none of these studies explicitly address flight-calls. Similarly, there is nothing known about the existence of character release in flight-calls: if this exists, what is the relationship between character release and diversity of related species?

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Are there potential applications for flight-calls? – Flight-calls are simple vocalizations (especially relative to songs) and could be useful behavioral characters in comparative analyses among taxa (Mundinger 1979, Farnsworth and Lovette 2005). Flight-calls also could aid in resolving cryptic species (Groth 1988) and delineating taxa (Mundinger 1979, Adkisson 1981, Groth 1988, 1993a, Hahn et al. 2001, Sewall et al. 2004). However, categorizing natural variation in flight-calls and expanding the sampling of spatial and temporal distributions of flight-call datasets are critical precursors to pursuing such directions (Sewall et al. 2004, Farnsworth and Lanzone in preparation). Flight-calls may also shed light on habitat preference and morphology (Groth 1993 a,b). For example, in phylogenetically controlled and uncontrolled analyses, Farnsworth and Lovette (2005) found little support for morphological constraints on flight-call frequencies in parulid wood-warblers. This pattern differs from the widely reported pattern of birds with larger body mass exhibiting vocalizations with lower frequencies (Greenewalt 1968, Wallschläger 1980). There are also diverse and potential powerful applications for monitoring flight-calls to document broad front patterns of species-specific nocturnal movements and altitudinal distribution of calling migrants (Tyler 1916, Ball 1952, Graber and Cochran 1960, Graber 1968, Evans 1994, Evans and Mellinger 1999, Evans and Rosenberg 2000, Evans 2000) and to identify the points of origin of calling migrants (Evans personal communication).

The patterns of nocturnal bird migration as detected by radar and acoustic methods do not always differ, although these methods do illuminate what are likely fundamental differences in patterns of behaviors (Ross et al. 1995, Larkin et al. 2002, Farnsworth et al. 2004). Nocturnal call counts of migrating birds can be useful as indices of nocturnal bird density aloft (Larkin et al.. 2002, Farnsworth et al. 2004), although extensive variation in calling rates (both among and within species) poses

major challenges for measuring bird density from flight-calls alone (Libby 1899, Graber 1968, Dierschke 1989, Evans and Mellinger 1999, Farnsworth 2001, Farnsworth et al. 2004). Moreover, there can be substantial differences between high volume of migration and high incidences of calling (Graber and Cochran 1960, Ross et al. 1995, Farnsworth et al. 2004). More detailed studies of nocturnal migration using radar and acoustic methods simultaneously, and studies that span even larger spatial and temporal scales are necessary to resolve these issues in greater detail. More studies using stand-alone methods based on flight-call counts are also valuable (Evans and Mellinger 1999), generating a database of departure and arrival data as well as relative proportions of species on different nights.

Concluding remarks

Many additional questions remain unanswered, and future studies of flight-calls clearly face challenges; however, they also provide excellent opportunities for improving the understanding of avian migration and life histories and the way these relate to such a variable behavior. Why do some species remain silent during nocturnal migration? Is the regular use of flight-calls related to other behavioral traits (flock foraging)? Do birds migrating in similar directions at similar times of the year show convergent vocalizations (Hamilton 1962 and 1967, Graber 1968, Thake 1981, 1983)? Do birds benefit from reciprocal calling by enhancing associations with conspecifics and, after landing, by reducing predation risk on the ground (after Hamilton 1971)? There are numerous applications for flight-calls in applied conservation, ecological, behavioral, and evolutionary studies. Intraspecific variation could be the result of proximate factors on a migratory route (dynamic environmental variation such as changing weather conditions, approaching ecological barriers), whereas interspecific variation could be the result of ultimate factors (evolution of migratory strategies, differences in foraging strategies). Regardless of the hypotheses

or the applications, it is important to remember that interpreting call counts or flight-calling behavior could be greatly misleading without considering such underlying behavioral information (Graber 1968, Evans and Mellinger 1999).

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CHAPTER TWO: EFFECTS OF WEATHER CONDITIONS ON FLIGHT-CALL
COUNTS OF NOCTURNALLY MIGRATING BIRDS[*]

Abstract

Monitoring flight-calls of migrating birds may be a useful way to quantify bird
numbers across space and time, but migrant density and call counts are only loosely
correlated. In an effort to determine additional sources of call count variation and to
improve upon simple density-call count models, we examined relationships between
10 weather variables and hourly call counts with and without removing statistically the
effects of bird density. We sampled radar, acoustic, and local climatic data hourly for
556 hours during 58 nights in western SC and southeastern NY. Although call counts
were significantly correlated to bird density and weather variables, call counts were
not significantly correlated to weather conditions after statistically controlling for
density effects. Weather factors improved explanatory power of simple density-call
count models, but additional variation in call counts remained unexplained.

Introduction

Conservation of migrant birds is a high priority (Andrew and Andres 2002, Donovan
et al. 2002, Ruth et al. 2003, Tankersley 2004, Kelly and Hutto 2005). Some current
migration monitoring programs have either used or proposed acoustic monitoring of
flight-calls as a method for quantifying migration, identifying species-specific routes,
and enhancing monitoring protocols with information about passing migrants that
traditional methods might not detect (Evans and Mellinger 1999, Evans 2000, Evans
and Rosenberg 2000, Hedges 2001). Flight-calls are vocalizations primarily given by
birds in sustained flight, and the vocalizations are usually single notes that are less

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[*] Andrew Farnsworth, Department of Ecology and Evolutionary Biology, Cornell Laboratory of
Ornithology, Cornell University, Ithaca, NY 14850; Sidney A. Gauthreaux, Jr., Department of
Biological Sciences, Clemson University, Clemson, SC 29630.

than one second in duration and that vary among species in frequency, modulation, and bandwidth (see Evans and O'Brien 2002 and Farnsworth 2005 for additional definitions).

Flight-call monitoring theoretically could be useful for generating estimates of the number of vocal birds passing at night (Evans and Mellinger 1999), but models based on radar reflectivity measurements of bird density suggest that call counts vary extensively from hour-to-hour and night-to-night (Larkin et al. 2002, Farnsworth et al. 2004). Additional variables might increase the explanatory power of such models and provide clues for understanding flight-calling behavior.

Atmospheric conditions that promote or inhibit bird migration are well known, and similar conditions generally correspond to similar migratory behaviors across a broad geographic range (for examples, see Lack 1960, Nisbet and Drury 1968, Able 1973, Richardson 1990, Erni et al. 2003). The relationships between weather conditions and flight-calling behavior are less clear and not sufficiently understood to be generally applicable across geographic regions. The following patterns are apparent (Farnsworth 2005): 1) call counts increase with increasing cloud cover and decreasing cloud ceiling, especially in the presence of artificial lighting (Cochran and Graber 1958, Graber and Cochran 1960, Ogden 1960, Graber 1968, Clemens 1978, Dorka 1966, Thake 1983, Evans and Mellinger 1999) and as birds approach frontal boundaries (Graber and Cochran 1960); 2) call counts of *Turdus* thrushes in Holland during autumn increased with the passage of cold fronts and decreasing temperature (Vleugel 1960); and 3) call counts correlated positively with 24-hour trends of falling temperatures in autumn and rising temperatures in the spring in Illinois (Graber and Cochran 1960). These studies suggest that increasing call counts associate with poor flying conditions and, perhaps more generally, with conditions associated with movements of areas of low air pressure (hereafter, frontal passages or boundaries).

Additionally, calling is density-dependent. Therefore, higher call counts may be associated with poor flying conditions and frontal passages or with large movements of birds, or both (Graber 1968).

Here, we test for the significance of the correlation between poor weather conditions and call counts. We examine relationships between local weather conditions and call counts of nocturnally migrating birds using a unique data set that combines local climatological data and previously published call count data and radar reflectivity measurements of bird density aloft (Farnsworth et al. 2004).

Methods

Data collection methods are described in Farnsworth et al. 2004. To summarize briefly, we sampled flight-calls of nocturnally migrating birds using a pressure zone microphone stationed on the roof of a house. We recorded the audio stream from each night to videocassettes and then digitized these data using software available on the Internet (www.oldbird.org). This software detects calls in user-defined frequency ranges based on the strength of the call signal relative to background noise levels, and time- and date-stamps the resultant .wav file. Additionally, we sampled radar reflectivity measurements of bird density from the displays of the WSR-88D radar during spring and fall 2000 in western South Carolina (Clemson and KGSP Greenville-Spartanburg) and southeastern New York (Rye and KOKX New York). We gathered base reflectivity and radial velocity data from the Clemson University Radar Ornithology Laboratory archive of WSR-88D products (Gauthreaux and Belser 1998, Gauthreaux et al. 2003). Detailed description of the screening, validation, and analysis procedures for these radar data are available in Farnsworth (2001), Gauthreaux et al. (2003), and Farnsworth et al. (2004). We sampled hourly for 556 hours during 58 nights (30 minutes after sunset to 30 minutes before sunrise). We also gathered local climatic data from weather recording stations at Greenville-Spartanburg

Airport, Greer, SC and Westchester County Airport, White Plains NY (approximately 60 km and 12 km from the audio recording locations, respectively; local climatological data are available online from National Climatic Data Center, www.ncdc.noaa.gov).

We used the following 10 weather variables in our analyses: local barometric pressure, visibility, dry bulb and wet bulb temperatures (dry bulb is air temperature typically reported by a thermometer, whereas wet bulb temperature is reported from a thermometer wrapped in a wet cloth reflecting the cooling effect of evaporating water), dew point temperature, relative humidity, meridional wind (–(wind speed) * cos (wind direction); a positive value indicates southerly winds), zonal wind (–(wind speed) * sin (wind direction); a positive value indicates westerly winds), sky cover, and cloud ceiling. Because these variables are not independent, we used the SAS version 9.1.3 PROC FACTOR statement (SAS 2000-2004) to remove the effects of dependence and reduce the number of variables in our models by extracting principal component (PC) axes. We selected PCs from this analysis for use in regression models. We chose components based on eigenvalue scores, excluding any component loading an eigenvalue less than one (these components explain less variation than any of the original variables). We used SAS version 9.1.3 PROC REG statements (SAS 2000-2004) to model relationships among call counts, bird density, and PCs extracted from the weather variables. We also used the residuals of call count-bird density models as a density control to regress call counts on the weather PCs with the effects of bird density removed. In addition, we included two other non-meteorological variables, Julian date and number of hours after sunset, in all models.

We set our initial significance level to $\alpha = 0.05$. However, we corrected for multiple comparisons by using a typical Bonferroni correction (e.g., Miller 1981), and we set our adjusted significance level to $\alpha = 0.002$ to account for 24 significance tests.

We also used a slightly less conservative sequential Bonferroni technique to generate a similar adjusted significance value (Holm's Method: see Holm 1979, Rice 1989; assessments use the statement $P_1 \leq \alpha/(1 + k - i)$ where k is the number of comparisons and i is the number of the sequential repetition from 0 to k). We use the term non-significant trend (trend) for any analyses producing significance values between P = 0.05 and P = 0.002.

We defined the following poor flying conditions (flying conditions: Lack 1960, Able 1973, Richardson 1990, Erni et al. 2003; frontal boundaries: Peterssen 1956) to assess the effects of seasonally appropriate weather on flight-call counts:

1) For spring, increasing barometric pressure, visibility, sky cover, cloud ceiling and zonal winds and decreasing dry bulb and wet bulb temperatures, dew point, relative humidity, and meridional winds. These conditions are associated with the passage of a low pressure center consistent with poor visibility, overcast conditions and easterly winds (pre-frontal) followed by cooler temperatures, lower humidity, clearing skies, and northerly winds (post-frontal).

2) For fall, decreasing barometric pressure, visibility, sky cover, cloud ceiling and zonal winds, dry bulb and wet bulb temperatures, dew point, relative humidity, and meridional winds. These conditions are associated with the approach of a low pressure center consistent with warmer temperatures, high humidity, southerly winds, and eventually poor visibility (pre-frontal) followed by westerly winds, cooler temperatures, and clearing skies (post-frontal).

We did not include precipitation in our analyses of call counts and weather conditions despite clear associations between precipitation and poor flying conditions (e.g. Erni et

al. 2003). Precipitation obscured birds on radar, making separation of birds and precipitation from radar imagery impossible in any areas where the two overlap in a radar scan. In addition, precipitation confounded audio recording because high levels of ambient noise associated with precipitation falling on the microphone made detecting relatively weak flight-call signals impossible.

Results

Principal Component Analysis

We extracted three PCs for the weather data in hourly call analyses that accounted for 97% of the variation in the 10 weather variables (Table 2.1). PC1 loaded positive correlations for barometric pressure and meridional and zonal winds and negative correlations for sky cover. PC2 loaded positive correlations of the three temperature variables. PC3 loaded positive correlations for relative humidity.

Call Count Relationships

In Clemson spring call counts exhibited significant correlations for each of the three PCs without statistical control of bird density (Table 2.2.) However, with density controls we found no significant patterns between the residuals of call counts and any PC. Fall relationships between call counts and PCs with and without density controls are similar to the patterns we found for spring analyses. The major distinction is that we found trends in count residuals with PC1 and PC3 (Table 2.2). The addition of Julian date and number of hours after sunset to each model by season did little to improve significant models (4-10% increase in variance explained, data not shown).

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Table 2.1. Results of a principal component analysis for 10 surface weather variables. Eigenvalue shows the value for each component extracted by the analysis. Proportion shows the proportion of variation explained by each component. Cumulative represents the total amount of variation in the data explained by each component. Factor Loadings are correlation coefficients for each component by weather variable. High scores indicate that variables are well-represented by a component.

	Principal Component	1	2	3
Eigenvalues	Eigenvalue	3.95	3.16	1.02
	Proportion	0.47	0.38	0.12
	Cumulative	0.47	0.85	0.97
Factor Loadings	Cloud Ceiling	0.56	-0.15	-0.22
	RelHum	0.06	0.10	0.97
	Sky Cover	-0.96	0.06	0.03
	Pressure	0.99	-0.02	0.05
	Visibility	0.04	-0.20	-0.45
	DryBulb	-0.07	1.00	-0.01
	WetBulb	-0.04	0.95	0.31
	DewPoint	-0.03	0.83	0.53
	EWWind	0.83	0.05	0.09
	NSWind	0.98	-0.01	0.05

In Rye spring call counts did not correlate significantly with any PC without controlling for bird density (Table 2.3). However, call count residuals showed a non-significant trend with each PC (Table 2.3). For fall data we found no significant relationship between call counts and any PC with and without controlling for bird density (Table 2.3). When we added Julian date and number of hours after sunset to Rye models, the percentage of variation explained improved drastically in some cases (Table 2.4). In particular, spring models with density controls for PC1 and PC3 showed greater than 4-fold improvements in variance explained when models included Julian date and number of hours after sunset. In addition to similar improvements in the fall, a non-significant relationship between calls without density controls and PC3 became significant (Table 2.4).

Table 2.2. Models of call counts with and without statistical controls for density effects for Clemson, SC. Each row represents a model from a given season of sample size N hours. Responses show call counts with and without density controls. Regressor represents the independent model terms. Correlated variables show which weather variables loaded high correlation coefficients from the PCA analysis for easing interpretation. R^2 and *P*-values come from model outputs. Sign of parameter estimate shows the model sign of the slope value for given regressors. Flying conditions and frontal location represent an analysis of seasonally appropriate weather conditions associated for the given model regressors.

N	Season	Response	Regressor	Correlated Weather Variables	R^2	P	Sign of Parameter Estimate	Flying Conditions	Frontal Location
124	Eigenvalue	Calls	Density, PC1	Barometric Pressure, Sky Cover, Meridional and Zonal Winds	0.11	0.0008	Negative	Poor	Passage
		Call Residuals	PC1		0	0.49	Negative	Poor	Passage
		Calls	Density, PC2	DryBulb, WetBulb, and DewPoint Temperatures	0.13	0.0003	Negative	Poor	Passage
		Call Residuals	PC2		0.02	0.09	Negative	Poor	Passage
		Calls	Density, PC3	Relative Humidity	0.11	0.0008	Positive	Favorable	Approach
		Call Residuals	PC3		0.01	0.23	Negative	Poor	Passage
216	Fall	Calls	Density, PC1	Barometric Pressure, Sky Cover, Meridional and Zonal Winds	0.17	< 0.0001	Negative	Favorable	Passage
		Call Residuals	PC1		0.03	0.01	Negative	Favorable	Passage
		Calls	Density, PC2	DryBulb, WetBulb, and DewPoint Temperatures	0.16	< 0.0001	Negative	Favorable	Passage
		Call Residuals	PC2		0	0.88	Positive	Poor	Approach
		Calls	Density, PC3	Relative Humidity	0.19	< 0.0001	Positive	Poor	Approach
		Call Residuals	PC3		0.04	0.02	Positive	Poor	Approach

Table 2.3. Models of call counts with and without statistical controls for density effects for Rye, NY. Each row represents a model from a given season of sample size N hours. Responses show call counts with and without density controls. Regressor represents the independent model terms. Correlated variables show which weather variables loaded high correlation coefficients from the PCA analysis for easing interpretation. R^2 and *P*-values come from model outputs. Sign of parameter estimate shows the model sign of the slope value for given regressors. Flying conditions and frontal location represent an analysis of seasonally appropriate weather conditions associated for the given model regressors.

N	Season	Response	Regressor	Correlated Weather Variables	R^2	P	Sign of Parameter Estimate	Poor Flying Conditions	Frontal Location
		Calls	Density, PC1	Barometric Pressure, Sky Cover, Meridional and Zonal Winds	0	0.94	Negative	Poor	Passage
		Call Residuals	PC1		0.08	0.01	Positive	Favorable	Approach
		Calls	Density, PC2	DryBulb, WetBulb, and DewPoint Temperatures	0	0.93	Negative	Poor	Passage
69	Eigenvalue	Call Residuals	PC2		0.17	0.003	Negative	Poor	Passage
		Calls	Density, PC3	Relative Humidity	0	0.93	Positive	Favorable	Approach
		Call Residuals	PC3		0.07	0.03	Positive	Favorable	Approach
		Calls	Density, PC1	Barometric Pressure, Sky Cover, Meridional and Zonal Winds	0.01	0.45	Negative	Poor	Approach
		Call Residuals	PC1		0.01	0.25	Positive	Favorable	Passage
		Calls	Density, PC2	DryBulb, WetBulb, and DewPoint Temperatures	0.03	0.09	Negative	Favorable	Passage
144	Fall	Call Residuals	PC2		0.01	0.15	Positive	Favorable	Passage
		Calls	Density, PC3	Relative Humidity	0.03	0.11	Negative	Favorable	Passage
		Call Residuals	PC3		0	0.8	Negative	Favorable	Passage

Table 2.4. Models of call counts with weather, Julian date, number of hours after sunset, and combined effects with and without controls for density effects for Rye, NY. Each row represents a model from a given season of sample size N hours. Responses show call counts with and without density controls. Regressor represents the independent model terms. Correlated variables show which weather variables loaded high correlation coefficients from the PCA analysis for easing interpretation. R^2 and *P*-values come from model outputs.

N	Eigenvalue	Response	Regressor	Weather		Weather+Julian		Weather+Sunset		Weather+Julian and Sunset	
				R^2	P	R^2	P	R^2	P	R^2	P
		Calls	Density, PC1	0.002	0.94	0.05	0.34	0.04	0.41	0.07	0.34
		Call Residuals	PC1	0.08	0.01	0.19	0.0009	0.18	0.002	0.33	<0.0001
69	Spring	Calls	Density, PC2	0.002	0.93	0.05	0.34	0.04	0.4	0.07	0.34
		Call Residuals	PC2	0.17	0.003	0.28	<0.0001	0.26	<0.0001	0.4	<0.0001
		Calls	Density, PC3	0.002	0.93	0.06	0.3	0.04	0.4	0.07	0.3
		Call Residuals	PC3	0.07	0.03	0.17	0.002	0.15	0.004	0.31	<0.0001
		Calls	Density, PC1	0.01	0.45	0.02	0.51	0.06	0.05	0.06	0.09
		Call Residuals	PC1	0.009	0.25	0.09	0.002	0.15	<0.0001	0.24	<0.0001
144	Fall	Calls	Density, PC2	0.03	0.09	0.03	0.19	0.06	0.03	0.06	0.06
		Call Residuals	PC2	0.01	0.15	0.08	0.004	0.19	<0.0001	0.24	<0.0001
		Calls	Density, PC3	0.03	0.11	0.03	0.18	0.12	0.0005	0.12	0.001
		Call Residuals	PC3	0.004	0.8	0.08	0.004	0.19	<0.0001	0.3	<0.0001

Poor Seasonally Appropriate Flying Conditions

Clemson

In analyses uncontrolled for bird density spring call counts showed significant negative correlations with PC1 and PC2 and a significant positive correlation with PC3 (Table 2.2). The conditions associated with these PCs are decreasing pressure, northerly and easterly winds, and increasing sky cover (negative PC1); decreasing dewpoint, dry bulb, and wet bulb temperatures (negative PC2); and increasing relative humidity (positive PC3). Weather associated with PC1 and PC2 are characteristic of poor flying conditions during spring associated with the passage of a cold front. Weather associated with PC3 is characteristic of more favorable flying conditions in advance of a frontal approach.

We found a similar pattern for fall counts uncontrolled for bird density with significant negative correlations between call count and PC1 and PC2 and a significant positive correlation between call count and PC3 (Table 2.2). These PCs correspond to increasing pressure, northerly and easterly winds, and increasing sky cover (negative PC1); decreasing dewpoint, dry bulb, and wet bulb temperatures (negative PC2); and increasing relative humidity (positive PC3). Weather associated with PC1 and PC2 are characteristic of favorable flying conditions during fall associated with the passage of a cold front. Weather associated with PC3 is characteristic of poorer flying conditions as a front approaches.

We did not find any significant correlations between call counts residuals and PCs in either season. However, there are two trends in the fall analyses. Call residuals showed non-significant trends with PC1 and PC3, corresponding to increasing pressure, northerly and easterly winds, and increasing sky cover (negative PC1) and increasing relative humidity (positive PC3).

Rye

In analyses uncontrolled for bird density we found no significant correlations between call counts and PCs in either season (Table 2.3). However, in analyses controlled for bird density spring count residuals showed significant negative correlations with PC2 ($R2 = 0.17$, $P = 0.003$). Weather conditions associated with this PC are decreasing dewpoint, dry bulb, and wet bulb temperatures (-PC2), characteristic of poor flying conditions after the passage of a cold front. We also found positive trends for count residuals and PC1 and PC3 ($P = 0.01$ and $P = 0.03$, respectively), associating increasing pressure, southerly and westerly winds, decreasing sky cover (+PC1) and increasing relative humidity (+PC3). Weather associated with PC1 is characteristic of poor flying conditions after a frontal passage, while conditions associated with PC3 are more favorable for flying. Fall analyses controlling for density effects did not show any significant relationships or trends between call counts and PCs.

Discussion

Despite positive correlations between flight-call counts and bird density, bird density alone does not always explain much of the variation in nocturnal call counts (Larkin et al. 2002; Table 2.5 displays specific results from Farnsworth 2001 and Farnsworth et al. 2004). Our results suggest that weather factors could explain some of the unexplained call count variation. For example, models from Clemson for both seasons showed improvement in R^2 values when PCs of weather variables are included (Table 2.2). Our results also suggest that higher call counts are associated with poor flying conditions and frontal passages in conjunction with large movements of birds (Tables 2.2 and 2.3). Clemson call counts without density controls correlated significantly with poor flying conditions (PC1 and PC2 in spring, PC3 in fall) or those conditions associated with the passage or approach of a frontal boundary (PC3 in spring, PC1 and PC2 in fall). However, in controlling for density effects our data showed only non-

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significant trends in associations between call count residuals and poor flying conditions or frontal passages.

The addition of Julian date and number of hours after sunset explained little additional variation in Clemson models. However, Rye models with and without density controls improved two- to four-fold in percentage of variance explained. The effect of number of hours after sunset followed a similar pattern at both site, suggesting that more calling occurs as hours after sunset increases. The effects of Julian date appear more complex: at Clemson, more calls are associated with later dates with and without density controls; at Rye, more calls are associated with earlier dates without density controls. Because Rye is a coastal location in the Northeastern US, the effects of the time of year and time of night may be more striking than at Clemson due to the composition of birds passing and the positions of origins and destinations.

Higher call counts may associate with frontal passages because large numbers of birds tend to be present under such conditions (Lack 1960, Graber 1968, Nisbet and Drury 1968, Able 1973, Richardson 1990, Larkin et al. 2002, Erni et al. 2003). Calling could hasten grouping or descent in the face of poor flying conditions, in agreement with theories describing the pattern of increased call counts as a function of descent at the end of a night of migration (Ball 1952, Lowery and Newman 1955, Newman 1956, Graber and Cochran 1960, Graber 1968). We speculate that calling facilitates communicating positional information or maintaining association during landing (or both) and may be adaptive for birds maintaining flock structure after landing (Hamilton 1962, Graber 1968, Griffin 1969, Thake 1983). This may be especially useful in the vicinity of frontal boundaries, where higher call counts could indicate that birds are attempting to stimulate conspecifics to organize or to land. As such, we would expect call counts to correlate with weather conditions regardless of

the migration density to support such a hypothesis. However, we found only non-significant trends to suggest that such a pattern might exist. Additional studies could clarify the meaning of these trends to support or to refute this hypothesis.

Table 2.5. Simple models of call counts and bird density from Farnsworth (2001) and Farnsworth et al. (2004). N is the sample size for each model representing total hour observations for each location by season.

Location	N	Season	R^2	P
New York	Eigenvalue	Spring	0.00	0.77
	144	Fall	0.01	0.21
South Carolina	124	Spring	0.11	0.0002
	216	Fall	0.16	< 0.0001

A number of drawbacks in the present study require attention in future studies. We sampled weather conditions at ground level and not at higher altitudes where birds are flying. We also sampled local climatic data and flight-calls at different locations; and although several studies suggest that generalizing local temperatures from lower resolution, regional data are still valid (i.e. downscaling; see Wilks 1989, Carbone and Bramante 1995, Brinkmann 2002, Tatli et al. 2005), the lack of geographic correspondence undoubtedly introduced error into our models. Furthermore, this study has the same potential sources of error as described by Farnsworth et al. (2004), stemming from an imperfect relationship between bird density and radar reflectivity measurements (Gauthreaux and Belser 1999). Finally, we did not control for artificial illumination, which probably contributes to changes in calling rates and flight behaviors in migrating birds (Cochran and Graber 1958, Graber 1968, Gauthreaux and Belser 2006).

More extensive studies of weather and call counts across multiple years and broader geographic range that incorporate more complete atmospheric profiles (for example, conditions aloft in the densest layers of migration) in close proximity to

recording stations could substantially improve our understanding of flight-calling behavior. However, while weather factors improve models of call count variation, much additional variation remains unexplained. We speculate that this additional variation could be the result of differences among species, including species-specific calling behaviors (such as rates and temporal pattern of calling), and species-specific migration timing. As such, future studies would also benefit from direct analysis of species-specific calling patterns and by including such variables into the models of call counts and bird density. Expanding studies in these ways could provide insight into observed patterns of flight-calling behavior as well as their functions.

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CHAPTER THREE: FLIGHT-CALLS OF WOOD-WARBLERS ARE NOT

EXCLUSIVELY ASSOCIATED WITH MIGRATORY BEHAVIORS[*]

Abstract

Wood-warblers (Parulidae), among many other species of birds, have species-specific

flight-calls given day and night in migratory periods. These vocalizations are not well

understood, although they are generally believed to maintain flocks and stimulate

migratory activity during periods of migration. However, flight-calls are not limited

to migratory periods, and they appear to have functions additional to those served

exclusively during migration.

Avian flight-calls are simple, species-specific notes that are usually less than 300 ms

in duration and generally in the 1-11 kHz range (Evans and O'Brien 2002). They are

usually single syllables and can be pure tones or modulated. These vocalizations are

narrow in bandwidth overall and high in frequency, distinctly different from broad-

bandwidth alarm calls or contact notes. Additionally, these calls are significantly

higher in frequency, narrower in bandwidth, and shorter in duration than most notes

that compose bird song (Farnsworth and Lovette 2005).

Many species of birds use flight-calls during migratory periods (Evans and

O'Brien 2002, Farnsworth 2005). However, flight-calls also occur in certain species'

repertoires outside of migration (for example, *Catharus* thrushes: Evans 1994; Evans

and O'Brien 2002). Because these vocalizations are not associated exclusively with

migratory behavior, comprehensive evaluation of the functions of flight-calls must

address their prevalence and use in both migratory and non-migratory periods. In this

paper, I present some of the first data available on seasonal patterns of flight-calling in

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23 species of wood-warblers (Parulidae, hereafter warblers) in non-migratory breeding and over-wintering periods.

Methods

Between December 2003 and January 2006, I observed 23 species of warblers during three different non-migratory periods that I define as: pre-fledging (hereafter the breeding period) from 1 June-14 July 2003, at which time no young birds were present outside the nest; post-fledging (hereafter the fledgling period) from 1 July-1 August 2004, when young had left the nest but still traveled in the company of adults; and the non-breeding over-wintering (hereafter the wintering period) from 27 December-27 February between 2003-2006, at which time birds traveled in flocks or individually or birds established territories (Tables 3.1 and 3.2). I observed individuals for randomly chosen 10-minute periods during daylight hours, noting presence and number of flight-calls. I recorded flight-calls using a Sennheiser MKH 70 microphone. I recorded analog data with a Sony TCM-5000 recorder and digital data with a Nagra Ares BB+ flash memory recorder. All flight-calls were either recorded or digitized at 16-bit, 22050 Hz sampling rates as uncompressed .wav files.

Results

I determined that flight-calls recorded during this study outside migratory periods are similar to those of known individuals recorded during migratory periods (Figure 3.1 and 3.2). Of the 16 species observed during the breeding period (140 periods of observations over 23 hours and 20 minutes total time), only Nashville Warbler ever gave flight-calls, all three of which were recorded during two periods (Table 3.2). Of the 10 species observed during fledgling periods (61 periods of observation over 10 hours and 10 minutes total time), five species gave a total of 42 flight-calls, recorded during 13 periods (Table 3.2). During the wintering period (248 periods of

observations over 41 hours and 20 minutes), 11 of 23 species (47.8%) gave a total of 127 flight-calls, recorded during 43 periods (Table 3.2). Of these 11 species, Nashville (48 of 127 calls) and Cape May (43 of 127 calls) Warblers represent 37.8 and 33.9% of the calls, respectively (Table 3.2). Standardizing call counts by observation periods, breeding period had an order of magnitude lower calls minute^{-1} than fledgling and wintering periods (Table 3.2).

Discussion

Literature on flight-calling behavior focuses predominantly on its occurrence during migratory periods, especially at night (Evans and O'Brien 2002; Farnsworth 2005). Individual warblers can produce more than 200 calls in a 10-minute period during migration (captive Tennessee Warbler, *Vermivora peregrina* in fall; Farnsworth and Lanzone, unpublished data). However, flight-calls are not restricted to these periods. While flight-calls outside of migration are less common than during migration, almost half of the total warbler species surveyed across all periods in this study gave diurnal flight-calls at some point during non-migratory periods. Nearly half of the species surveyed in winter and in post-fledging periods also gave flight-calls. Only one species, Nashville Warbler, gave flight-calls during the breeding season, and these were rare.

Clearly, non-migration related flight-calling behavior is substantially more prevalent during winter and post-fledging period (17.4% and 21.3% of time periods in each, respectively) than during the pre-hatching period of the breeding season (1.4% of time periods). This pattern is particularly striking when calls are standardized by observation time (Table 3.2). The fact that flight-calls are a regular, albeit small, part of warbler vocal repertoires during much of the year suggests a general function for these calls the transcends any specific function they have during migration.

Table 3.1. Date, location, and season of observations of flight-calling behavior for 23 species of warblers.

Year	Location	Dates	Days	Observation Periods	Species Recorded	Species giving calls	Life History
2003	Adirondacks and Finger Lakes	1 June-14 July	27	140	16	1	Breeding
2004	Adirondacks and Finger Lakes	1 July-1 August	10	61	10	5	Fledging
2004	Eastern Cuba[a]	31 January-27 February	22	189	18	9	Wintering
2003-2004	Morelos[b]	27 December-2 January	7	18	9	3	Wintering
2004-2005	Morelos[b]	27 December-3 January	8	17	6	2	Wintering
2005-2006	Morelos, Jalisco[c]	27 December-7 January	12	24	6	2	Wintering

a) Cayo Guam, Bahia de Taco, Nuevo Mundo, Barrio Nuevo, Uvero, Santiago, Gran Piedra
b) Cuernavaca
c) Cuernavaca and Careyes

Table 3.2. Seasonal prevalence of flight-calls and numbers of calls counted for 23 species of warblers. Each period represents a 10-minute observation.

Season	Breeding[a]				Fledging[b]				Winter[c,d,e,f]				All
Species	Calling Periods	Total Periods	Calls	Calls/Minute	Calling Periods	Total Periods	Calls	Calls/Minute	Calling Periods	Total Periods	Calls	Calls/Minute	Total Periods
American Redstart	0	11	0	0	3	12	12	0.1	2	14	3	0.02	37
Black-and-white Warbler[g]	0	8	0	0	0	4	0	0	4	14	6	0.04	26
Black-throated Blue Warbler	0	9	0	0	2	7	4	0.06	2	37	4	0.01	53
Black-throated Gray Warbler[h]									0	5	0	0	5
Black-throated Green Warbler[g]	0	10	0	0	2	6	12	0.2	0	9	0	0	25
Cape May Warbler									14	34	43	0.13	34
Chestnut-sided Warbler	0	5	0	0	4	8	11	0.14					13
Common Yellowthroat	0	11	0	0	0	6	0	0	2	9	4	0.04	26
Hooded Warbler	0	1	0	0	2	7	3	0.04	0	1	0	0	9
Louisiana Waterthrush	0	2	0	0	0	2	0	0	0	1	0	0	5
MacGillivray's Warbler[h]									0	5	0	0	5

a) Adirondacks and Finger Lakes 2003: 27 days, 140 observations, June 1-July 14
b) Adirondacks and Finger Lakes 2004: 10 days, 61 observations, July 1-August 1
c) Cuba 2004: 22 days, 189 observations, January 31-February 27
d) Mexico 2003-2004: 8 days, 18 observations, December 27-January 2
e) Mexico 2004-2005: 8 days, 17 observations, December 27-January 3
f) Mexico 2005-2006: 8 days, 24 observations, December 27-January 7
g) Cuba and Mexico
h) Mexico

Table 3.2 (Continued).

Season	Breeding[a]				Fledging[b]				Winter[c,d,e,f]				All
Species	Calling Periods	Total Periods	Calls	Calls/ Minute	Calling Periods	Total Periods	Calls	Calls/ Minute	Calling Periods	Total Periods	Calls	Calls/ Minute	Total Periods
Nashville Warbler[h]	2	15	3	0.02					11	21	48	0.23	36
Northern Parula	0	5	0	0					1	14	2	0.01	19
Northern Waterthrush	0	10	0	0	0	5	0	0	0	5	0	0	20
Orange-crowned Warbler[h]									4	10	15	0.15	10
Ovenbird	0	8	0	0	0	4	0	0	0	11	0	0	23
Palm Warbler	0	12	0	0					0	15	0	0	27
Prairie Warbler	0	2	0	0					1	11	1	0.01	13
Wilson's Warbler[h]									0	8	0	0	8
Worm-eating Warbler									1	5	0	0	5
Yellow Warbler	0	12	0	0					0	3	0	0	15
Yellow-rumped Warbler[g]	0	19	0	0					0	12	0	0	31
Yellow-throated Warbler									1	4	1	0.03	4
Total	2	140	3	0.002	13	61	42	0.07	43	248	127	0.05	449

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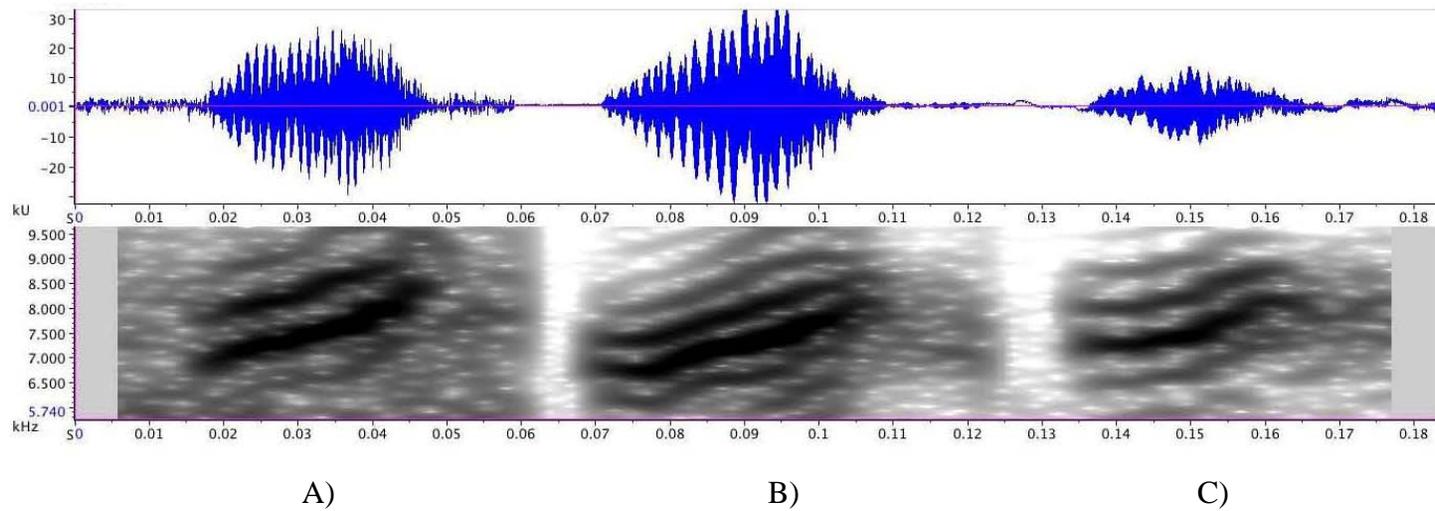
Figure 3.1. Flight-calls of Nashville Warbler (*Vermivora ruficapilla*) recorded during three different seasonal periods: A) migration (Fall 2004, Ithaca, NY), B) breeding (Summer 2003, Adirondacks SP, NY), and C) wintering (December 2004, Morelos, Mexico). The flight-calls are shown as waveform (upper ordinate axis) and spectrogram (lower ordinate axis) representations.
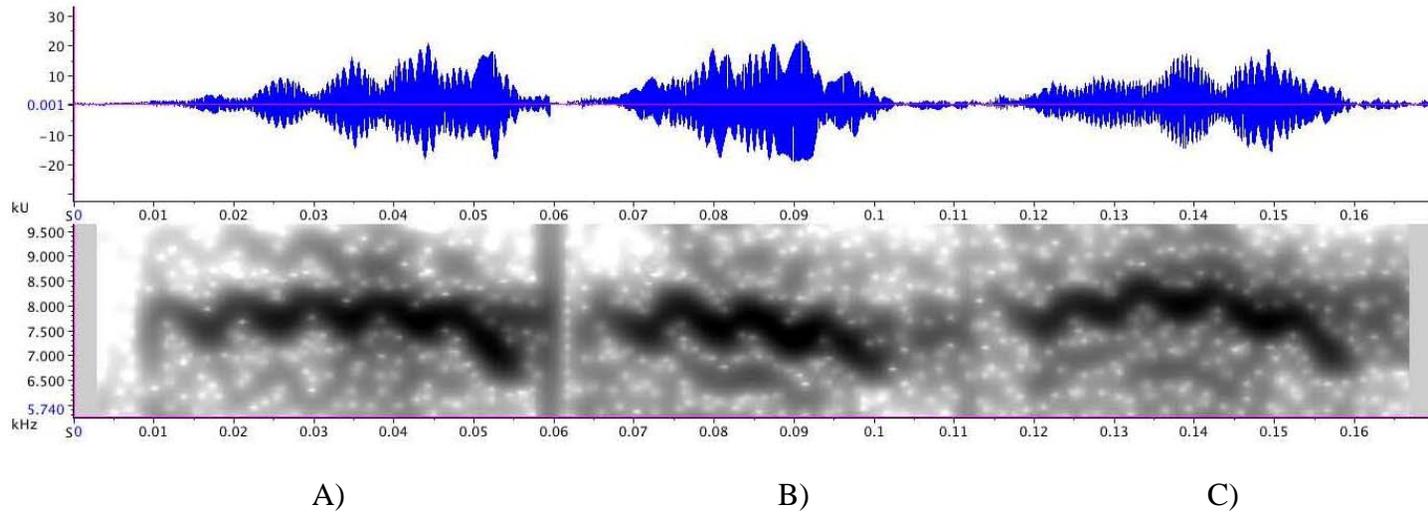
Figure 3.2. Flight-calls of Cape May Warbler (*Dendroica tigrina*) recorded during two different seasonal periods: A) migration (Spring 2005, New York, NY and B) wintering (February 2004, Humboldt NP, Cuba). The flight-calls are shown as waveform (upper ordinate axis) and spectrogram (lower ordinate axis) representations.

Flight-calls are short, high frequency, narrow bandwidth vocalizations, perfect for short-distance communication outside the range of many predators' hearing (Dooling 1982, Okanoya and Dooling 1987, Langemann et al. 1998, Gill and Sealy 2003, Farnsworth and Lovette 2005). Possibly, flight-calls serve a grouping role among recently fledged birds foraging with adults in family groups. Additionally, warblers that give flight-calls in winter may use flight-calls in much the same way as they are used for recently fledged young birds traveling with adults. For example, Nashville Warblers forage in inter- and conspecific flocks in winter in western Mexico (Howell and Webb 1995; Hutto 1980, 1994; Williams 1996), and this species gives flight-calls with some regularity (Table 3.2). Similarly, Cape May Warblers in Cuba gave flight-calls more than any other local species observed, and nearly as often as Nashville Warbler (Table 3.2). Both Nashville and Cape May Warbler also engage in local facultative movements often involving groups (Baltz and Latta 1998).

Not all species that form or join flocks in winter give flight-calls, and the reasons behind such variation are not yet understood. For example, Palm Warbler winters in large numbers in Cuba (Wilson 1996) and occasionally forms large flocks in which birds do not use flight-calls but instead produce another call type ("chip" notes; Farnsworth personal observations). Similarly, Yellow-rumped Warblers, which flock extensively on wintering grounds, rarely use their flight-call diurnally in place of the ubiquitous chip note. Interestingly, this species engages in facultative nocturnal migration after typical migration seasons end (Terrill and Ohmart 1984, Terrill and Crawford 1988), though it is unknown whether birds use flight-calls during these movements. Examining these facultative nocturnal movements could provide additional insights into the functions of flight-calls both during migration and beyond.

Non-migratory flight-calling could be an important behavioral clue for understanding both the evolution and the ontogeny of these calls. Research on

specific behavioral contexts associated with flight-calls is needed. Additional

sampling of the annual cycle is also crucial. Such research is especially important for

determining the prevalence of flight-calls during periods such as hatching for which

information is still scant.

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CHAPTER FOUR: INTER- AND INTRASPECIFIC VARIATION IN FLIGHT-CALLS AMONG WOOD-WARBLERS[*]

Abstract

Flight-calls of wood-warblers differ in duration and frequency, both within and among species. To evaluate these differences, we recorded 3,405 flight-calls from 171 captive individuals of known identity, age, and sex representing 14 warbler species. We measured spectral and temporal energy distributions from spectrograms of these calls, using mixed models to quantify variance in flight-call characteristics among species and individuals as well as between ages and sexes. Among-species and among-individual variances were significantly greater than random among-call variance for 10 spectral and temporal measurements of flight-call spectrograms, while age- and gender-related variance were not significantly greater for any measurements. Median frequency and median frequency contour exhibited substantial variation among individuals, but both were even more variable among species. These findings, the first such assessment for any avian flight-calls, support the hypotheses that flight-calls are species-specific and more functional as species identifiers rather than as a method of individual recognition. We suggest that incorporating the information available in individually identifiable flight-call measurements into current methods for monitoring flight-calls of nocturnal migrants could increase the power of these methods for counting vocal nocturnal migrants. It remains unknown if variation among individuals within species is recognizable and biologically relevant to warblers.

[*] Andrew Farnsworth, Department of Ecology and Evolutionary Biology, Cornell Laboratory of Ornithology, Cornell University, Ithaca NY 14850; Michael Lanzone, Carnegie Museum of Natural History, Powdermill Avian Research Center, 1847 Route 381, Rector, PA 15677.

Introduction

Variation in bird vocalizations reflects adaptation for signal transmission in local habitats, provides a basis for individual recognition, and encodes information about the individual sender (Martens and Marler 1977, Morton 1975, Morton 1977, Richards and Wiley 1982, Wiley 1991, Naguib et al. 2001, Slabbekoorn and Smith 2002). While birds' songs are the primary source for this information, the diverse vocal repertoires of many birds include numerous types of calls that also exhibit variation. While singing is mostly associated with breeding behaviors, calling behavior is far more opportunistic and erratic.

Avian calls are primarily transient signals with highly variable patterns in the timing and context of calls, and such diversity may increase their potential to communicate an array of messages dependent on their contextual associations (for example, birds often use different calls for alarm, group cohesion, and aggressive interactions). In contrast, a song likely contains an important but highly specific type of information (such as displaying male quality or defining territorial boundaries). Although calls are structurally simple, and usually monosyllabic, variation in calls may play an important role in communication in some species of birds. Yet bird calls are generally neglected in the study of bird communication (Baptista and Gaunt 1994, Marler 2004).

In this paper, we describe inter- and intra-specific variation in flight-call characteristics of 14 species of North American wood-warblers. Warbler flight-calls are species-specific vocalizations usually given as single notes. They are often amplitude- and frequency-modulated (sometimes rapidly), usually less than a second in duration, and between 3-11 kHz in frequency (Evans and O'Brien 2002, Farnsworth 2005).

Recent studies have provided insights into the temporal and seasonal patterns of flight-calling behavior (Evans 1994, Evans and O'Brien 2002, Larkin et al. 2002, Farnsworth et al. 2004, Farnsworth and Lovette 2005), and interest in flight-calls as a method for monitoring bird migration is increasing (Evans and Mellinger 1999, Evans and Rosenberg 2000, Mills 2000, Hedges 2001). However, information on intraspecific variation is generally lacking (also for interspecific variation, but see Evans and O'Brien 2002). Moreover, there is no information available about sex- and age-related variation in flight-calls.

Methods

Recordings of warbler flight-calls from migrant North American species occurring east of the Rocky Mountains are available as part of a published compilation (Evans and O'Brien 2002). Although this compilation provides some information on intraspecific variation in some species, its primary focus is differences among species. We recorded 3,405 flight-calls of 171 captively held warblers of 14 species at two different locations: Powdermill Avian Research Center near Pittsburgh, PA and Mormon Lake near Phoenix, AZ (Table 4.1). By recording flight-calls from captive warblers, we could gather calls from known individuals to examine intraspecific individual variation. We captured birds using mist nets, banded each individual with a USFWS band, and recorded its age (HY, hatching-year including second year birds; AHY, after-hatching-year including after second year birds, unknown) and sex (male, female, unknown). We placed birds for 10 minutes in an apparatus equipped with a microphone, designed to hold birds and to record any vocalizations they produced (Lanzone and Farnsworth in preparation). If a bird did not call during this 10-minute period, we released it. Upon release, when possible, we followed birds with a shotgun microphone (Sennheiser MKH70, www.sennhesier.com for specifications) to record any flight-calls given during free-flight.

Table 4.1. Total number of flight-calls and individuals for 14 species of warblers and total number of flight-calls and individuals from age-sex sub-sample for six species of warblers.

Species	Calls	Individuals
American Redstart *Setophaga ruticilla**	283	10
Black-throated Blue Warbler *Dendroica caerulescens*	159	8
Black-throated Green Warbler *Dendroica virens**	318	13
Common Yellowthroat *Geothlypis trichas*	23	3
Chestnut-sided Warbler *Dendroica pennsylvanica**	162	9
Grace's Warbler *Dendroica graciae*	154	14
Hooded Warbler *Wilsonia citrina*	164	12
Magnolia Warbler *Dendroica magnolia**	1147	51
Nashville Warbler *Vermivora ruficapilla**	273	16
Ovenbird *Seiurus auricapillus*	257	10
Palm Warbler *Dendroica palmarum*	131	6
Tennessee Warbler *Vermivora peregrina*	213	10
Virginia's Warbler *Vermivora virginiae*	34	3
Yellow-rumped Warbler *Dendroica coronata**	87	6
Total Sample	3405	171
Age-Sex Sample*	2270	105

*Species used in age-sex sampling

The acoustic cone contained a pressure zone microphone with a Knowles EK3132 microphone element (see applications by Evans and Mellinger 1999, Evans and Rosenberg 2000, Farnsworth et al. 2004) with a flat ($\pm$ 1 dB) frequency response in the 2000 - 10000 Hz range, connected to a digital recording device (Terapin Mine, www.terapintech.com) that recorded 22,050 kHz, 16-bit WAV files. Before analysis, all digital files were filter-decimated to a 22,050 Hz sampling rate. We used Raven 1.2.1 (Charif et al. 2004) to edit flight-call spectrograms, and after editing flight-call samples contained approximately 20-40 ms initial and terminal portions of ambient noise that were not part of the call. We excluded any flight-calls if spectrograms contained noise that interfered with the call signal, and all calls from birds of unknown age or sex.

We used XBAT 0.6.3 (www.xbat.org; Figueroa 2002) to compute spectrograms representing the time-varying distribution of sound intensity level in a call. All spectrograms were computed with identical parameters (Hamming window, 87.5% overlap, 256-point FFT, 256-point frame length) resulting in temporal and frequency resolutions of 11.6 ms and 112 Hz. We implemented a feature extraction process to measure automatically acoustic characteristics of flight-calls. This set of features was a subset of those based on ACUSTAT (Fristrup and Watkins 1992, 1993), and XBAT 0.6.3 provided the analytical environment to implement a customized auto-feature-measurement routine. Measuring acoustic properties involved selecting a signal of interest (in this case, a flight-call) by drawing a box around a flight-call onscreen using the cursor. This box represents the bounds within which the feature extraction process occurred, extracting measurements automatically and logging these in a data file. For these analyses, each spectrogram's amplitude-time envelope (aggregate power as a function of time) and power spectrum envelope (power as a function of frequency) were treated conceptually as probability density functions in the time and frequency dimensions, respectively. More details of this procedure are available in Chapter 5 and from the Cornell Laboratory of Ornithology Bioacoustic Research Program (Cortopassi, www.birds.cornell.edu/brp/research/algorithms/RSM.html.)

XBAT records 120 measures from the aggregate distributions and contour extractions of each signal analyzed. However, many of these measurements are redundant and highly correlated with one another. We produced a correlation matrix among all characters and removed variables in the matrix with correlation coefficients greater than r=0.71 (> 50% of the variation of original variables, based on R^2 values), keeping only the variables to which these eliminated variables correlated. (We chose not to perform principal component analysis because of the difficulties involved in

accounting for non-independent, nested levels within our data and in interpreting any resultant component axes, such as flight-calls of individuals of species; for additional information on this issue, see Longford and Muthen 1992; K. Grace-Martin personal communication.) We reduced our total number of uniquely descriptive measurements of each flight-call from 120 to 28: 16 from the amplitude-time and power spectrum envelopes and 12 concentration measures derived from sorted probability density functions of the time-varying features in the spectral frames, 9 from the amplitude-time envelope and 3 from the power spectrum envelope. The following are brief descriptions for each of these 28 ACUSTAT measurements. Table 4.2 is a look-up table to match the terms given here with those in ACUSTAT as implemented in XBAT.

1) Median, equivalent-duration and skewness of the amplitude-time envelope (MeENV, EqENV, and SkENV, in seconds);

2) Median, equivalent-bandwidth and skewness of the power spectrum envelope (MePS, EqPS, and SkPS, in Hz);

3) Median, equivalent-width and skewness of the discrete Fourier transform of the amplitude-time envelope, computing the frequency spectrum of the amplitude-time envelope and measuring from that (MeENVM, EqENVM, and SkENVM, in Hz);

4) Median, equivalent-width and skewness of the discrete Fourier transform of the median frequency contour from the amplitude-time envelope weighted by ¼ power of the amplitude-time envelope (MeAFM, EqAFM, and SkAFM in Hz);

5) Attack fraction (ATTACKFR, unitless), fraction of data blocks that have higher energy than the previous block, similar to the musical definition of a crescendo;

6) Up-sweep fraction (UPSWFR, unitless), fraction of data blocks that have higher frequency (based on the peak frequency contour) that the previous block;

7) Up-sweep mean (UPSWM, in Hz), average slope of the peak frequency contour;

8) Sweep magnitude (SWMAG, in Hz), sum of the absolute value of the derivative of the peak frequency contour;

9) Median, spread and skewness of the median-frequency contour (MeFMED, EqFMED, and SkFMED, in Hz), where FMED is the vector of the median-frequency values in each spectral frame of the power spectrum (Figure 4.1);

10) Median, spread and skewness of the frequency-concentration contour (MeFCC, EqFCC, and SkFCC, in Hz), where FCC is the vector of the number of bins needed to accumulate 50% of the total energy in the sorted energy distribution for each spectral frame;

11) Median, spread and skewness of the equivalent-bandwidth contour (MeEBC, EqEBC, and SkEBC, in Hz), where EBC is the vector of equivalent-bandwidth values for each spectral frame;

12) Median, spread and skewness of the frequency-skewness contour (MeFSKEW, EqFSKEW, and SkFSKEW in Hz), where FSKEW is the vector of skewness values for each spectral frame;

Species in our dataset did not have equal numbers of flight-calls when parsed by individual or by species, so, for all our analyses, we used mixed-model approaches that account for unbalanced experimental design (Herr 1986, Shaw and Mitchell-Olds 1993, Littell et al. 1996, Langsrud 2003). Analysis of our data using a stratified random sample of flight-calls to create a balanced design experiment revealed only slight differences from the patterns observed in the complete, unbalanced dataset. We used two different mixed models to analyze our data, one to examine variance components and another to model fixed and random effects. We corrected for multiple comparisons by using Tukey-Kramer multiple comparison adjustments (PROC MIXED, option LSMEANS; SAS Institute 1999) to adjust all p-values and confidence limits for the differences among least-squares means (Kramer 1956); all significant p-values we report presented adjusted values.

We assessed the variance components for the different sound measures in our sample by modeling them against the following effects as random effects: species, individuals, age, and gender (Littell et al. 1996). The SAS output for such an analysis includes a ratio of variance (PROC MIXED, RATIO option, SAS Institute 1999) attributable to the random effects relative to residual variation attributable to a model without any effects. The value of this ratio describes variance in sound measures resulting from random effects relative to the variance in sound measures of a model with no effects. In this case, a model with no effects represents variance in sound measures among calls irrespective of any additional effects of species, individuals, ages, or sexes (PROC MIXED, SAS Institute 1999). In SAS output, residual variance is always equal to 1, so all variance components are scaled to this value.

Table 4.2. XBAT energy-distribution measurements recorded from each flight call spectrogram.

Measurement	Analogous ACUSTAT Measurement	Description	Estimates
1) Amplitude Time Envelope (ENV, in sec)	Energy Envelope (ENV)	Amplitude time envelope from the aggregate energy envelope	Median (Me), Equivalent Duration (EQD), Skewness (Sk)
2) Power Spectrum Envelope (PS, in Hz)	Frequency Bandwidth (TS)	Power spectrum envelope from the aggregate power spectrum	Median (Me), Equivalent Bandwidth (EQB), Skewness (Sk)
3) Frequency Spectrum of Amplitude Time Envelope (ENVM, in Hz)	Amplitude Modulation (AM)	Discrete Fourier transform of the amplitude-time envelope, computing the frequency spectrum of the amplitude-time envelope and measuring from that	Median (Me), Equivalent Bandwidth (EQB), Skewness (Sk)
4) Median Frequency Contour Spectrum of Amplitude Time Envelope (AFM, in Hz)	Amplitude-Frequency Modulation (AFM)	Discrete Fourier transform of the median frequency contour from the amplitude-time envelope weighted by ¼ power of the amplitude-time envelope	Median (Me), Equivalent Bandwidth (EQB), Skewness (Sk)
5) Attack Fraction (ATTACKFR, unitless)	Attack Fraction (ATTACKFR)	Fraction of data blocks that have higher energy than the previous block	
6) Up-sweep Fraction (UPSWP, unitless)	Up-sweep Fraction (UPSWFR)	Fraction of data blocks that have higher frequency (peak frequency contour) that the previous block	
7) Up-sweep Mean (UPSWM, in Hz)	Up-sweep Mean (UPSWM)	Average slope of the peak frequency contour	
8) Sweep Magnitude (SWMAG, in Hz)	Sweep Magnitude (SWMAG)	Sum of the absolute value of the derivative of the peak frequency contour	
9) Median Frequency Contour (FMED, in Hz)	Median Frequency Contour (FMED)	The vector of the median-frequency values in each spectral frame of the power spectrum	Median (Me), Spread (Sp), Skewness (Sk)
10) Frequency Concentration Contour (FCC, in Hz)	Frequency Concentration Contour (CONC)	The vector of the number of bins needed to accumulate 50% of the total energy in the sorted energy distribution for each spectral frame	Median (Me), Spread (Sp), Skewness (Sk)
11) Equivalent Bandwidth Contour (EBC, in Hz)	Equivalent Bandwidth Contour (MODW)	The vector of equivalent-bandwidth values for each spectral frame	Median (Me), Spread (Sp), Skewness (Sk)
12) Frequency Skewness Contour (FSKEW, in Hz)	Frequency Asymmetry Contour (FASYM)	The vector of skewness values for each spectral frame	Median (Me), Spread (Sp), Skewness (Sk)

Parenthetical notation represents the abbreviations used in XBAT. Estimates refer to order statistics used to describe measurements. Measures and estimates (for example FMED and ME = FMEDME) describe the acoustic characteristics of flight-calls measured.

We also used a more traditional approach to produce least squares means from a mixed model of fixed and random effects (Little et al. 1996). We modeled fixed and random effects, choosing species, age, sex, and age*sex interactions (hatching-year male or female, after-hatching-year male or female) as fixed effects and individuals as random effects. By using a restricted maximum likelihood method (REML), PROC MIXED generates parameter estimates that are best linear unbiased predictors (BLUPS, Littel et al. 1996) for intercepts (model without fixed effects) and fixed effects. Plots of these estimates display the deviation of a model with effects from a model without effects, with the intercept representing a null hypothesis to test for differences in the sound measure response variable. We produced BLUPS for fixed effects of age, sex, and age*sex interactions for each sound measurement, and we plotted these against the intercept value to depict differences among effects for each sound measurement.

Results

Warbler flight-calls exhibited variation in acoustic characteristics within species (Table 4.3) and among species (Table 4.4). As such, flight-call characteristics were not necessarily distinctly different for each species, nor were flight-calls uniformly variable among all species. Flight-calls of Virginia's warbler (*Vermivora virginiae*) and Black-throated Blue warbler (*Dendroica caerulescens*) had significantly wider frequency concentration contour (MeFCC) than the remaining 12 species and differed significantly from each other (Figure 4.1). However, these same species did not differ significantly in equivalent bandwidth contour (MeEBC), despite exhibiting significantly wider values than the remaining 12 species (Figure 4.1). Additionally, flight-calls of Palm warbler (*Dendroica palmarum*), Virginia's warbler, Grace's warbler (*Dendroica graciae*), and Nashville warbler (*Vermivora ruficapilla*) are significantly lower in median frequency (MePS) than all other species, but the median

frequencies of these species' flight-calls not significantly different from each other
(Figure 4.2). Also, flight-calls of Magnolia Warbler (*Dendroica magnolia*) showed
the maximum range for eight measurements of acoustic characteristics, while flight-
calls of Common Yellowthroat (*Geothlypis trichas*) showed the minimum range for
eight measurements of acoustic characteristics (Table 4.3).
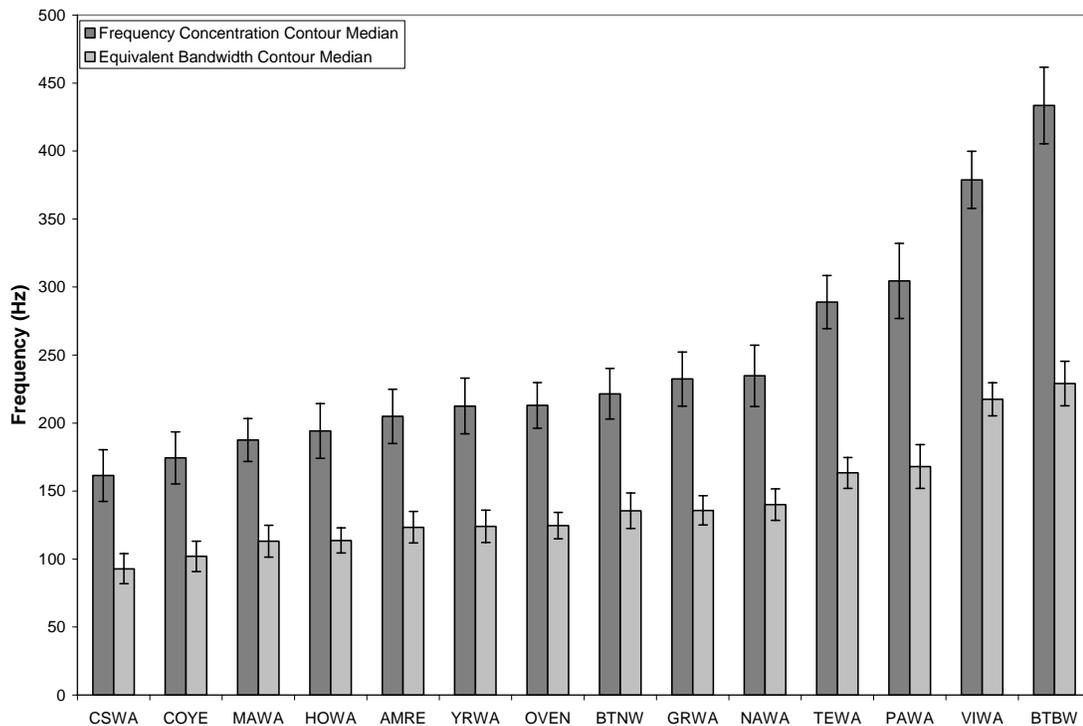
Figure 4.1. Least squares means and standard errors for frequency concentration
contour median (MeFCC) and equivalent bandwidth contour median (MeEBC)
measurements for flight-calls of 14 species of warbler.

Although all measurements of acoustic characteristics of flight-calls varied to
some extent among species and individuals and between ages and sexes, this variation
was most significant and extensive among species. Mixed model results showed that
variance among species was higher relative to random, among-call variance than
variance among individuals and between ages and sexes in 10 variables (Table 4.5).
The measurements with the highest among-species to among-call ratios were median

frequency (MePS) and median frequency contour median (MeFMED). This species-level variability is also apparent in plots of median frequency (MePS, Figure 4.3a) and median frequency contour (MeFMED, Figure 4.3b). While among-species variance was several times greater than among-individual variance for these measurements, variance among individuals in median frequency (MePS) and median frequency contour median (MeFMED) was also significantly greater than residual, random variation among calls. These were the only measurements among individuals that were significantly greater than random among-call variation.
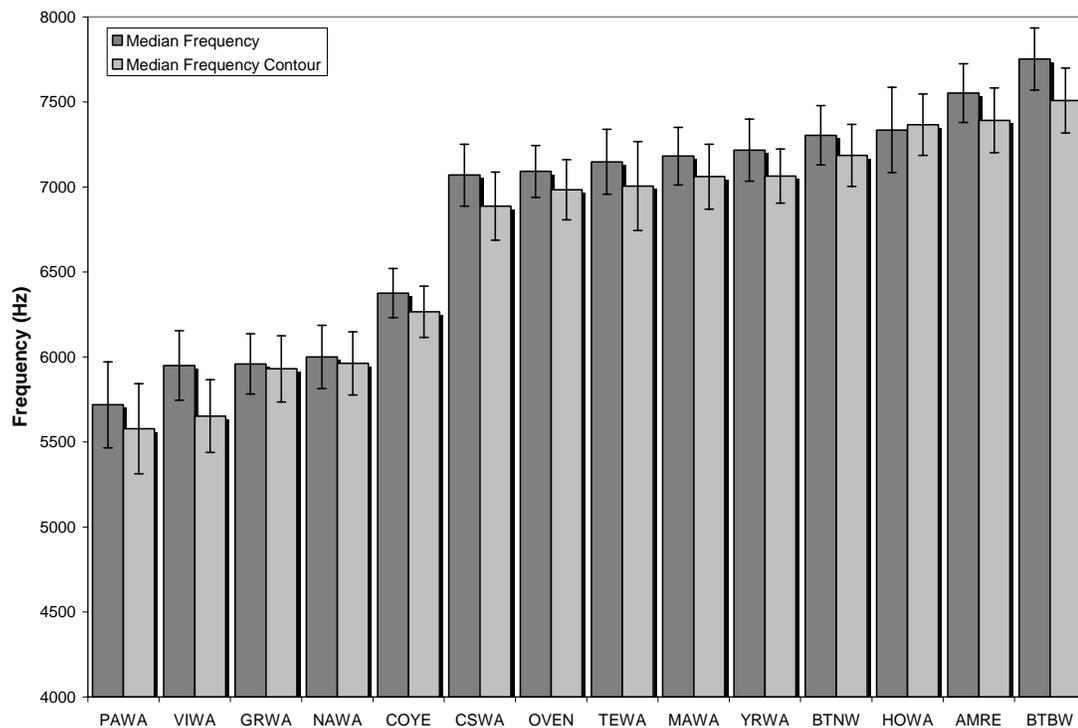
Figure 4.2. Least squares means and standard errors for median frequency (MePS) and median frequency contour median (MeFMED) measurements for flight-calls of 14 species of warbler.

Table 4.3. Pooled median, interpercentile range, and range for 28 measurements recorded from flight-calls of 14 species of warblers, with the species with minimum and maximum range for each of 28 flight-call measurements.

Measurement*	Median	Range extremes	
		Minimum	Maximum
SkAFM	0.62 ± 0.1 (0.89)	Palm Warbler	Magnolia Warbler
MeAFM	16.55 ± 5.06 (53.87)	Palm Warbler	Magnolia Warbler
EqAFM	8.63 ± 3 (21.61)	Virginia's Warbler	Magnolia Warbler
SkENVM	0.59 ± 0.08 (0.85)	Virginia's Warbler	Magnolia Warbler
MeENVM	14.81 ± 4.1 (45.32)	Common Yellowthroat	Magnolia Warbler
EqENVM	7.17 ± 2.12 (14.93)	Common Yellowthroat	American Redstart
ATTACKFR	0.55 ± 0.17 (0.76)	Common Yellowthroat	Black-throated Green Warbler
SkFCC	0.43 ± 0.27 (0.98)	Common Yellowthroat	Magnolia Warbler
MeFCC	208.35 ± 75.44 (615.89)	Yellow-rumped Warbler	Black-throated Blue Warbler
SpFCC	106.51 ± 80.08 (679.17)	Common Yellowthroat	Grace's Warbler
SkENV	0.1 ± 0.23 (0.66)	Black-throated Blue Warbler	Ovenbird
MeENV	0.05 ± 0.02 (0.08)	Virginia's Warbler	Black-throated Green Warbler
EqENV	0.02 ± 0.01 (0.03)	Black-throated Blue Warbler	Chestnut-sided Warbler
SkFSKEW	0.48 ± 0.26 (0.92)	Common Yellowthroat	Tennessee Warbler
MeFSKEW	0.3 ± 0.16 (0.68)	Common Yellowthroat	Tennessee Warbler
SpFSKEW	0.29 ± 0.15 (0.73)	Common Yellowthroat	Tennessee Warbler
SkFMED	0.64 ± 0.35 (0.98)	Palm Warbler	Grace's Warbler
MeFMED	7051.24 ± 754.46 (5258)	Virginia's Warbler	Grace's Warbler

*Based on Table 4.1

Table 4.3 (Continued).

Measurement*	Median	Range extremes	
		Minimum	Maximum
SPFMED	538.01 ± 674.88 (5199)	Hooded Warbler	Palm Warbler
SkEBC	0.42 ± 0.25 (0.94)	Chestnut-sided Warbler	Magnolia Warbler
MeEBC	122.94 ± 45.65 (391.34)	Yellow-rumped Warbler	Black-throated Blue Warbler
SPEBC	64.27 ± 49.02 (388.89)	Chestnut-sided Warbler	Palm Warbler
SWMAG	287.33 ± 205.27 (1843)	Yellow-rumped Warbler	Grace's Warbler
SkPS	0.37 ± 0.28 (0.91)	Common Yellowthroat	Grace's Warbler
MePS	7127.27 ± 748.92 (4219)	Virginia's Warbler	Black-throated Blue Warbler
EqPS	163.82 ± 92.86 (713.1)	Grace's Warbler	Black-throated Blue Warbler
UPSWFR	0.56 ± 0.27 (0.92)	Virginia's Warbler	Magnolia Warbler
UPSWM	137.35 ± 183.04 (2262)	Yellow-rumped Warbler	Palm Warbler

Table 4.4. Species-specific median, standard error, and range for 28 measurements recorded from flight-calls of 14 species of warblers.

Measurement*	American Redstart	Black-throated Blue Warbler	Black-throated Green Warbler	Chestnut-sided Warbler	Common Yellowthroat
SkAFM	0.65 ± 0 (0.38)	0.66 ± 0.01 (0.36)	0.64 ± 0 (0.36)	0.6 ± 0.01 (0.5)	0.57 ± 0.02 (0.41)
MeAFM	18.38 ± 0.25 (35.68)	24.13 ± 0.35 (21.58)	16.48 ± 0.17 (21.39)	12.5 ± 0.2 (19.9)	13.11 ± 0.79 (13.6)
EqAFM	9.26 ± 0.11 (15.8)	13.08 ± 0.25 (14.93)	8.53 ± 0.1 (12.6)	5.99 ± 0.12 (9.96)	6.01 ± 0.49 (8.73)
SkENVM	0.61 ± 0.01 (0.54)	0.65 ± 0.01 (0.31)	0.6 ± 0 (0.27)	0.55 ± 0.01 (0.34)	0.5 ± 0.01 (0.13)
MeENVM	15.56 ± 0.19 (23.83)	21.94 ± 0.2 (13.01)	15.41 ± 0.13 (18.27)	11.32 ± 0.19 (18.03)	11.67 ± 0.42 (8.41)
EqENVM	7.43 ± 0.1 (14.12)	11.35 ± 0.11 (6.72)	7.48 ± 0.07 (8.34)	5.21 ± 0.09 (6.67)	5.18 ± 0.23 (4.28)
ATTACKFR	0.53 ± 0.01 (0.62)	0.45 ± 0.01 (0.63)	0.5 ± 0.01 (0.7)	0.47 ± 0.01 (0.44)	0.53 ± 0.02 (0.3)
SkFCC	0.45 ± 0.01 (0.85)	0.52 ± 0.02 (0.89)	0.4 ± 0.01 (0.82)	0.44 ± 0.01 (0.76)	0.52 ± 0.04 (0.64)
MeFCC	231.65 ± 3.93 (356.98)	374.2 ± 9.62 (530.33)	159.86 ± 2.22 (250.86)	208.12 ± 2.5 (203.63)	429.42 ± 17.72 (359.67)
SpFCC	165.56 ± 4 (336.03)	172.5 ± 6.1 (435.51)	111.51 ± 4.21 (539.45)	79.86 ± 2.4 (184.24)	141.41 ± 10.58 (179.72)
SkENV	0.11 ± 0.01 (0.56)	0 ± 0 (0.16)	0.08 ± 0.01 (0.5)	0.31 ± 0.01 (0.6)	0.25 ± 0.03 (0.49)
MeENV	0.05 ± 0 (0.07)	0.04 ± 0 (0.06)	0.05 ± 0 (0.07)	0.06 ± 0 (0.06)	0.06 ± 0 (0.05)
EqENV	0.02 ± 0 (0.02)	0.01 ± 0 (0.01)	0.01 ± 0 (0.01)	0.02 ± 0 (0.03)	0.02 ± 0 (0.01)
SkFSKEW	0.48 ± 0.01 (0.87)	0.45 ± 0.02 (0.78)	0.44 ± 0.01 (0.92)	0.54 ± 0.01 (0.89)	0.49 ± 0.03 (0.58)
MeFSKEW	0.29 ± 0.01 (0.57)	0.39 ± 0.01 (0.47)	0.18 ± 0.01 (0.47)	0.35 ± 0.01 (0.56)	0.41 ± 0.02 (0.32)
SpFSKEW	0.34 ± 0.01 (0.54)	0.26 ± 0.01 (0.6)	0.32 ± 0.01 (0.64)	0.27 ± 0.01 (0.5)	0.21 ± 0.02 (0.3)
SkFMED	0.64 ± 0.01 (0.89)	0.63 ± 0.02 (0.94)	0.7 ± 0.01 (0.91)	0.54 ± 0.02 (0.84)	0.79 ± 0.04 (0.7)
MeFMED	7553.58 ± 28.37 (2712.75)	6450.46 ± 50.28 (3361.45)	7168.97 ± 22.97 (1656.61)	5942.69 ± 29.73 (2605.99)	5536.6 ± 90.7 (1483.28)
SPFMED	932.78 ± 22.49 (2117.7)	813.64 ± 66.11 (4515.4)	476.3 ± 26.79 (2504.29)	497.37 ± 26.9 (2028.13)	808.98 ± 161.41 (2602.01)
SkEBC	0.42 ± 0.01 (0.81)	0.41 ± 0.01 (0.83)	0.4 ± 0.01 (0.91)	0.45 ± 0.01 (0.64)	0.41 ± 0.04 (0.67)
MeEBC	133.8 ± 2.69 (245.8)	208.04 ± 5.68 (360.22)	98.13 ± 1.5 (133.36)	123.1 ± 1.58 (113.63)	231.81 ± 8.41 (165.06)
SPEBC	113.39 ± 2.83 (254.45)	108.65 ± 3.94 (279.73)	64.43 ± 2.14 (254.37)	50.37 ± 1.28 (96.59)	108.81 ± 6.53 (122.96)
SWMAG	381.89 ± 9.97 (908.42)	432.44 ± 24.05 (1688.23)	198.88 ± 5.32 (599.37)	256.09 ± 8.5 (628.02)	466.82 ± 40.4 (1001.82)
SkPS	0.41 ± 0.01 (0.85)	0.48 ± 0.01 (0.7)	0.21 ± 0.01 (0.75)	0.39 ± 0.01 (0.71)	0.46 ± 0.03 (0.54)
MePS	7368.35 ± 33.48 (2970.81)	6635.78 ± 47.77 (3315.34)	7303.94 ± 21.61 (1545.05)	6038.61 ± 29.03 (2342.52)	5701.38 ± 94.02 (1641.92)
EqPS	168.97 ± 4.39 (343.25)	310.91 ± 10.08 (634.57)	111.54 ± 3.13 (266.61)	182.73 ± 4.12 (278.24)	388.77 ± 20.18 (423.27)
UPSWFR	0.45 ± 0.01 (0.78)	0.6 ± 0.01 (0.69)	0.72 ± 0.01 (0.58)	0.36 ± 0.01 (0.62)	0.54 ± 0.02 (0.42)
UPSWM	35.54 ± 8.12 (740.08)	198.22 ± 16.47 (1329.19)	127.71 ± 4.38 (543.95)	59.61 ± 7.27 (446.66)	163.93 ± 18.7 (342.23)

*Abbreviation from Table 4.1
Values are median ± standard error (range)

Table 4.4 (Continued).

Measurement*	Grace's Warbler	Hooded Warbler	Magnolia Warbler	Nashville Warbler	Ovenbird
SkAFM	0.58 ± 0.01 (0.28)	0.64 ± 0.01 (0.62)	0.64 ± 0 (0.89)	0.61 ± 0 (0.52)	0.61 ± 0 (0.36)
MeAFM	15.89 ± 0.29 (23.37)	18.44 ± 0.38 (28.91)	14.82 ± 0.3 (53.69)	16.62 ± 0.2 (35.88)	16.16 ± 0.12 (13.51)
EqAFM	7.42 ± 0.17 (13.68)	9.47 ± 0.22 (16.21)	7.76 ± 0.11 (20.29)	8.82 ± 0.1 (14.63)	8.42 ± 0.08 (8.24)
SkENVM	0.57 ± 0 (0.25)	0.56 ± 0 (0.26)	0.59 ± 0 (0.85)	0.59 ± 0 (0.32)	0.59 ± 0.01 (0.44)
MeENVM	15.47 ± 0.21 (14.97)	15.16 ± 0.2 (15.13)	12.99 ± 0.09 (44.45)	16.53 ± 0.13 (16.68)	15.46 ± 0.18 (24.08)
EqENVM	7.19 ± 0.12 (7.19)	6.59 ± 0.1 (7.22)	6.41 ± 0.04 (13.11)	8.02 ± 0.07 (8.93)	7.23 ± 0.09 (8.27)
ATTACKFR	0.53 ± 0.01 (0.54)	0.4 ± 0.01 (0.66)	0.57 ± 0 (0.64)	0.58 ± 0.01 (0.55)	0.5 ± 0.01 (0.59)
SkFCC	0.29 ± 0.02 (0.89)	0.47 ± 0.02 (0.87)	0.45 ± 0.01 (0.96)	0.43 ± 0.01 (0.85)	0.43 ± 0.01 (0.84)
MeFCC	151.75 ± 3.95 (299.53)	272.93 ± 4.01 (266.42)	217.02 ± 1.25 (259.71)	210.53 ± 2.96 (479.67)	191.17 ± 2.07 (183.12)
SpFCC	154.4 ± 10.73 (675.35)	95.41 ± 3.27 (285.96)	88.88 ± 1.32 (437.25)	115.2 ± 4.4 (578.98)	98.21 ± 2.59 (235.27)
SkENV	0.07 ± 0.01 (0.43)	0.26 ± 0.01 (0.55)	0.13 ± 0 (0.54)	0 ± 0.01 (0.38)	0.17 ± 0.01 (0.66)
MeENV	0.05 ± 0 (0.06)	0.04 ± 0 (0.07)	0.06 ± 0 (0.06)	0.05 ± 0 (0.05)	0.05 ± 0 (0.05)
EqENV	0.02 ± 0 (0.01)	0.02 ± 0 (0.02)	0.02 ± 0 (0.02)	0.01 ± 0 (0.01)	0.02 ± 0 (0.02)
SkFSKEW	0.3 ± 0.02 (0.82)	0.51 ± 0.01 (0.82)	0.5 ± 0.01 (0.85)	0.49 ± 0.01 (0.9)	0.49 ± 0.01 (0.89)
MeFSKEW	0.09 ± 0.01 (0.53)	0.4 ± 0.01 (0.45)	0.32 ± 0 (0.65)	0.27 ± 0.01 (0.56)	0.28 ± 0.01 (0.55)
SpFSKEW	0.3 ± 0.02 (0.71)	0.24 ± 0.01 (0.44)	0.25 ± 0 (0.58)	0.3 ± 0.01 (0.63)	0.35 ± 0.01 (0.57)
SkFMED	0.76 ± 0.02 (0.97)	0.42 ± 0.02 (0.91)	0.64 ± 0.01 (0.9)	0.62 ± 0.01 (0.92)	0.69 ± 0.02 (0.91)
MeFMED	7394.29 ± 65.32 (3772)	5887.29 ± 24.14 (1644.98)	7093.78 ± 10.08 (2333.04)	7196.97 ± 23.35 (2214.21)	7384.82 ± 23.72 (2641.24)
SPFMED	742.95 ± 69.43 (3062.92)	286.82 ± 18.76 (1319.91)	310.21 ± 11.14 (2828.45)	692.12 ± 46.17 (3448.17)	1048.67 ± 21.35 (2138.19)
SkEBC	0.34 ± 0.01 (0.85)	0.43 ± 0.01 (0.79)	0.43 ± 0.01 (0.92)	0.47 ± 0.01 (0.93)	0.42 ± 0.01 (0.8)
MeEBC	90.54 ± 2.47 (170.19)	153.75 ± 2.32 (139.94)	126.14 ± 0.76 (168.25)	132.41 ± 1.78 (256.01)	108.93 ± 1.28 (122.4)
SPEBC	92.27 ± 5.32 (367.16)	61.75 ± 1.99 (128.25)	52.89 ± 0.8 (280.16)	70.6 ± 1.93 (236.7)	60.03 ± 1.46 (129.56)
SWMAG	397.59 ± 23.55 (1842.75)	304.05 ± 13.1 (955.93)	270.61 ± 3.74 (713.9)	350.19 ± 8.69 (914.7)	272.6 ± 5.34 (612.31)
SkPS	0.04 ± 0.01 (0.64)	0.46 ± 0.01 (0.72)	0.39 ± 0.01 (0.81)	0.36 ± 0.01 (0.8)	0.34 ± 0.02 (0.85)
MePS	7547.98 ± 46.91 (2425.52)	5912.5 ± 24.72 (1618.15)	7112.32 ± 10.72 (2793.39)	7367.12 ± 20.86 (1821.41)	7631.26 ± 23.49 (2373.23)
EqPS	82.92 ± 2.54 (135.63)	213.38 ± 4.79 (293.81)	163.16 ± 1.57 (356.37)	191.69 ± 4.53 (423.24)	167.86 ± 4.04 (359.15)
UPSWFR	0.38 ± 0.02 (0.75)	0.38 ± 0.01 (0.67)	0.5 ± 0.01 (0.91)	0.78 ± 0.01 (0.49)	0.67 ± 0.01 (0.61)
UPSWM	27.64 ± 13.01 (1148.45)	6.22 ± 10.37 (660.8)	122.34 ± 3.14 (825.69)	256.36 ± 7.89 (956.11)	197.48 ± 5.36 (553.52)

Table 4.4 (Continued).

Measurement*	Palm Warbler	Tennessee Warbler	Virginia's Warbler	Yellow-rumped Warbler
SkAFM	0.56 ± 0 (0.24)	0.63 ± 0.01 (0.54)	0.59 ± 0.01 (0.35)	0.63 ± 0.01 (0.29)
MeAFM	18.79 ± 0.18 (10.86)	18.08 ± 0.28 (29.17)	20.4 ± 0.55 (16.02)	16.71 ± 0.33 (15.47)
EqAFM	9.51 ± 0.11 (8.42)	9.41 ± 0.17 (19.05)	10.77 ± 0.31 (7.67)	8.69 ± 0.2 (10.21)
SkENVM	0.58 ± 0.01 (0.46)	0.6 ± 0 (0.22)	0.56 ± 0.01 (0.12)	0.61 ± 0.01 (0.24)
MeENVM	18.11 ± 0.22 (22.16)	17.39 ± 0.11 (11.01)	19.33 ± 0.47 (14.91)	14.97 ± 0.27 (12.37)
EqENVM	9.54 ± 0.1 (5.72)	8.47 ± 0.07 (6.37)	9.56 ± 0.29 (9.46)	7.13 ± 0.14 (7.31)
ATTACKFR	0.67 ± 0.01 (0.44)	0.5 ± 0.01 (0.5)	0.6 ± 0.02 (0.48)	0.5 ± 0.01 (0.45)
SkFCC	0.36 ± 0.02 (0.86)	0.35 ± 0.02 (0.9)	0.55 ± 0.04 (0.74)	0.42 ± 0.02 (0.77)
MeFCC	213.56 ± 7.59 (430.16)	194.19 ± 3.37 (224.22)	312.7 ± 13.27 (309.49)	183.06 ± 3.95 (171.37)
SpFCC	229.58 ± 10.36 (631.48)	127.52 ± 6.25 (484.41)	143.3 ± 9.96 (211.68)	90.5 ± 5.8 (238.11)
SkENV	0 ± 0.01 (0.38)	0 ± 0.01 (0.41)	0 ± 0.01 (0.33)	0.09 ± 0.01 (0.43)
MeENV	0.04 ± 0 (0.03)	0.05 ± 0 (0.05)	0.04 ± 0 (0.03)	0.05 ± 0 (0.06)
EqENV	0.02 ± 0 (0.01)	0.01 ± 0 (0.01)	0.01 ± 0 (0.01)	0.01 ± 0 (0.01)
SkFSKEW	0.36 ± 0.02 (0.87)	0.5 ± 0.02 (0.92)	0.51 ± 0.03 (0.81)	0.44 ± 0.02 (0.88)
MeFSKEW	0.14 ± 0.01 (0.48)	0.26 ± 0.01 (0.68)	0.34 ± 0.02 (0.46)	0.25 ± 0.02 (0.51)
SpFSKEW	0.28 ± 0.01 (0.66)	0.35 ± 0.01 (0.71)	0.27 ± 0.02 (0.43)	0.33 ± 0.01 (0.58)
SkFMED	0.84 ± 0.02 (0.67)	0.74 ± 0.02 (0.96)	0.54 ± 0.03 (0.9)	0.64 ± 0.02 (0.69)
MeFMED	5891.36 ± 43.59 (2774.66)	6993.02 ± 23.34 (2845.1)	6983.62 ± 43.59 (1072.97)	6251.91 ± 30.94 (1809.87)
SPFMED	1666.22 ± 129.53 (5163.41)	632.71 ± 55.47 (3253.72)	889.17 ± 66.03 (1413.79)	636.05 ± 31.04 (1420.14)
SkEBC	0.43 ± 0.02 (0.8)	0.4 ± 0.01 (0.91)	0.49 ± 0.04 (0.79)	0.41 ± 0.02 (0.72)
MeEBC	119.51 ± 4.19 (249.55)	116.66 ± 2.32 (153.72)	167.45 ± 6.17 (147.43)	110.62 ± 2.41 (111.15)
SPEBC	120.44 ± 4.93 (372.67)	76.63 ± 2.74 (214.34)	77.68 ± 5.69 (130.7)	52.02 ± 2.8 (126.04)
SWMAG	765.8 ± 35.62 (1743.68)	328.03 ± 12.46 (1000.4)	421.56 ± 32.64 (793.85)	185.69 ± 6.55 (319.98)
SkPS	0.13 ± 0.02 (0.91)	0.34 ± 0.02 (0.91)	0.5 ± 0.02 (0.63)	0.32 ± 0.02 (0.66)
MePS	6028.45 ± 18.78 (1508.7)	7103.38 ± 26.89 (2333.66)	7396.35 ± 38.51 (1153.42)	6341.43 ± 30.68 (1916.75)
EqPS	110.67 ± 4.69 (250.65)	149.28 ± 4.81 (398.81)	254.99 ± 13.71 (351.05)	147.5 ± 5.64 (242.84)
UPSWFR	0.6 ± 0.02 (0.72)	0.73 ± 0.01 (0.58)	0.69 ± 0.02 (0.39)	0.72 ± 0.01 (0.45)
UPSWM	583.72 ± 35.82 (2142.11)	218.69 ± 8.91 (866.6)	304.79 ± 24.76 (724)	97.43 ± 4.9 (240.34)

Table 4.5. Ratios significantly greater than 1 for among species and among individual variance in flight-call measurements relative to among-call (residual) variance.

Variable	Species		Individuals	
	Variance Ratio	P	Variance Ratio	P
Median Frequency (MePS)	6.7804	0.0102	1.7918	<.0001
Median Frequency Contour Median (MeFMED)	5.4274	0.0106	1.7011	<.0001
Frequency Concentration Contour Median (MeFCC)	3.4071	0.0105	*	
Energy Envelope Median (EqENV)	2.5383	0.0102	*	
Equivalent Bandwidth Contour Median (MeEBC)	2.2734	0.0111	*	
Frequency Mode Width (EqPS)	2.0226	0.0106	*	
Amplitude Modulation Mode Width (EqENVM)	1.9338	0.0099	*	
Upsweep Fraction (UPSWFR)	1.583	0.0098	*	
Amplitude Modulation Median (MeENVM)	1.2802	0.0115	*	
Sweep Magnitude (SWMAG)	1.0377	0.0133	*	

*Variance ratio < 1
+ No variance ratio for ages, sexes and age*sex classes were significantly greater than 1.
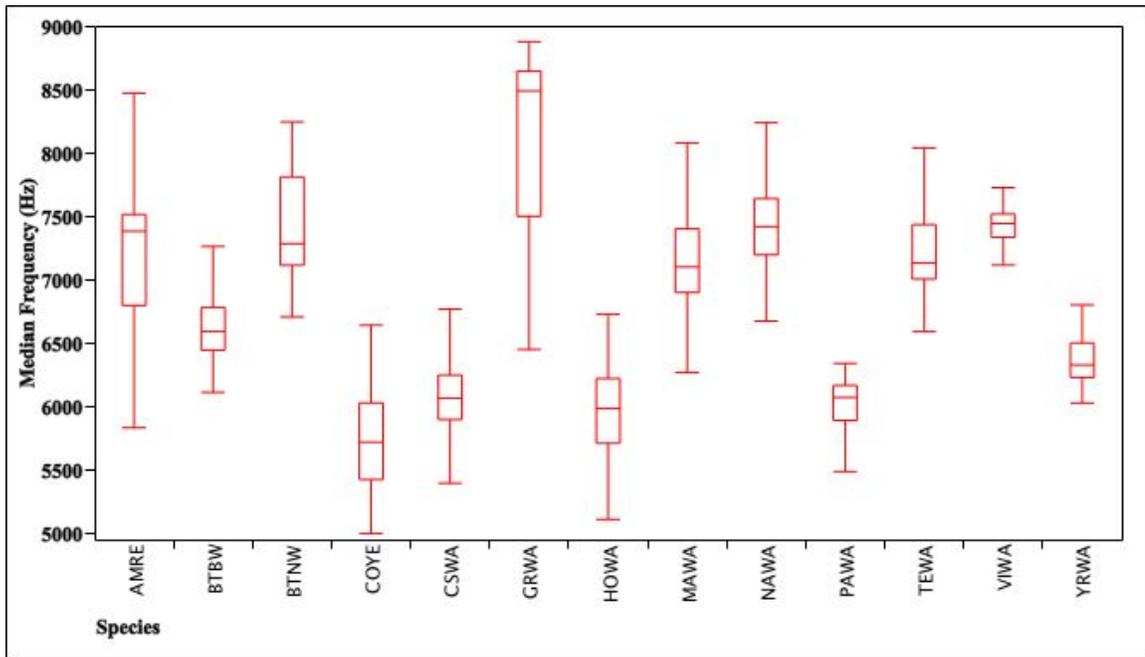
A)
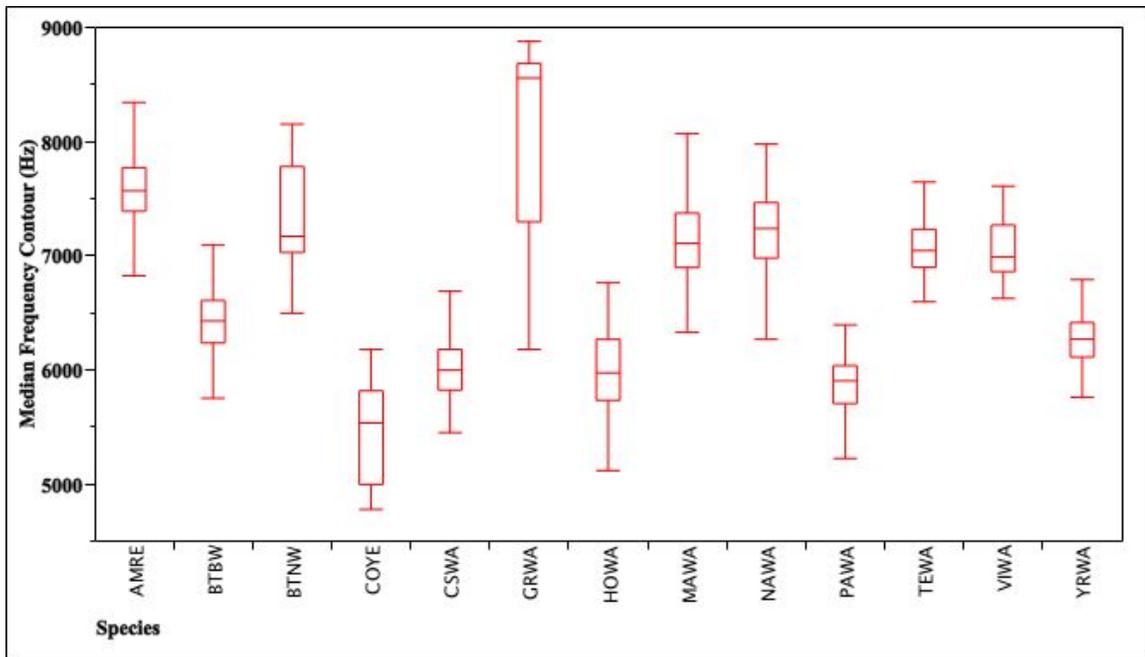
B)

Figure 4.3. Box plots of variation in flight-call frequency characteristics among warbler species. A) Median frequency (MePS). B) Median frequency contour median (MeFMED).

Age, sex, and age-sex interaction accounted for no significant, additional variance in sound measures. However, some subtle and significant differences existed in the flight-call characteristics of these classes (Table 4.6, Figure 4.4). For example, female Magnolia Warblers showed significantly lower frequencies in their flight-calls, while AHY Magnolia Warblers had significantly higher frequencies. Additionally, flight-calls of American Redstart (*Setophaga ruticilla)* and Yellow-rumped Warbler (*Dendroica coronata)* females exhibited lower values than males for all measurements that differed significantly between sexes, whereas the reverse was true for Nashville Warbler (Table 4.6). Flight-calls of Black-throated Green Warbler (*Dendroica virens)* showed higher values for two of the three measurements that differed significantly between sexes, whereas female Chestnut-sided Warblers (*Dendroica pennsylvanica)* showed higher values for one of the three measurements that differed significantly between sexes. Between ages, AHY Black-throated Green Warbler, Nashville Warbler, and Yellow-rumped Warbler flight-calls exhibited higher values than HY birds for all measurements that differed significantly between ages, whereas AHY American Redstart and Chestnut-sided Warbler flight-calls exhibited higher values than HY birds for half (for both species, respectively) of the measurements that differed significantly between ages (Table 4.6). Although means of 16 measurements differed significantly for age*sex interaction classes within species, no measurements differed significantly among values for all four age*sex interaction classes within species (Table 4.7). In summary, we found no consistent and significant differences in the four age*sex classes to describe each class uniquely.

Table 4.6. Differences between sexes and ages in least squares mean values by flight-call measurement and species.

Species	Measurement[A]	Age/Sex*	Estimate	Standard Error	Age/Sex*	Estimate	Standard Error	Difference[+]	Standard Error	P
American Redstart	EqAFM	AHY	8.99	0.24	HY	9.97	0.20	-0.98	0.31	0.00
American Redstart	SkFCC	AHY	0.40	0.02	HY	0.48	0.02	-0.07	0.03	0.01
American Redstart	SpEBC	AHY	152.53	16.70	HY	95.03	13.75	57.50	21.63	0.01
American Redstart	SpFCC	AHY	219.37	22.16	HY	139.76	18.26	79.61	28.71	0.01
American Redstart	EqENVM	Female	7.05	0.27	Male	7.92	0.25	-0.87	0.37	0.02
American Redstart	UPSWFR	Female	0.39	0.02	Male	0.48	0.02	-0.09	0.03	0.01
Black-throated Green Warbler	EqPS	AHY	183.01	21.62	HY	117.21	8.77	65.80	23.33	0.01
Black-throated Green Warbler	MeEBC	Female	115.33	6.50	Male	96.17	4.05	19.16	7.66	0.01
Black-throated Green Warbler	MeFCC	Female	193.81	9.61	Male	165.34	5.99	28.46	11.32	0.01
Black-throated Green Warbler	UPSWFR	Female	0.64	0.03	Male	0.71	0.02	-0.07	0.03	0.03
Chestnut-sided Warbler	ATTACKFR	AHY	0.53	0.02	HY	0.47	0.02	0.06	0.03	0.03
Chestnut-sided Warbler	EqAFM	AHY	6.80	0.20	HY	6.15	0.17	0.65	0.26	0.02
Chestnut-sided Warbler	EqPS	AHY	173.68	6.71	HY	195.82	5.45	-22.14	8.64	0.01
Chestnut-sided Warbler	MeAFM	AHY	13.68	0.44	HY	12.53	0.35	1.15	0.56	0.04
Chestnut-sided Warbler	MeFSKEW	AHY	0.32	0.02	HY	0.36	0.01	-0.05	0.02	0.02
Chestnut-sided Warbler	SpEBC	AHY	49.03	2.08	HY	55.96	1.69	-6.93	2.68	0.01
Chestnut-sided Warbler	SkEBC	Female	0.47	0.01	Male	0.41	0.02	0.06	0.02	0.00
Chestnut-sided Warbler	SkENVM	Female	0.55	0.01	Male	0.58	0.01	-0.03	0.01	0.02
Chestnut-sided Warbler	SpFSKEW	Female	0.25	0.01	Male	0.31	0.01	-0.06	0.01	<0.0001

All estimates significant at $P < 0.0001$
[A] Abbreviations from Table 1
* AHY, after hatching year; HY, hatching year
+ Differences are relative to Female and AHY estimates.

Table 4.6 (Continued).

Species	Measurement[A]	Age/Sex*	Estimate	Standard Error	Age/Sex*	Estimate	Standard Error	Difference[+]	Standard Error	P
Magnolia Warbler	EqAFM	AHY	8.58	0.35	HY	9.91	0.32	-1.33	0.47	0.00
Magnolia Warbler	MeENV	AHY	0.06	0.00	HY	0.06	0.00	0.00	0.00	0.01
Magnolia Warbler	MeFMED	AHY	7168.88	64.09	HY	6969.13	57.85	199.75	86.33	0.02
Magnolia Warbler	MePS	AHY	7199.32	63.38	HY	6985.92	57.21	213.40	85.38	0.01
Magnolia Warbler	MeFMED	Female	6967.96	59.21	Male	7160.45	62.62	-192.49	86.18	0.03
Magnolia Warbler	MePS	Female	6980.00	58.24	Male	7195.26	61.52	-215.26	84.71	0.01
Magnolia Warbler	SWMAG	Female	243.70	13.00	Male	283.27	13.30	-39.58	18.59	0.03
Magnolia Warbler	UPSWFR	Female	0.47	0.02	Male	0.53	0.02	-0.06	0.03	0.03
Magnolia Warbler	UPSWM	Female	90.12	10.26	Male	134.11	10.45	-43.99	14.65	0.00
Nashville Warbler	EqENVM	AHY	0.61	0.00	HY	0.60	0.00	0.01	0.01	0.04
Nashville Warbler	MeFMED	AHY	7217.86	142.67	HY	6862.30	87.56	355.56	167.39	0.03
Nashville Warbler	MePS	AHY	7413.27	131.48	HY	7069.27	80.30	344.00	154.06	0.03
Nashville Warbler	SkENVM	AHY	0.60	0.00	HY	0.58	0.00	0.02	0.01	0.00
Nashville Warbler	EqENV	Female	0.01	0.00	Male	0.01	0.00	0.00	0.00	0.01
Nashville Warbler	MeEBC	Female	150.29	7.07	Male	127.13	5.88	23.16	9.19	0.01
Nashville Warbler	MeFCC	Female	241.75	11.53	Male	208.77	9.60	32.98	15.00	0.03
Yellow-rumped Warbler	MeFMED	AHY	6402.81	65.12	HY	6185.34	54.17	217.47	84.70	0.01
Yellow-rumped Warbler	MePS	AHY	6488.44	62.18	HY	6307.34	52.65	181.10	81.48	0.03
Yellow-rumped Warbler	SpFCC	Female	84.87	11.44	Male	123.95	14.28	-39.09	18.29	0.04
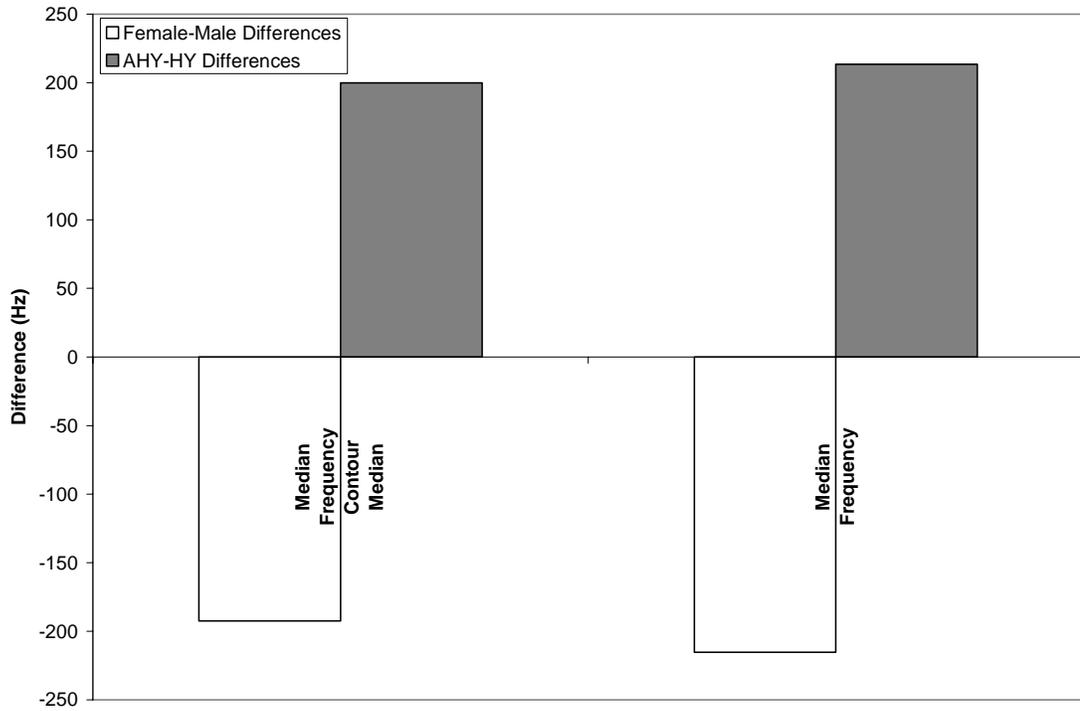
Figure 4.4. Difference in least squares mean values for median frequency (MePS) and median frequency contour median (MeFMED) between Magnolia Warbler sexes and ages.

Table 4.7. Significant differences in least squares mean values of flight-call characteristics between age-sex interaction classes.

Species	Measurement*	Age-Sex Interaction Comparison		Difference	Standard Error	P
American Redstart	SpEBC	AHY,F	HY,F	102.92	34.87	0.02
American Redstart	SpFCC	AHY,F	HY,F	144.26	43.72	0.01
American Redstart	SpFCC	AHY,M	HY,F	81.76	29.59	0.03
American Redstart	UPSWFR	AHY,M	HY,F	0.11	0.04	0.05
Black-throated Green Warbler	EqPS	AHY,F	HY,M	108.71	34.94	0.01
Black-throated Green Warbler	EqPS	AHY,F	HY,F	109.09	37.35	0.02
Black-throated Green Warbler	SpFMED	AHY,F	HY,F	1492.15	429.97	<0.0001
Black-throated Green Warbler	SpFMED	AHY,F	HY,M	1372.94	398.05	<0.0001
Black-throated Green Warbler	SpFMED	AHY,F	AHY,M	1422.25	513.29	0.03
Black-throated Green Warbler	UPSWFR	AHY,M	HY,F	0.16	0.05	0.01
Chestnut-sided Warbler	EqPS	AHY,M	HY,F	-27.53	10.38	0.04
Chestnut-sided Warbler	SpFSKEW	AHY,M	HY,F	0.06	0.02	0.01
Chestnut-sided Warbler	SpFSKEW	AHY,F	AHY,M	-0.07	0.03	0.05
Magnolia Warbler	EqAFM	AHY,M	HY,F	-1.87	0.63	0.02
Magnolia Warbler	MeENV	AHY,F	HY,F	0.01	0.00	0.03
Magnolia Warbler	MeFMED	AHY,M	HY,F	337.82	111.88	0.01
Magnolia Warbler	MePS	AHY,M	HY,F	371.26	109.34	<0.0001
Magnolia Warbler	UPSWM	AHY,M	HY,F	61.60	19.48	0.01
Nashville Warbler	EqENV	AHY,M	HY,F	0.00	0.00	0.05
Nashville Warbler	MeEBC	AHY,M	HY,F	-40.04	15.12	0.04
Nashville Warbler	SkENV	AHY,F	AHY,M	0.07	0.02	0.01
Nashville Warbler	SkENVM	AHY,M	HY,F	0.04	0.01	<0.0001
Nashville Warbler	SkENVM	AHY,M	HY,M	0.03	0.01	<0.0001
Nashville Warbler	SkENVM	AHY,F	HY,F	0.02	0.01	0.03
Yellow-rumped Warbler	EqENVM	AHY,F	AHY,M	1.58	0.48	0.01
Yellow-rumped Warbler	EqENVM	AHY,F	HY,F	1.19	0.43	0.03
Yellow-rumped Warbler	MeEBC	AHY,F	HY,F	-31.14	7.95	<0.0001
Yellow-rumped Warbler	MeFMED	AHY,F	HY,F	300.83	75.25	<0.0001
Yellow-rumped Warbler	MeFMED	AHY,F	HY,M	363.45	78.53	<0.0001
Yellow-rumped Warbler	MePS	AHY,F	HY,F	267.50	96.76	0.03
Yellow-rumped Warbler	SpFMED	AHY,F	AHY,M	-302.80	77.17	<0.0001
Yellow-rumped Warbler	SpFMED	AHY,F	HY,F	-313.01	72.03	<0.0001
Yellow-rumped Warbler	SpFMED	AHY,F	HY,M	-426.02	75.17	<0.0001
Yellow-rumped Warbler	SpFSKEW	AHY,F	HY,M	-0.13	0.03	<0.0001
Yellow-rumped Warbler	SpFSKEW	HY,F	HY,M	-0.09	0.03	0.02
Yellow-rumped Warbler	UPSWM	AHY,F	HY,M	-37.74	13.56	0.03

*Abbreviation from Table 4.1

Discussion

The most important message from our findings is that flight-calls are most variable among species, and most variation in the flight-call characteristics results from differences among species. Variation among individuals, between sexes, and between ages, though significant, is much more subtle and contributes little to the total variance of the flight-call measurements. In a broader context that includes additional call properties such as syllable structure (i.e., spectrographic shape, see Chapter 7), such results imply that flight-call species-specificity may be even more apparent. Our research provides the first quantitative assessment of the suite of flight-call spectrographic measurements that are most variable and the levels at which these measurements vary most significantly (i.e., among species rather than within individuals or between ages or sexes).

Median frequency (MePS) and median frequency contour median (MeFMED) were the most variable acoustic characteristics we measured. These measurements showed higher variances both among species and among individuals than any other measurements, with highest levels of variation at the species level rather than among individuals or between ages or sexes. Frequency of bird vocalizations generally varies as a function of vegetation structure in signals propagating through different vegetation types (Wiley 1991). This may also be true for flight-call frequency, which appears to co-vary with several different habitat characteristics (Chapter 7).

In addition to the median frequency characteristics, eight flight-call measurements also exhibited significant among-species variation. This suite of measurements may represent a group of features that could be useful for species recognition, and therefore might be useful for researchers interested in classifying warbler flight-calls by species. Furthermore, the potential utility of these measurements may apply to among-individual recognition or classification,

particularly for the two median frequency (MePS, MeFMED) measurements with significant among-individual variance.

Individual recognition based on vocal variation may be a widespread phenomenon in avian social and vocal systems (e.g., Mammen and Nowicki 1981, Beecher 1991, Robisson et al. 1993, Mathevon 1997, Lefebvre et al. 1998, Jouventin et al. 1999, Baker et al. 2000, Charrier et al. 2001, Molles and Vehrencamp 2001, Naguib et al. 2001, Wanker and Fischer 2001, Mathevon et al. 2003, Lovell and Lein 2005). However, while individual differences in call characteristics may allow a human observer to identify individuals reliably, such differences do not imply necessarily that individual recognition actually occurs among the birds themselves (after Falls 1982). Furthermore, single measurements in isolation may not suffice for representing or expressing individuality in bird vocalizations, and may not have biological relevance (Morton and Young 1986, Robisson 1992, Farquhar 1993, Otter et al. 1994, Otter 1996, Stoddard 1996). Individuality also depends on physiological capabilities to produce and to detect variation. Flight-calls are short and high in frequency relative to the limitations of hearing in birds (Dooling 1980, Dooling et al. 1987, Beecher 1988, 1989, Nelson 1989, Weary 1990, Medvin et al. 1993). Furthermore, the propagation distance of these calls as well as the information encoded in them are constrained by their short, high frequency, and narrow bandwidth features (Farnsworth and Lovette 2005; but see Aubin et al. 2004).

A trait that functions to signal individual identity should be highly variable with polymodal distributions, and should lack dependence on physical condition, change in cost for production and maintenance (i.e. traits should be cheap to produce and to maintain), or association with fitness differences (Dale et al. 2001). Flight-calls of warblers are variable among individuals, but whether these calls are independent of physical conditions and individual fitness is unknown. Additionally, warbler produce

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flight-calls in a variety of contexts, most commonly during migratory flights (Chapter 3), but the cost of producing these calls while flying or of maintaining them relative to other vocal abilities also is unknown. Therefore, we cannot currently determine whether a biological function exists for the observed variation among individuals of the same species.

Calls may also mediate social interactions not governed by song across a wide diversity of behavioral contexts (Mundinger 1970, 1975, Marler and Mundinger 1971, Dahlin et al. 2005, Sharp and Hatchwell 2006). Warblers produce flight-calls during diurnal and nocturnal migration under a variety of atmospheric conditions and across a wide range of geographic locations. Flight-calls are also staple vocalizations of many species' non-breeding repertoires, and these calls are associated with young birds traveling in family-flocks with parents and siblings (Chapter 3). Some nocturnal recordings of flight-calls also suggest the possibility that even greater variation may exist than we detected in this study. Some species may even use several types of flight-calls in different contexts (W. Evans, personal communication). Whether these vocalizations evolved for specific contexts or whether a single vocalization type is useful across multiple contexts, detailed studies of the ontogeny of flight-calls and the onset of flight-calling behavior is needed to clarify these usage patterns and to illuminate flight-call function.

Additional experimental study of the effects of age and sex variation in flight-calls is also necessary to determine whether the any of the differences we recorded have biological meaning. For example, AHY American Redstarts have less compact flight-calls in frequency and duration than HY birds, while females have more compact call durations and lower upsweep fractions than males (Table 4.6). In contrast, AHY Chestnut-sided Warblers have more compact frequency bandwidths, higher attack fractions, less symmetrically distributed frequencies, and less compact

durations than HY birds, while females have less symmetrical signal duration relative to median, less symmetrical frequency distribution, and more asymmetrical frequency concentrations than males (Table 4.6). Although such differences in flight-call measurements may be relevant for communication, connections between these differences, communication requirements, and warbler ecology are not known. Additionally, whether the features of warbler flight-calls with greater among-species variation represent important cues for species recognition is unknown.

Experiments may also clarify whether warblers elaborate the structure of their flight-calls to facilitate individual recognition. Some birds elaborate vocalizations, specifically calls, to contain more information (Medvin et al. 1993, Robisson et al. 1993, Searby et al. 2004, Searby and Jouventin 2005), an adaptation that may enhance parent-offspring recognition. If recognizing kin during post-fledging, pre-migratory period is an important part of an individual warbler's life history, elaboration may be important. A short, high-frequency call for communicating across short distances to maintain family groups may contain enough information to identify individuals, but not at the expense of disclosing the location of the group to a predator (Langemann et al. 1998, Jurisevic and Sanderson 1998, Swanson and Sanderson 1999, Farnsworth and Lovette 2005).

Our results have potentially important applications for conservation. Flight-calls are useful for monitoring passing, vocal nocturnal migrants. Ideally, counting calls would yield a count of individuals passing. However, variation in calling rates across seasons, species, and meteorological conditions confounds the ideal. By including information about individual differences among flight-call measurements in existing monitoring methods, refining estimates of passing individuals and counting individuals may be possible. Additional research focused on classifying individuals

using sound measurements is necessary, and a larger and more diverse sample of flight-calls must be tested for individuality before applying such methodology.

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CHAPTER FIVE: A COMPARISON OF SOUND ANALYSIS METHODS USING WARBLER FLIGHT-CALLS, A SIMPLE AVIAN VOCALIZATION[*]

Abstract

Recent studies using a number of different methods have demonstrated individual distinctiveness in the calls of a wide variety of birds. However, whether or not commonly used methods produce the same results qualitatively or quantitatively remains unclear. We applied three common methods to analyze a simple type of signal, flight-calls of New World warblers. We compared: 1) spectrographic cross-correlation (SPCC) matrices ordinated by principal coordinate analysis; 2) energy-distribution (ED) measurement matrices ordinated by principal coordinate analysis; and 3) classification tree analysis (CTA) of multiple ED measurements. Sufficient individuality in flight-call measurements exists to distinguish among individuals, and we compared the ability of each method to assign calls correctly to known caller for five warbler species using linear discriminant analysis. Results show that SPCC data yielded the lowest misclassification rates, suggesting that this form of data is best for representing individual differences in flight-calls. Additionally, SPCC and ED measurements did not show concordant patterns of correlations with unordinated spectral and temporal measurements of sound, indicating that these two approaches for characterizing sounds do not represent common acoustic features.

Introduction

Warbler flight-calls are single-syllable, short, high frequency, and narrow-bandwidth calls that are probably used for short distance communication. These simple calls may

[*] Andrew Farnsworth, Department of Ecology and Evolutionary Biology, Cornell Laboratory of Ornithology, Cornell University, Ithaca NY 14850; Michael Lanzone, Carnegie Museum of Natural History, Powdermill Avian Research Center, 1847 Route 381, Rector, PA 15677; Kathy Cortopassi, Bioacoustic Research Program, Cornell Laboratory of Ornithology, Cornell University, Ithaca NY 14850.

have several functions including maintaining flock structure, stimulating conspecifics, coordinating movements, or some combination of these (Marler 1955, Hamilton 1962, Griffin 1969, Evans and O'Brien 2002, Farnsworth and Lovette 2005). In addition, these calls exhibit unique acoustic properties among species and individuals as well as between ages and sexes (Chapter 4).

Numerous studies have demonstrated that individual differences exist in the calls of a wide variety of birds (e.g. Robertson 1996, Price 1999, Dahlin et al. 2005, Searby and Jouventin 2005, Sharp and Hatchwell 2006). A number of different methods have been invoked to demonstrate individual distinctiveness, including visual inspection, spectrographic cross-correlation (SPCC), and comparisons based on objective statistical analyses of acoustic measurements. Despite several efforts to compare methods (Nowicki and Nelson 1990, Baker and Logue 2003, Preatoni et al. 2005), it remains unclear whether commonly used methods will produce the same answers qualitatively or quantitatively.

Here, we take advantage of recent studies of New World warblers' (Parulidae) flight-calls (Chapter 4), using this simple type of signal to compare three popular methods of comparing sounds: a) SPCC matrices ordinated by principal coordinate analysis (e.g. Cortopassi and Bradbury 2000, 2006); b) multiple measurements on each sound reduced to similarity matrices and ordinated using principal coordinate or principal component analysis (e.g. Baker and Logue 2003) and c) classification tree analysis using multiple measurements on each sound (e.g. Van Opzeeland and Van Parijs 2004, Preatoni et al. 2005). We compare the ability of each acoustic analysis method to assign flight-calls correctly to individual caller for five warbler species. Based on these results we discuss the degree to which these methods are concordant in their rankings of different acoustic features.

Methods

The dataset consisted of 3405 warbler flight-calls from 171 individuals of 14 species previously recorded from captive birds. All data were collected in a specially designed recording device (Lanzone and Farnsworth in preparation) using a pressure zone microphone with a Knowles EK3132 microphone element (see applications by Evans and Mellinger 1999, Evans and Rosenberg 2000, Farnsworth et al. 2004) with a flat (± 1 dB) frequency response in the 2000 - 10000 Hz range. Before analysis, all digital files were filter-decimated to a 22,050 Hz sampling rate. We used Raven 1.2.1 (Charif et al. 2004) to edit flight-call spectrograms, and after editing flight-call samples contained approximately 20-40 ms initial and terminal portions of ambient noise that were not part of the call. We excluded any flight-calls if spectrograms contained noise that interfered with the call signal.

Because species and individuals did not have uniform representation in this dataset, we limited our analysis to species represented by at least four individuals: at least one male, one female, one after-hatching-year (> 1 year-old) bird, and one hatching-year (< 1 year-old) bird (Lanzone and Farnsworth in preparation). Five species (American Redstart *Setophaga ruticilla*, Chestnut-sided Warbler *Dendroica pennsylvanica*, Magnolia Warbler *Dendroica magnolia*, Nashville Warbler *Vermivora ruficapilla*, and Yellow-rumped Warbler *Dendroica coronata*) met this criterion, and we sampled randomly 10 flight-calls from each individual across these species (see Figure 5.1 for flight-call examples). If the sample set for a species had more than one individual for a given age or sex class, we sampled randomly to choose the individual. This procedure yielded a new sample of 200 flight calls from five species, each represented by four individuals with 10 flight-calls per individual.

We applied spectrogram cross-correlation and comparative analysis of call features to compare quantitatively calls within and among individuals of the same

species. For both analyses, we used XBAT 0.6.3 (www.xbat.org; Figueroa 2002) to compute spectrograms representing the time-varying distribution of sound intensity level in a call. All spectrograms were computed with identical parameters (Hamming window, 87.5% overlap, 256-point FFT, 256-point frame length) resulting in temporal and frequency resolutions of 11.6 ms and 112 Hz. Spectrogram cross-correlation was applied to comparatively measure the similarity between pairs of calls (SPCC, Clark et al. 1987, Cortopassi and Bradbury 2000). This process returns a single value between 0 and 1, where 0 represents no similarity and 1 represents identical sounds.
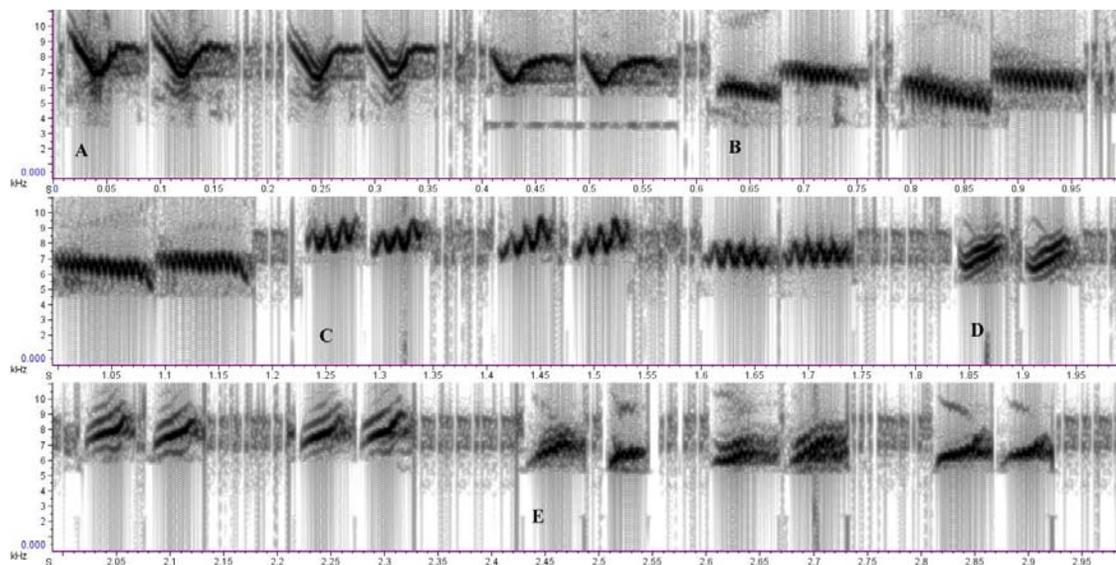
Figure 5.1. Spectrograms of the flight-calls of five warbler species, with two flight-calls from each of three individuals per species. A) American Redstart, B) Chestnut-sided Warbler, C) Magnolia Warbler, D) Nashville Warbler, and E) Yellow-rumped Warbler. Note that the general pattern of the signal is often consistent within a species, whereas flight-calls vary in frequency and time within a species.

We implemented a feature extraction process to measure automatically acoustic characteristics of flight-calls. This set of features was a subset of those based on ACUSTAT (Fristrup and Watkins 1992, 1993), and XBAT provided the analytical environment to implement a customized auto-feature-measurement routine. Measuring acoustic properties involved selecting a signal of interest (in this case, a

flight-call) by drawing a box around a flight-call onscreen using the cursor. This box represents the bounds within which the feature extraction process occurred, extracting measurements automatically and logging these in a data file. For these analyses, each spectrogram's amplitude-time envelope (aggregate power as a function of time) and power spectrum envelope (power as a function of frequency) were treated conceptually as probability density functions in the time and frequency dimensions, respectively (Figure 5.2).
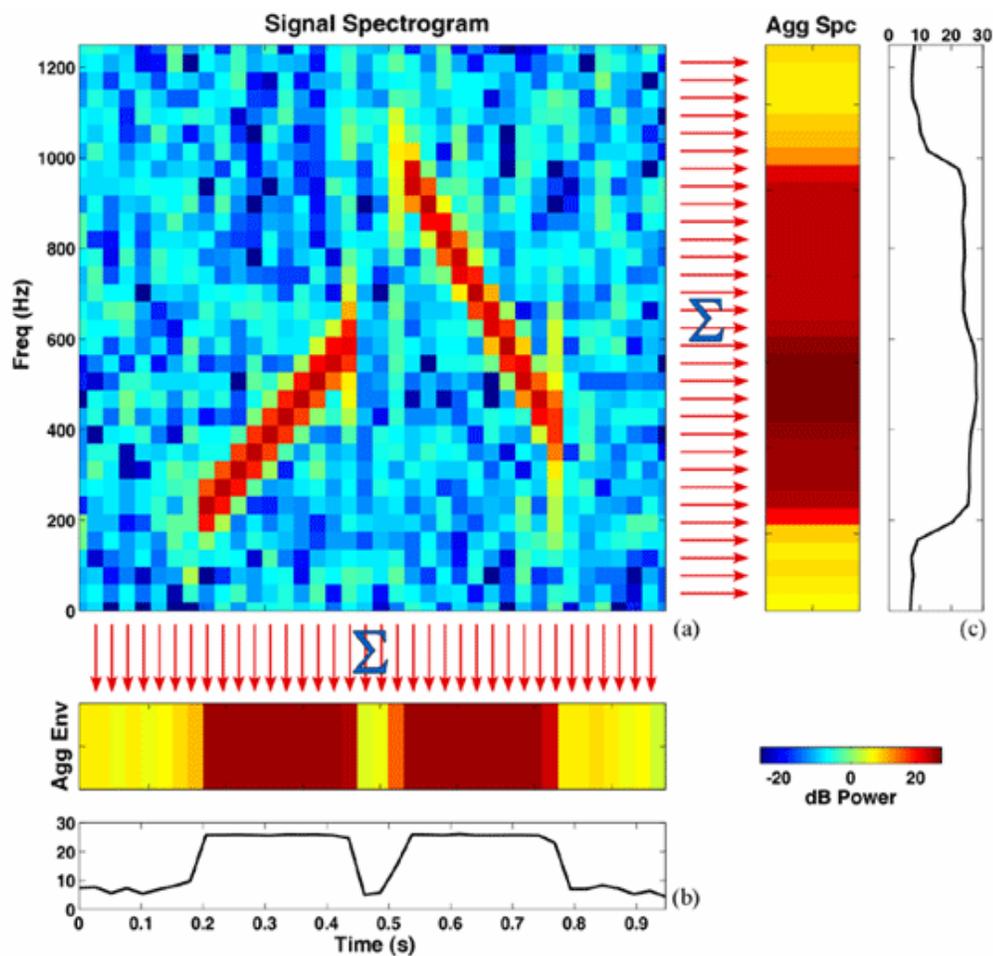
Figure 5.2. Spectrogram representation (a) of a signal, generating an aggregate time envelope (b) and a frequency spectrum (c) by summing power values in each short-time spectrum or narrow-band envelope, respectively. The resulting aggregates (once normalized to have unit area) are treated like probability density functions with time and frequency as variates.

We used 50% of the total flight-call signal energy in the amplitude-time and power spectrum envelopes to measure statistical quartiles and inter-quartile ranges, where "median" (Me) is the 50th percentile, "initial" (P1) is the 25th percentile, "terminal" (P2) is the 75th percentile, "inter-percentile range" (W) encompasses 50% of the signal energy distribution, and "skewness" is (Me-P1)/W. We use the highest and lowest values that bound the top 50% of the probability distribution of the amplitude-time or power spectrum envelope to calculate the spread (highest minus lowest) in the distribution, which is then used to calculate "skewness" in the amplitude-time or power spectrum envelope. We also use equivalent width to describe amplitude-time (equivalent-duration) and power spectrum (equivalent bandwidth) data (Figure 5.3).
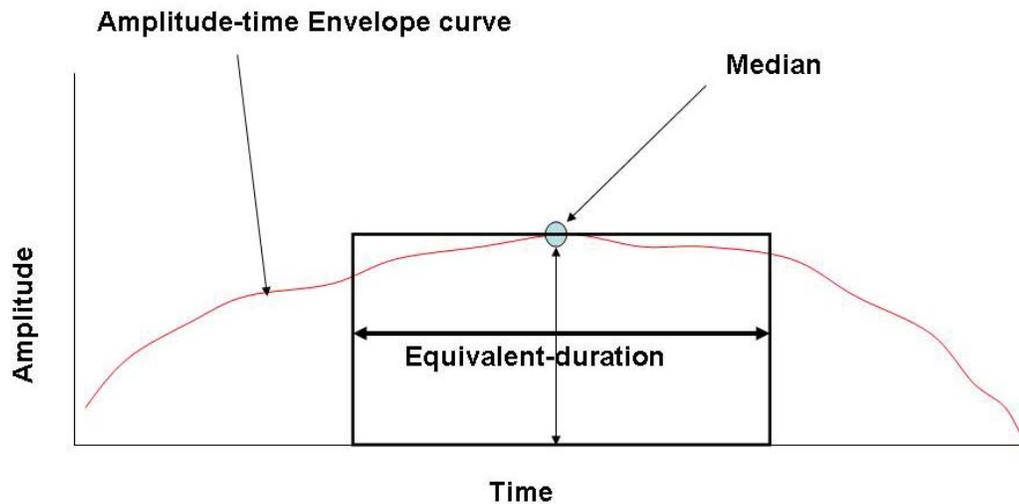
Figure 5.3. Equivalent-duration is the width of the rectangle whose height is the value of the median, centered on the median such that the area in the rectangle is equal to the total area under the amplitude-time envelope curve (see Table 5.1, measure 1; ENV). When the curve is the power spectrum (see Table 5.1, measure 2; PS), this width is referred to as equivalent-bandwidth. Note: when the curve is the FFT of the amplitude-time envelope curve (AM, AFM; Table 5.1, measures 3 and 4), then it is neither a "duration" or a "bandwidth" in an easy to understand sense (i.e., abstract); we refer to it as an "equivalent width."

XBAT extracted measurements to quantify a signal's compactness by sorting the amplitude-time and power spectrum envelopes, referred to as concentration measures (Figure 5.4). The value of concentration in relation to interpercentile range reveals how densely or loosely the signal's energy is distributed. Detailed descriptions of this procedure and these energy-distribution measurements are available from the Cornell Laboratory of Ornithology Bioacoustic Research Program (Cortopassi, www.birds.cornell.edu/brp/research/algorithms/RSM.html).
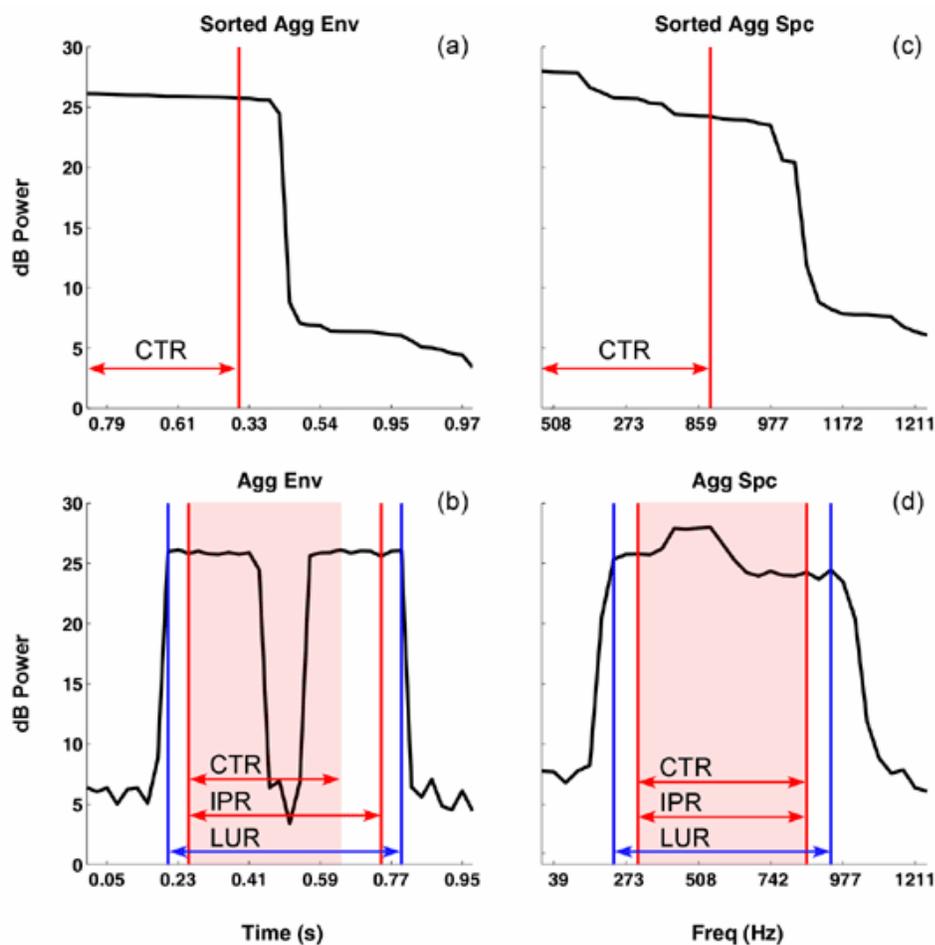
Figure 5.4. Sorted aggregate time envelope (a) and frequency spectrum (c) of a signal. Notice how the time and frequency indices are not sequential. The segment needed to accumulate a fraction P = 0.75 of the total signal energy is marked, and denoted as concentration (CTR). The concentration, interpercentile range (IPR), and lower-upper range (LUR) are shown together overlaid on the aggregate time envelope (b) and frequency spectrum (d).

There were 28 measurements taken: 16 from the amplitude-time and power spectrum envelopes and 12 concentration measures derived from sorted probability density functions of the time-varying features in the spectral frames, 9 from the amplitude-time envelope and 3 from the power spectrum envelope. The following are brief descriptions for each of these 28 ACUSTAT measurements. Table 5.1 is a look-up table to match the terms given here with those in ACUSTAT as implemented in XBAT.

1) Median, equivalent-duration and skewness of the amplitude-time envelope (MeENV, EqENV, and SkENV, in seconds);

2) Median, equivalent-bandwidth and skewness of the power spectrum envelope (MePS, EqPS, and SkPS, in Hz);

3) Median, equivalent-width and skewness of the discrete Fourier transform of the amplitude-time envelope, computing the frequency spectrum of the amplitude-time envelope and measuring from that (MeENVM, EqENVM, and SkENVM, in Hz);

4) Median, equivalent-width and skewness of the discrete Fourier transform of the median frequency contour from the amplitude-time envelope weighted by ¼ power of the amplitude-time envelope (MeAFM, EqAFM, and SkAFM in Hz);

5) Attack fraction (ATTACKFR, unitless), fraction of data blocks that have higher energy than the previous block, similar to the musical definition of a crescendo;

6) Up-sweep fraction (UPSWFR, unitless), fraction of data blocks that have higher frequency (based on the peak frequency contour) that the previous block;

7) Up-sweep mean (UPSWM, in Hz), average slope of the peak frequency contour;

8) Sweep magnitude (SWMAG, in Hz), sum of the absolute value of the derivative of the peak frequency contour;

9) Median, spread and skewness of the median-frequency contour (MeFMED, EqFMED, and SkFMED, in Hz), where FMED is the vector of the median-frequency values in each spectral frame of the power spectrum (Figure 5.5);

10) Median, spread and skewness of the frequency-concentration contour (MeFCC, EqFCC, and SkFCC, in Hz), where FCC is the vector of the number of bins needed to accumulate 50% of the total energy in the sorted energy distribution for each spectral frame;

11) Median, spread and skewness of the equivalent-bandwidth contour (MeEBC, EqEBC, and SkEBC, in Hz), where EBC is the vector of equivalent-bandwidth values for each spectral frame;

12) Median, spread and skewness of the frequency-skewness contour (MeFSKEW, EqFSKEW, and SkFSKEW in Hz), where FSKEW is the vector of skewness values for each spectral frame;

Table 5.1. XBAT energy-distribution measurements recorded from each flight call spectrogram.

Measurement	Analogous ACUSTAT Measurement	Description	Estimates
1) Amplitude Time Envelope (ENV, in sec)	Energy Envelope (ENV)	Amplitude time envelope from the aggregate energy envelope	Median (Me), Equivalent Duration (EQD), Skewness (Sk)
2) Power Spectrum Envelope (PS, in Hz)	Frequency Bandwidth (TS)	Power spectrum envelope from the aggregate power spectrum	Median (Me), Equivalent Bandwidth (EQB), Skewness (Sk)
3) Frequency Spectrum of Amplitude Time Envelope (ENVM, in Hz)	Amplitude Modulation (AM)	Discrete Fourier transform of the amplitude-time envelope, computing the frequency spectrum of the amplitude-time envelope and measuring from that	Median (Me), Equivalent Bandwidth (EQB), Skewness (Sk)
4) Median Frequency Contour Spectrum of Amplitude Time Envelope (AFM, in Hz)	Amplitude-Frequency Modulation (AFM)	Discrete Fourier transform of the median frequency contour from the amplitude-time envelope weighted by ¼ power of the amplitude-time envelope	Median (Me), Equivalent Bandwidth (EQB), Skewness (Sk)
5) Attack Fraction (ATTACKFR, unitless)	Attack Fraction (ATTACKFR)	Fraction of data blocks that have higher energy than the previous block	
6) Up-sweep Fraction (UPSWP, unitless)	Up-sweep Fraction (UPSWFR)	Fraction of data blocks that have higher frequency (peak frequency contour) that the previous block	
7) Up-sweep Mean (UPSWM, in Hz)	Up-sweep Mean (UPSWM)	Average slope of the peak frequency contour	
8) Sweep Magnitude (SWMAG, in Hz)	Sweep Magnitude (SWMAG)	Sum of the absolute value of the derivative of the peak frequency contour	
9) Median Frequency Contour (FMED, in Hz)	Median Frequency Contour (FMED)	The vector of the median-frequency values in each spectral frame of the power spectrum	Median (Me), Spread (Sp), Skewness (Sk)
10) Frequency Concentration Contour (FCC, in Hz)	Frequency Concentration Contour (CONC)	The vector of the number of bins needed to accumulate 50% of the total energy in the sorted energy distribution for each spectral frame	Median (Me), Spread (Sp), Skewness (Sk)
11) Equivalent Bandwidth Contour (EBC, in Hz)	Equivalent Bandwidth Contour (MODW)	The vector of equivalent-bandwidth values for each spectral frame	Median (Me), Spread (Sp), Skewness (Sk)
12) Frequency Skewness Contour (FSKEW, in Hz)	Frequency Asymmetry Contour (FASYM)	The vector of skewness values for each spectral frame	Median (Me), Spread (Sp), Skewness (Sk)

Parenthetical notation represents the abbreviations used in XBAT. Estimates refer to order statistics used to describe measurements. Measures and estimates (for example FMED and ME = FMEDME) describe the acoustic characteristics of flight-calls measured

Figure 5.5. Spectrogram representation (a) of a signal with an overlay of the median frequency contour (FMED), which is based on the medians of the successive short-time spectra. The median (M), initial percentile (P1), terminal percentile (P2), and interpercentile range (IPR) values are shown for the aggregate time envelope (b) and frequency spectrum (c) for an energy fraction P = 0.75.

The SPCC algorithm (Cortopassi unpublished data; similar application, Cortopassi and Bradbury 2000, 2006) calculates peak correlation coefficients for all pair-wise correlations of flight-calls and generates a matrix of these values. The algorithm convolves the two spectrogram matrices over each other in both time and frequency to compute their fit (Clark et al. 1987, Cortopassi and Bradbury 2000; also see ambiguity functions, Woodward 1953, Angelari 1970). As such, SPCC incorporates spatial and temporal elements of spectrograms in a repeatable and objective way to generate correlations rather than using a suite of more subjective individual measures of time and frequency to characterize a signal (Clark et al. 1987, Cortopassi and Bradbury 2000, Baker and Logue 2004). Whereas some previous applications of SPCC convolved only on a single scale (e.g. time scale, Cortopassi and

Bradbury 2000), convolution on both scales was necessary in our analyses; flight-call similarity across individuals and species may shift in both time *and* frequency (i.e., a pair of flight-calls may show differences in their durations, differences in their frequency distributions or differences in both duration and frequency distribution.) Before computing the spectrograms for a pair of calls, the program adds data samples of zero value to the length of the shorter call so as to have it match the duration of the longer call, a process called zero-padding (Qi 1992, Cortopassi and Bradbury 2000, Lucero and Koenig 2000). For all correlation calculations, we used the given spectrographic frequency and filter resolution of the Hamming window and frequency convolution of $\pm$ 1000 Hz for frequencies (based on previous visual inspection confirming that calls did not vary in center and bandwidth frequency by more than this amount). We cross-correlated 10 flight-calls from each of four individuals for each of the five species, yielding five different, species-specific, symmetrical 40-by-40 correlation matrices, each containing 780 unique pair-wise values.

We extracted 5 principal coordinates (PCOs) from each species' SPCC matrix (generated using a PCO option in the SPCC algorithm, Cortopassi unpublished data) and from each species' ED matrix (SAS 9.1.3, PROC MDS based on Euclidean distances between XBAT measurements, PROC DISTANCE, SAS Institute 2006). PCOs explained 94-99% of the variance in the SPCC matrices and 93-99% of the variance in the ED matrices (Table 5.2). Principal coordinate analysis of correlation matrices reduces and ordinates sound data into independent measures (latent orthogonal object measures; Gower 1966, Neff and Marcus 1980, Gower 1987, Legendre and Legendre 1998, Everitt and Dunn 2001) useful for grouping sounds and associating sounds with extrinsic variables (Cortopassi and Bradbury 2000, Baker 2004). In these analyses, negative eigenvalues represented less than 1% of the

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cumulative variation explained by all eigenvalues, and none of the first five PCOs

extracted from our samples contained negative eigenvalues.

Table 5.2. Cumulative goodness of fit of five principal coordinate axes extracted from flight-call correlation matrices of spectrographic cross-correlation data (SPCC) and XBAT energy-distribution measurement data (ED).

	Cumulative goodness of fit	
Species	SPCC	XBAT
American Redstart	99%	98%
Chestnut-sided Warbler	98%	97%
Magnolia Warbler	98%	96%
Nashville Warbler	94%	93%
Yellow-rumped Warbler	96%	99%

Goodness of fit is represented in percentage of variance explained. None of the PCOs we extracted contained negative eigenvalues.

For each species we classified individuals using a linear discriminant analysis

(LDA) with cross-validation of PCO data extracted from SPCC and ED measurements

of spectrograms (PROC DISCRIM, SAS 9.1.3, SAS Institute 2006). We used

individuals as output variables and PCOs as input variables to generate

misclassification rates for misidentifying calls to known caller. By this procedure,

misclassification rates represent a common metric for assessing the abilities of the

LDA to discriminate among individuals.

We performed two separate series of stepwise regressions, one for the SPCC-

PCO and one for the ED-PCO datasets, against the 28 ED measurements (PROC

REG, SAS 9.1.3) to examine the relationships between the SPCC-PCO and ED-PCO

datasets and linear combinations of the acoustic ED measurements. The goal of this

analysis was two-fold: 1) to determine which, if any, acoustic measures correlated

significantly to the PCO data; and 2) to compare any such correlations of acoustic

measures between SPCC-PCO and ED-PCO datasets. We also used stepwise

regression to investigate relationships between cross-correlation and energy-

distribution representations of flight-calls and to search for significant linear

combinations of SPCC-PCO and ED-PCO datasets. In addition to this stepwise regression for SPCC-PCO and ED-PCO datasets, we performed a canonical correlation analysis (CCA) to correlate the linear combinations of these PCO data (PROC CANCORR, SAS Institute 2006). We used Holm's method for sequential Bonferroni correction (Holm 1979, Rice 1989) with an adjusted critical value of p = 0.002. We designated any critical value of $0.002 < p < 0.05$ as a near-significant trend.

We performed classification tree analysis (CTA) using CART 5.0 (Salford Systems; Steinberg and Colla 1997) to explore the misclassification rates and variable importance among species for each individual. CTA is a statistical method for partitioning categorical data by constructing decision rules for splitting groups (Breiman et al. 1984, Clark and Pregibon 1992, Friedman 1989, Steinberg and Colla 1997, De'ath and Fabricius 2000, Perlich et al. 2003, Prasad et al. 2006). Binary splits based on single predictor variables generate successively smaller group partitions, to a point after which no smaller partitions are possible and to a point at which the largest class representation within a partition defines the group (also called plurality, Steinberg and Colla 1997). However, single trees may misrepresent data because of variability in data sampling (Freund and Schapire 1996, Breiman 1996, Prasad et al. 2006). To reduce the effects of variable data sampling, we used a procedure of resampling and combining trees based on the performance of prior trees (ARCing, or adaptive resampling and combining; Breiman 1996, Freund and Schapire 1996, Steinberg and Colla 1997). Successive samples are not random but skewed in favor of classes with higher, prior misclassification rates (in contrast, see bootstrapping aggregates: Steinberg and Colla 1997).

We combined 200 trees using ARCING in CART 5.0 with 50 redraws, withholding 25% of the population sample, and using a power exponent of four (the

larger this exponent, the greater the weight on previously misclassified cases). We used a Gini splitting rule to maximize the number of nodes with as few target classes of individuals as possible. We cross-validated to produce a minimum cost - one standard error tree (additional detail: Steinberg and Colla 1997), using misclassification rate to assess the accuracy of tree models. We assessed variable importance by examining the reductions in sum of squares based on all partitions associated with a given sound measurement and its role as a primary and surrogate splitter (details: Steinberg and Colla 1997). We do not present classification trees in our results because we produced no single representative tree for each species, a result of combining 200 trees for each analysis.

Results

Flight-call PCOs showed patterns of individual grouping within species in both the SPCC and ED data (data shown for PCOs 1 and 2: Figure 5.6, SPCC; Figure 5.7, ED). However, substantial variation exists in the degree of individual separation among the five species, and substantial differences in individual separation exist between SPCC and ED data for the same species. American Redstart flight-calls formed distinct clusters of individuals, and this pattern is apparent in the scatterplot of SPCC-PCO 1 against SPCC-PCO 2 (Figure 5.6a). In contrast, Yellow-rumped Warbler flight-calls formed indistinct and overlapping clusters of individuals (Figure 5.6e). The same relationships for ED-PCOs exhibit much less distinct separation among individuals for both species (Figures 5.7a and 5.7e, respectively).
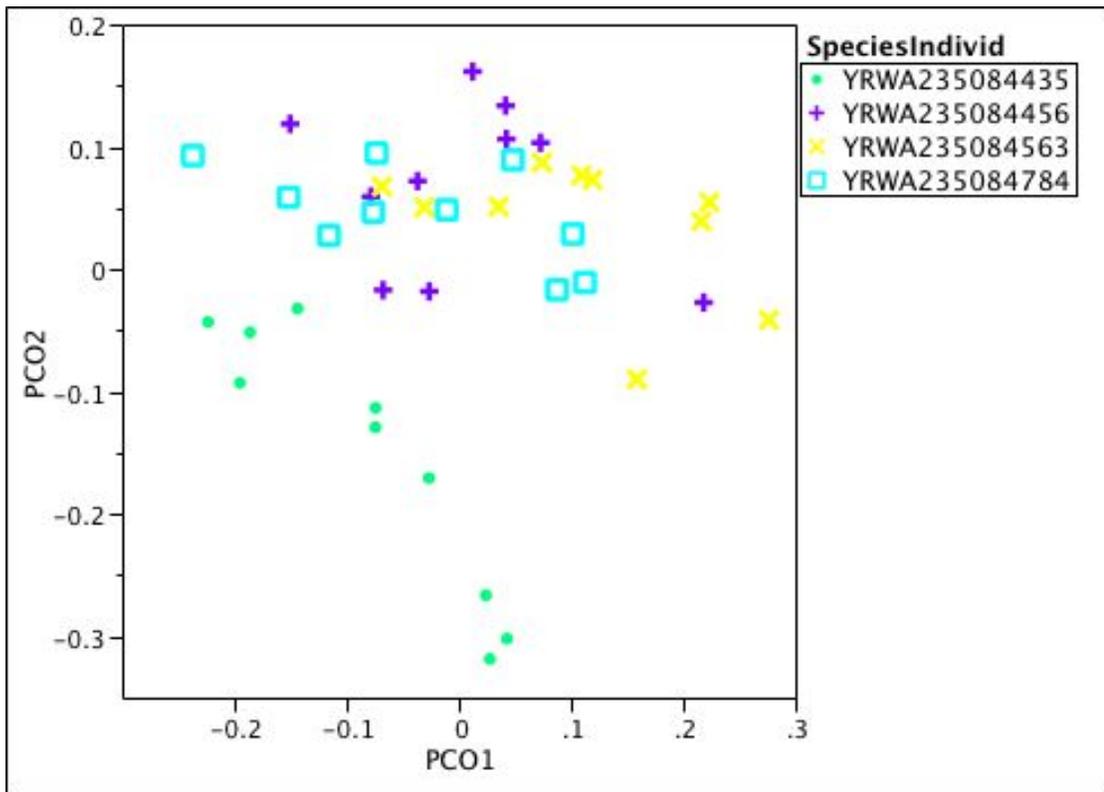
A)

Figure 5.6. Scatterplot matrix of SPCC PCOs 1 and 2 of flight-calls of five species of warblers. A) American Redstart, B) Chestnut-sided Warbler, C) Magnolia Warbler, D) Nashville Warbler, E) Yellow-rumped Warbler. Each individual is labeled with a unique marker and color in the legend.

Figure 5.6 (Continued).
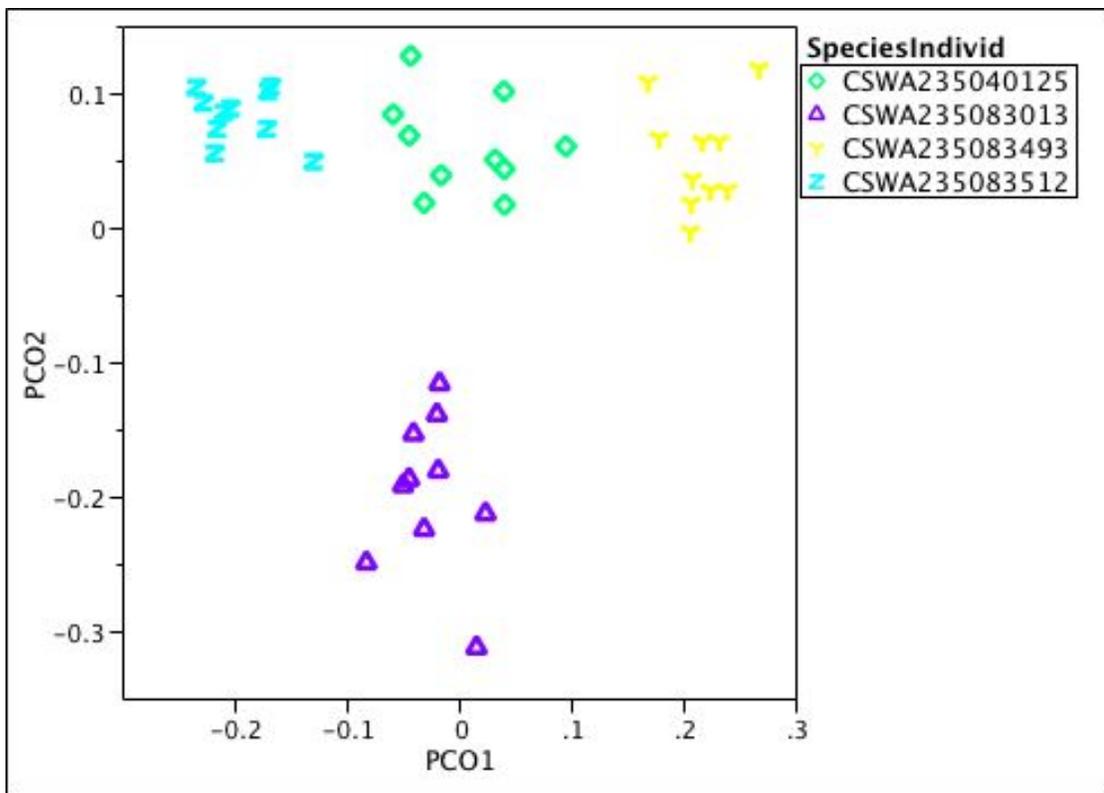
B)

Figure 5.6 (Continued).

C)
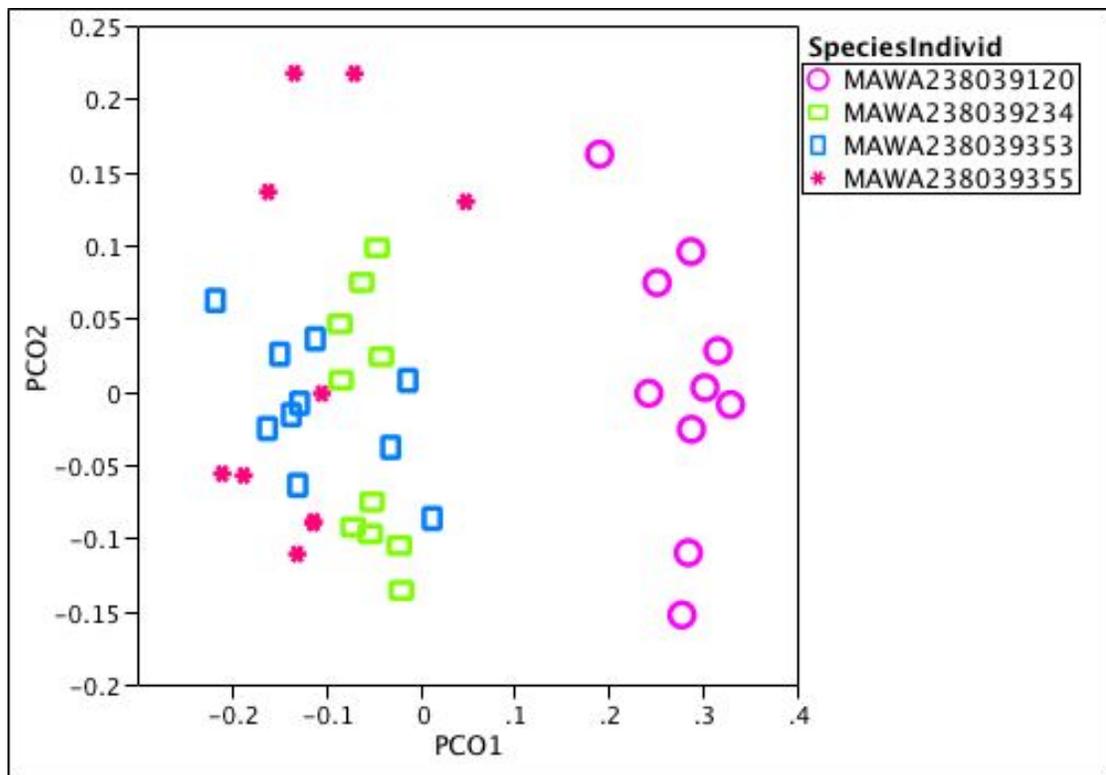
Figure 5.6 (Continued).

D)
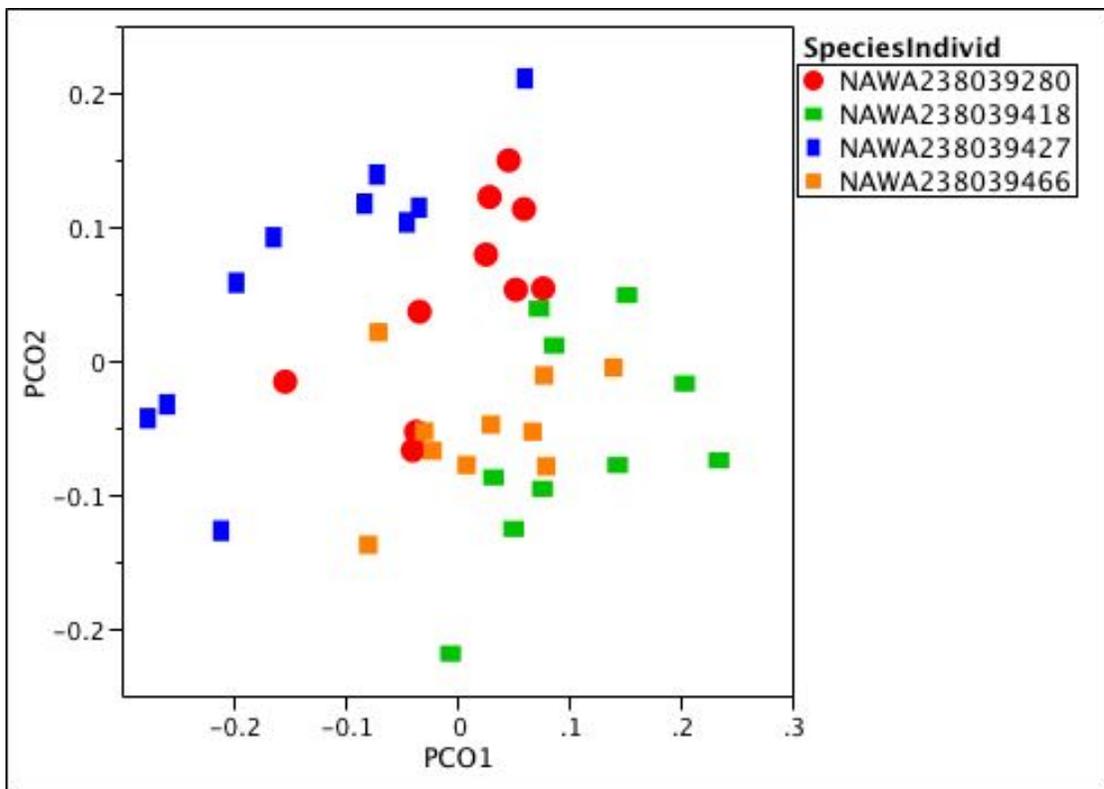
Figure 5.6 (Continued).
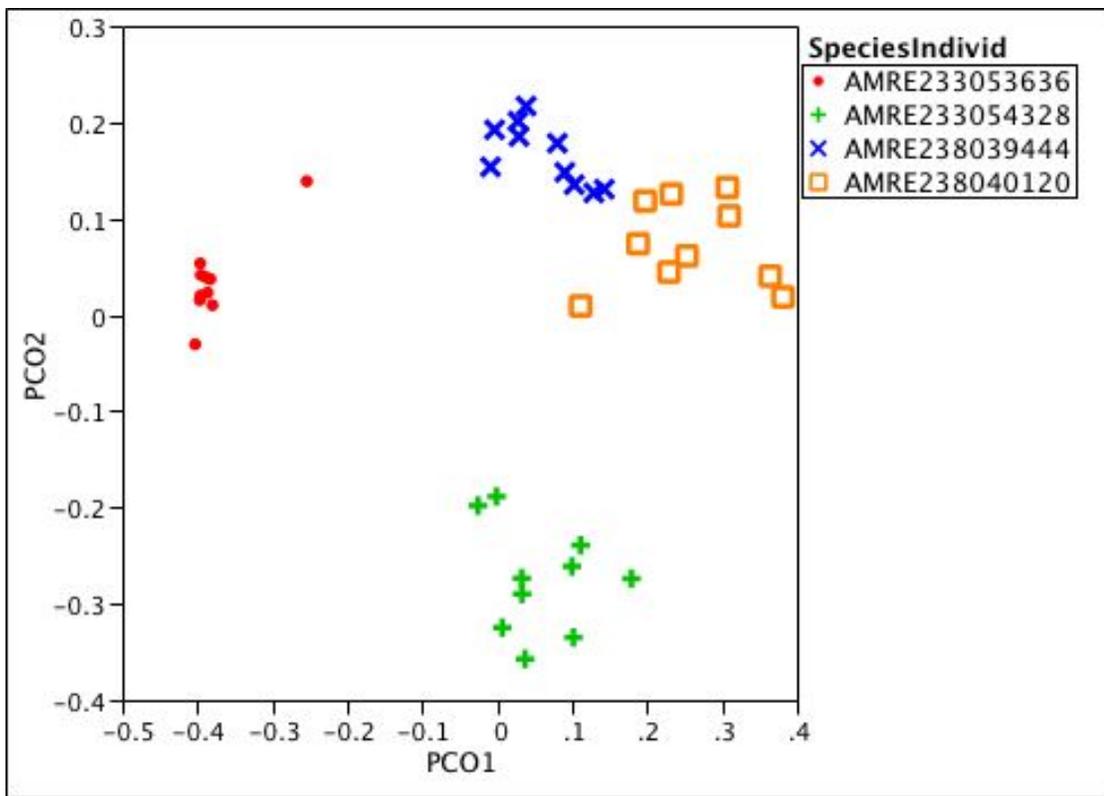
E)
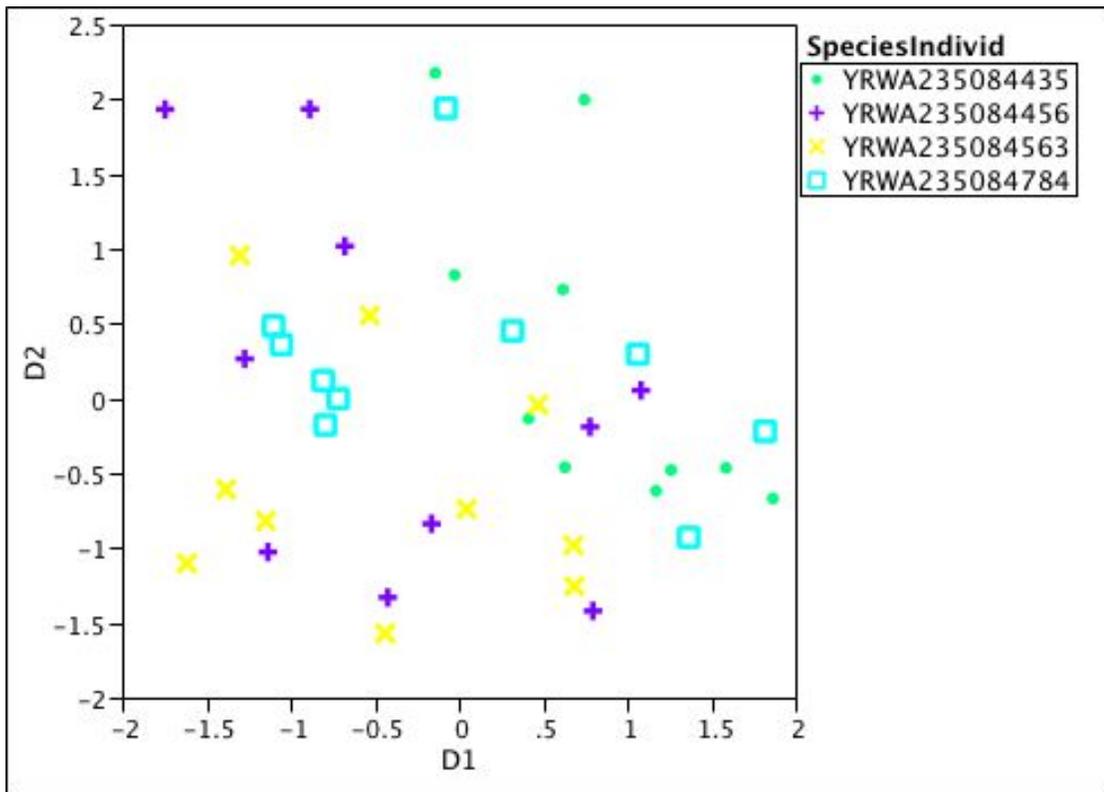
A)

Figure 5.7. Scatterplot matrix of ED PCOs 1 and 2 of flight-calls of five species of warblers. A) American Redstart, B) Chestnut-sided Warbler, C) Magnolia Warbler, D) Nashville Warbler, E) Yellow-rumped Warbler. Each individual is labeled with a unique marker and color in the legend.

Figure 5.7 (Continued).
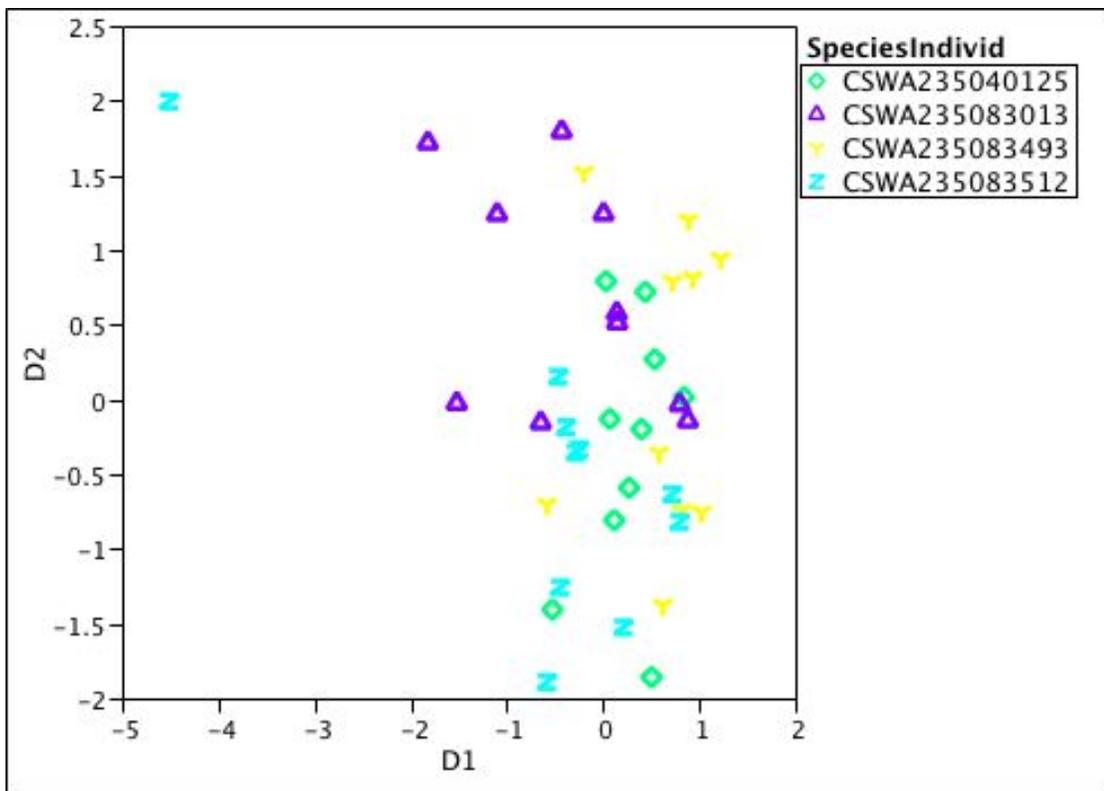
B)

Figure 5.7 (Continued).
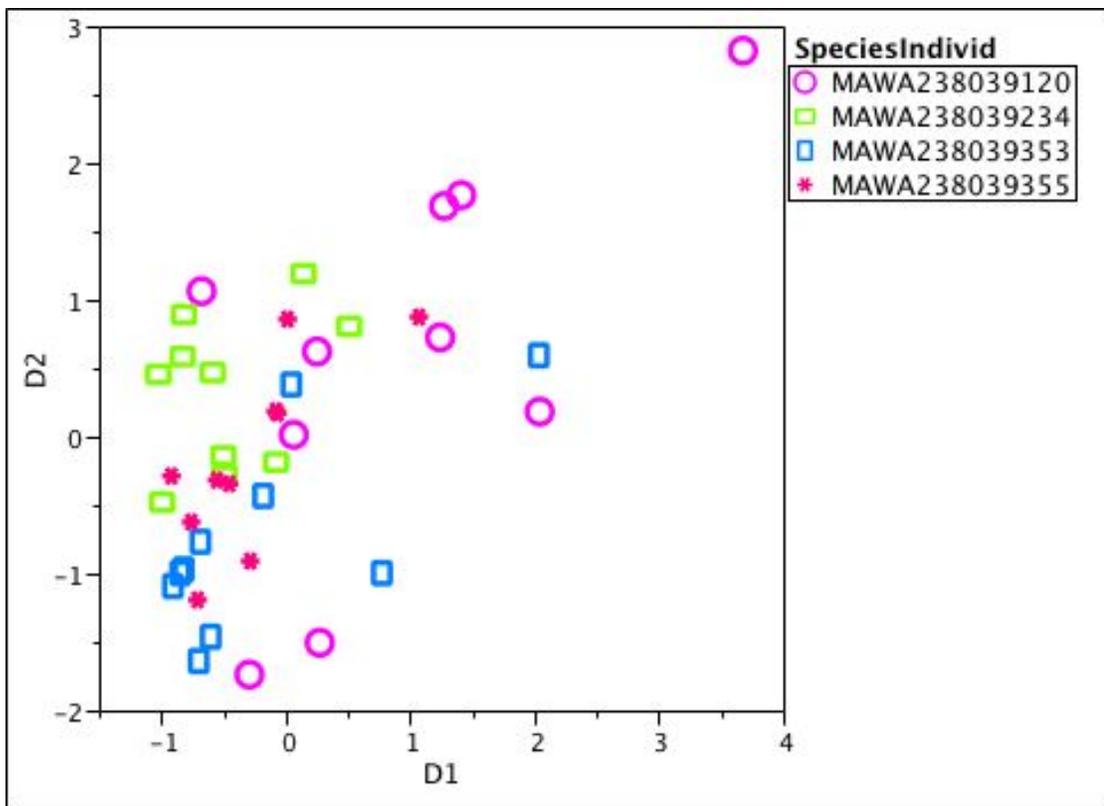
C)

Figure 5.7 (Continued).

D)
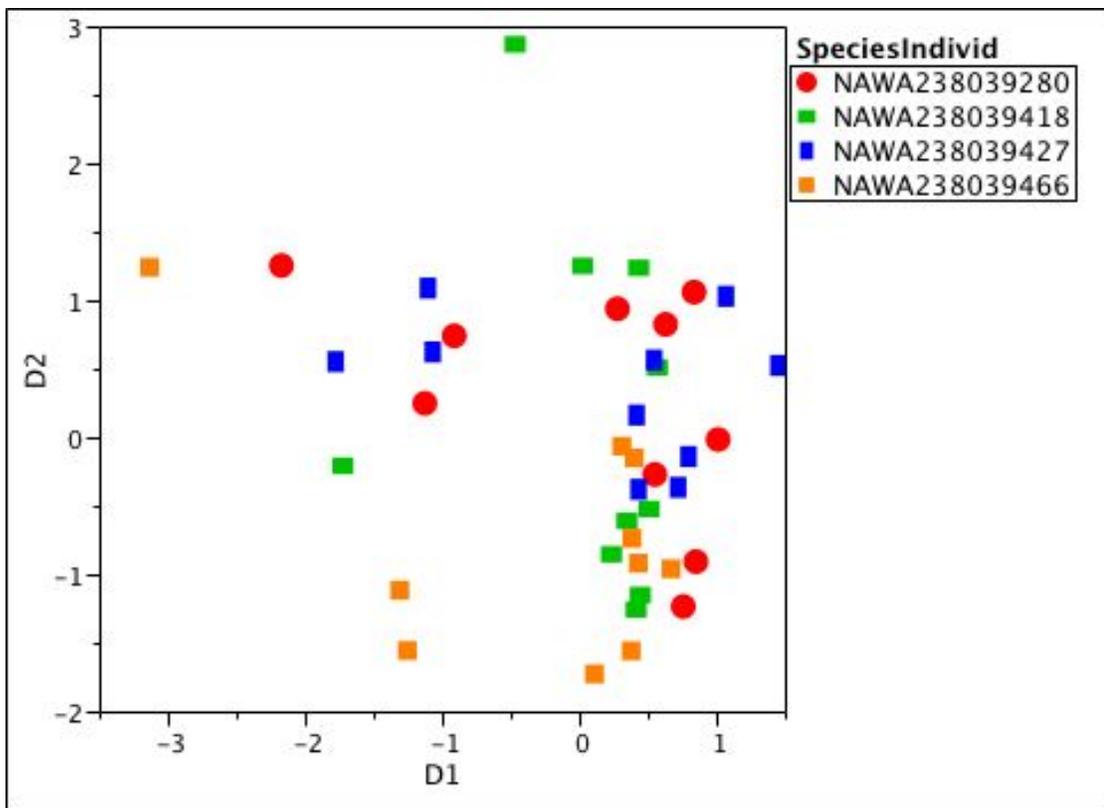
Figure 5.7 (Continued).
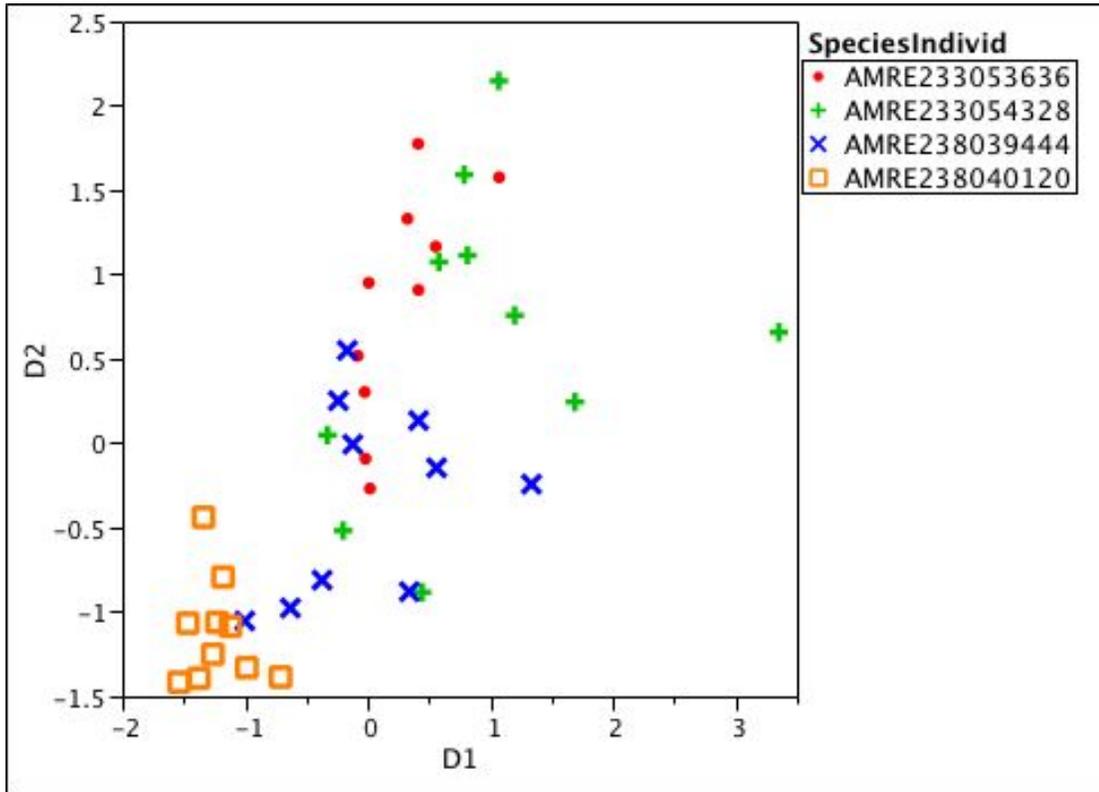
E)

SPCC-PCO data performed better at correctly classifying flight-calls than did ED-PCO data for each species (Table 5.3). LDA classification of individuals using PCO data as input variables yielded misclassification rates of individuals of 0-70% for SPCC data and 10-100% for ED data. American Redstart and Chestnut-sided Warbler were not misclassified for SPCC-PCO data, while Yellow-rumped Warbler showed the highest misclassification rates up to 70% with these data. American Redstart and Chestnut-sided Warbler were misclassified for ED-PCO DATA (10-70% and 40-70% respectively). Nashville Warbler showed the highest misclassification rates using ED-PCO data (60-100%).

Table 5.3. Misclassification rate means and ranges by species for misclassifying flight-calls to known flight-caller.

Species	Classification Method	Input Data	Average Misclassification Rate	Range
American Redstart	CART	ED	25.2%	15-35%
		SPCC	15.4%	5-45%
		XBAT	16.2%	10-25%
	LDA	SPCC	0.0%	0%
		XBAT	35.2%	10-70%
Chestnut-sided Warbler	CART	ED	65.0%	50-85%
		SPCC	8.3%	0-25%
		XBAT	43.2%	30-55%
	LDA	SPCC	0.0%	0%
		XBAT	50.0%	40-70%
Magnolia Warbler	CART	ED	45.3%	35-50%
		SPCC	21.7%	10-35%
		XBAT	37.8%	30-40%
	LDA	SPCC	22.6%	0-50%
		XBAT	47.5%	10-60%
Nashville Warbler	CART	ED	35.0%	30-40%
		SPCC	35.0%	10-45%
		XBAT	32.4%	25-40%
	LDA	SPCC	12.5%	0-30%
		XBAT	77.3%	60-100%
Yellow-rumped Warbler	CART	ED	55.2%	30-65%
		SPCC	40.0%	20-45%
		XBAT	43.2%	35-50%
	LDA	SPCC	35.0%	0-70%
		XBAT	52.5%	30-80%

CTA, classification tree analysis; LDA, linear discriminant analysis; ED, energy-distribution measurements prior to ordination by PCO; ED, PCO of XBAT energy-distribution measurements; SPCC, PCO of spectrographic cross-correlation data.

PCOs of both SPCC and ED data exhibited significant relationships with linear combinations of ED measurements from XBAT (Table 5.4). In particular, SPCC-PCO 2 and ED-PCO 2 exhibited significant models with the linear combinations of the most energy-distribution measurements: SPCC-PCO2 correlated significantly with a linear combination of amplitude modulation median, total frequency spectrum mode width,

energy envelope mode width, median frequency contour median and skewness, and frequency skewness contour skewness, this combination explaining 26% of the variation in SPCC-PCO2; and ED-PCO2 correlated significantly with a liner combination of weighted amplitude modulation median, median frequency, upsweep fraction, upsweep mean, sweep magnitude, median frequency contour median and spread, and frequency skewness contour spread, this combination explaining 54% of the variation in ED-PCO2. We also found significant correlations between SPCC-PCO and ED-PCOs (Table 5.4). While two of five PCOs showed no significant relationships with any respective linear PCO combination (SPCC-PCOs 4 and 5; ED-PCOs 3 and 5), the remaining three PCOs exhibited significant relationships with a single PCO or a linear combination of PCOs. SPCC-PCO2 and ED-PCO2, in particular, exhibited significant relationships with linear combinations of PCOs. Canonical correlation analysis confirmed this result, indicating that the first SPCC and ED canonical variables with high correlation loadings of SPCC-PCO2 and ED-PCO2 exhibited a significant correlation ($r = 0.40$, $F = 1.86$, $P = 0.0007$, Table 5.5).

Among the five species' flight-calls we examined, CTA produced a broad range of misclassification rates (Table 5.3). These rates were generally higher than misclassification rates of LDA, especially for SPCC-PCO data. Additionally, with only a single exception (Nashville Warbler), ED-PCO data generally yielded higher misclassification rates than SPCC-PCO data in CTA (Table 5.3). The most important variables for classifying individuals using CTA varied by species, especially for classifications using unordinated ED measurements (Table 5.6).

Table 5.4. Stepwise regression of PCOs against each other and PCOs against energy-distribution measurements.

Data for regression	Response	R^2	F-value*	Regressor
PCO Data	SPCC PCO 1	0.03	5.96	ED PCO 2
	SPCC PCO 2	0.11	7.93	ED PCO 1, ED PCO 2, ED PCO 4
	SPCC PCO 3	0.03	6.47	ED PCO 4
	SPCC PCO 4	-	-	-
	SPCC PCO 5	-	-	-
	ED PCO 1	0.06	11.77	SPCC PCO 2
	ED PCO 2	0.07	7.1	SPCC PCO 1, SPCC PCO 2
	ED PCO 3	-	-	-
	ED PCO 4	0.03	6.47	SPCC PCO 3
	ED PCO 5	-	-	-
Energy Distribution (ED) Data	SPCC PCO 1	0.11	8.26	AFMEQB, ENVME, EBCSP
	SPCC PCO 2	0.26	11.53	ENVMME, PSEQB, ENVEQD, FMEDME, FMEDSK, FSKEWSK
	SPCC PCO 3	0.05	4.72	FCCME, EBCSK
	SPCC PCO 4	0.09	6.32	ENVMEQB, ENVEQD, UPSWFR
	SPCC PCO 5	0.03	6.53	EBCME
	ED PCO 1	0.25	16.01	ATTACKFR, SWMAG, FMEDSP, FSKEWME
	ED PCO 2	0.51	24.53	AFMME, PSME, UPSWFR, UPSWM, SWMAG, FMEDME, FMEDSP, FSKEWSP
	ED PCO 3	0.24	15.32	PSEQB, PSSK, UPSWFR, SWMAG
	ED PCO 4	0.02	4.92	ENVME
	ED PCO 5	0.06	6.51	FMEDSP, EBCSK

* $P < 0.002$
⁻ no significant variables entered the model
Response is the PCO regressed on spectrogram cross correlation (SPCC) or energy-distribution (ED) measurements. R^2 is the percentage of variation explained by the model, with its associated F-statistic. Regressor represent the SPCC or ED variables on which we stepwise-regressed the response.
* denotes a significant correlation at $P < 0.002$; - denotes a PCO for which no significant variables entered the stepwise regression.

Table 5.5. Canonical correlations for first canonical variables extracted from SPCC and ED PCO data.

PCO Data	Canonical Variable 1 for SPCC	Canonical Variable 1 for ED
SPCC PCO1	0.2993	0.1193
SPCC PCO2	0.8227	0.3281
SPCC PCO3	-0.4281	-0.1707
SPCC PCO4	0.2162	0.0862
SPCC PCO5	-0.0596	-0.0238
	Canonical Variable 1 for ED	Canonical Variable 1 for SPCC
ED PCO1	-0.4667	-0.1861
ED PCO2	-0.6623	-0.2641
ED PCO3	0.1289	0.0514
ED PCO4	0.2786	0.1111
ED PCO5	-0.2186	-0.0872

PCO Data come from spectrographic cross correlation (SPCC) or energy-distribution (ED) measurements. Second column from the left represents the patterns of PCO loadings for each canonical variable. Third column from the left represents the patterns of PCO loadings on the opposing canonical variable.

Table 5.6. Variable importance for classification tree analysis (CTA) of individual warblers by species.

Species	Most Common Primary and Surrogate Splitter		
	ED	SPCC-PCO	ED-PCO
American Redstart	FCCSp	PCO 1	PCO 1
Chestnut-sided Warbler	ENVMEQB	PCO 1	PCO 1
Magnolia Warbler	UPSWFR	PCO 1	PCO 2
Nashville Warbler	PSMe	PCO 3	PCO 4
Yellow-rumped Warbler	AFMSk	PCO 3	PCO 3

ED, the un-ordinated energy-distribution measurements; SPCC-PCO, ordinated spectrographic cross-correlation data; and ordinated ED-PCO, energy-distribution measurements. PCOs of SPCC and ED data correspond to ED measurements in Table 5.4.

Discussion

Both spectrographic cross-correlation and energy-distribution measurements of

warbler flight-call spectrograms grouped individuals significantly. Our results suggest

that both approaches to representing and comparing simple acoustic signals may be

useful for identifying subtle individual differences. Qualitative inspection of the PCO scatter plots suggests that the SPCC-PCO analytical approach yielded more distinct individual flight-call groups than the ED-PCO approach (e.g., American Redstart). Moreover, LDA and CTA confirmed this quantitatively (Table 5.3). We conclude that individuality in warbler flight-calls may be expressed more effectively with the linear discriminant analysis LDA as applied to the SPCC-PCO approach to sound measurement.

Although slight overlap exists in the two basic patterns of correlation for energy-distribution measurements with SPCC-PCO and ED-PCO data (Table 5.4; for example, SPCC-PCO2 versus ED-PCO1 and ED-PCO2), these patterns of correlations with the PCO variables are largely different. Therefore, while there may be some overlap in the representative abilities of the reduced and ordinated measures (PCOs) from spectrographic cross-correlations and energy-distribution measurements, the two analysis approaches depict different quantitative measures of sound. To our knowledge this is the first report of a statistical association between ordinated, reduced cross-correlation measurements and spectral-temporal measurements of sounds (SPCC-PCO data versus ED measurements, Table 5.4) and between two sets of different principal coordinate measurements (SPCC-PCO versus ED-PCO datasets, Table 5.5). Without comparisons of PCO data with ED measurements, we would have missed this important conclusion. As such, we believe this study represents an important step forward: 1) for understanding the relationship between more traditional sound measurements approaches and SPCC approaches; 2) for developing more automated and objective techniques for processing and comparing sounds; and 3) for highlighting the value of comparing multiple approaches to measuring sounds, particularly in relation to interpreting variation in signals and to classifying signals.

No single spectral or temporal measurement was common to all species in classification tree analysis that identified individuals by their flight-call measurements. Five of the 28 ED measurements that we recorded were important for classifying individuals by their flight-calls (Table 5.6). PCO data exhibited less variation and greater redundancy of important variables, although all CTA based on PCOs included at least two PCO variables (Table 5.6). While different patterns of important classification variables (unordinated or ordinated and reduced) across species may relate to classification and measurement methods, the patterns may also have biological relevance. Individual recognition of vocalizations in birds is likely a function of multiple parameters, rather than single, isolated acoustic features of vocalizations. In addition, both sound production and perception abilities may differ among individuals and among species (e.g. Beecher 1989, Stoddard 1996, Slabbekoorn and Ten Cate 1998 a,b, Jouventin and Aubin 2002). Regardless of their underlying cause, the patterns revealed by the analysis presented here emphasize the importance of choosing multiple or ordinated variables to classify individuals by measurements of their vocalizations as well as the importance of such choices and comparing different approaches of representing sounds.

While any set of signal measures could miss important features associated with particular biological or behavioral contexts (Cortopassi and Bradbury 2000, Baker and Logue 2003), we chose an analysis approach to include measures that were robust to human measurement error and as descriptive as possible.

SPCC does not have the constraints associated with subjective sound measurement sets, and therefore may have the important advantage of incorporating features into sound measurements that more subjective measures may not represent. However, previous analyses using SPCC have highlighted drawbacks to this method, especially related to interpreting results in terms consistent with more typical methods

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for representing sound. Specifically, there is the difficulty in interpreting results relative to more traditional measures of sound arises because 1) SPCC measurements are not user-defined but data-defined (SPCC convolves entire spectrograms that can be viewed as a n x m matrix of features with high local co-variance, in contrast to sets of specific feature measurements from spectrograms); and 2) principal coordinate analysis extracts new, reduced and ordinated axes that do not necessarily correspond to intuitively salient time and frequency features (Cortopassi and Bradbury 2000, Baker and Logue 2003). Additionally, shortcomings of spectrographic analysis with regard to time standardization may be problematic, particularly when comparing two entire sounds: 1) cross-correlating two sounds similar in frequency features but different in lengths may produce inaccurate similarity values; and 2) frequency-modulated signals may have artificially low cross-correlation values despite their similarity in shape as a result of tiny differences in length (e.g. Deecke and Janik 2006). As such, SPCC analysis may not account for differences in signal stretching and compression or frequency dilation and compression. However, flight-calls are short vocalizations, and such differences in duration and frequency among individuals or species are not as extreme as such differences present in bird songs. Finally, separating a human's ability to discriminate between acoustic objects and a bird's ability to discriminate between acoustic objects is critically important. To understand a bird's powers of discrimination requires much more knowledge of bird behavior, signal production and content, and perceptive abilities in order to weight properly a comparative map in spectrographic space.

Our approach indicates that there may be instances where interpreting SPCC-PCO data may be possible, such that correlation and regression analyses of SPCC-PCO data with spectral and temporal (ED) measurements yield interpretations in accordance with more traditional and easy-to-interpret acoustic measurements.

Additionally, the increasing ease of processing digital data likely will facilitate more extensive studies of the relationships between SPCC-PCO and ED-PCO data and lead to further improvements in interpretive power and ability. Even using SPCC for comparing more complex vocalizations such as songs, though a much greater challenge than analysis of simple sounds, may prove within reach, facilitating analysis of complex vocal behaviors in novel and powerful ways. Yet, for simple vocalizations, particularly flight-calls, SPCC analysis may be even more powerful, enhancing abilities to automate sound classification of species and individuals. Monitoring flight-calls has wide applicability to various conservation goals (Evans and Mellinger 1999, Evans and Rosenberg 2000, Larkin et al. 2002). Automatic classification of flight-calls by SPCC could prove invaluable for speeding the assessment process, especially assessing the magnitude, timing, and location of species' migration routes.

Separating a human's ability to discriminate between acoustic objects and a bird's ability to discriminate between acoustic objects is critically important. To understand a bird's powers of discrimination requires much additional knowledge of bird behavior, signal production and content, and perceptive abilities in order to weight properly a comparative map of a vocalization in spectrographic space. Furthermore, SPCC gives equal weight to each cell in a similarity matrix, when in reality observer intuition and experience as well as experimental evidence suggest that this is not always true; rather, that a flourish or subtle difference could make a substantive difference in content or acoustic properties that SPCC would not reveal.

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CHAPTER SIX: EVOLUTION OF NOCTURNAL FLIGHT-CALLS IN
MIGRATING WOOD-WARBLERS: APPARENT LACK OF MORPHOLOGICAL
CONSTRAINTS*

Abstract

Many migratory songbirds produce flight-calls that vary, sometimes strikingly, among
species in duration, frequency, modulation, and pattern, and little is known about what
factors are responsible for this variation. Negative correlations between body mass or
bill length and song frequencies are well documented in birds, but no studies have
examined these associations for flight-calls. We explored relationships between
flight-call and song frequencies and body mass or bill length in 33 species of wood-
warblers. Phylogenetically controlled and uncontrolled analyses showed no
significant relationship between body mass or bill length and flight-call frequency;
however, we found significant differences between flight-call and song frequencies
and a significant relationship between maximum frequencies of flight-calls and songs.
Our findings suggest that factors other than body mass and bill length are responsible
for variation in flight-call frequencies in wood-warblers. We suggest that different
ecological and atmospheric properties might play important roles in selection for
flight-call frequencies.

Evans and O'Brien (2002) define flight-calls as the primary vocalization given during
sustained avian flight, particularly the long, sustained flight characteristic of
migration. Many birds produce these vocalizations, which are usually short in duration
(usually less than a second and frequently less than half a second) and high in

* Andrew Farnsworth, Department of Ecology and Evolutionary Biology, Cornell University, Ithaca,
NY 14853 USA; Irby J. Lovette, Evolutionary Biology Program, Cornell Laboratory of Ornithology,
159 Sapsucker Woods Road, Ithaca, New York, 14850, USA. Dr. Roland Sandberg granted permission
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frequency (in the 2-10 kHz range for most passerines), while migrating at night (Ball 1952; Graber and Cochran 1959; Evans and Mellinger 1999). Although some of these vocalizations may appear similar, flight-calls are species-specific, varying especially in their fine structure in frequency, duration, modulation, and pattern among taxa (Figure 6.1). Little is known about the function of flight-calls, although they may serve to maintain flocks and to communicate information among members of a flock (Hamilton 1962, Thake 1981) and perhaps among flocks (Griffin 1969).

Negative relationships between body mass and song frequencies are well documented in many avian groups (e.g., Greenewalt 1968, Wallschläger 1980, Ryan and Brenowitz 1985, Tubaro and Mahler 1998, Palacios and Tubaro 2000, Laiolo and Rolando 2003). Body mass and the mass of vibrating structures (such as syringeal membranes) are often positively correlated (e.g., Greenewalt 1968; Bowman 1983). Because frequency decreases as the mass of a vibrating structure increases, thicker syringeal membranes associated with larger body mass allow larger birds to produce lower frequency vocalizations. Additionally, larger birds are more likely to produce longer wavelength (i.e., lower frequency) vocalizations, particularly given the constraints that smaller birds face when attempting to produce vocalizations with wavelengths exceeding their body size (i.e., acoustical short-circuiting; see Bradbury and Vehrencamp 1998). Several studies have also reported that resonating properties of the suprasyringeal vocal tract affect song frequency spectra (e.g., Nowicki 1987, Nowicki and Marler 1988, Gaunt and Nowicki 1998). Changes in suprasyringeal characteristics of the vocal tract such as changing bill gape correlate with changing song frequencies – see e.g., *Zonotrichia*, *Melospiza* : Westneat et al. (1993); *Melospiza*: Podos et al. (1995); *Geospiza*: Podos (2001), Podos et al (2004). Additionally, several studies report negative correlations between bill length and vocalization frequency (Palacios and Tubaro 2000, song frequencies in woodcreepers

– Dendrocolaptidae; Slabbekoorn and Smith 2000, song frequency in *Pyrenestes ostrinus*); however, Laiolo and Rolando 2003 report that rattle call frequencies are higher in larger-billed *Corvus* and *Nucrifraga* (i.e., the opposite relationship), although rattle calls are non-tonal and appear not to fit the vocal tract-resonance model (Podos et al 2004).

Despite the prevalence of flight-calls in the repertoire of many songbird taxa, no published studies examine body mass or bill length relative to variation in flight-call frequencies. We examined body mass and bill length as possible sources for the variation in flight-call frequency among 33 species of wood-warblers (Parulidae). We tested the null hypotheses that there are no relationships between body mass or bill length and flight-call frequencies in wood-warblers. For comparison with the flight-call data, we also tested similar hypotheses using songs in place of flight-calls. In addition, we examined whether differences exist between flight-call and song frequencies and whether flight-call and song frequencies are related. Warblers provide a tractable group for studies of flight-call evolution because they exhibit a diversity of patterns and frequencies in flight-calls, recordings of flight-calls are available (Evans and O'Brien 2002), and a robust phylogenetic hypothesis for these taxa is available (Lovette and Bermingham 2001, 2002). In testing relationships among morphology and flight-call frequencies, we followed methodologies of several similar studies that used phylogenetic data as a foundation for creating independent contrasts between taxa (e.g., Tubaro and Mahler 1998, Palacios and Tubaro 2000).
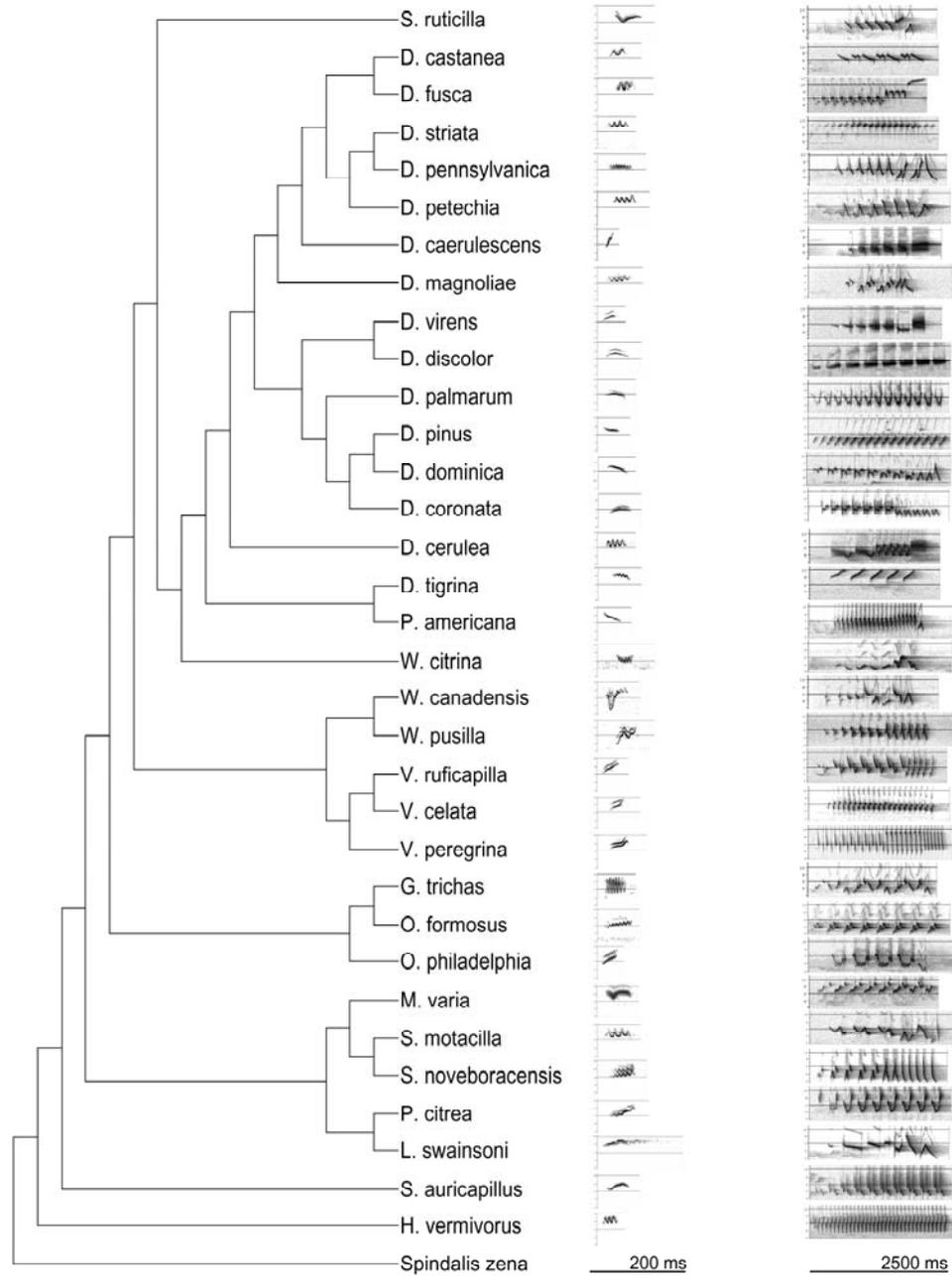
Figure 6.1. Phylogenetic hypothesis with a *Spindalis zena* outgroup for 33 species of wood-warblers with associated spectrograms of flight-calls and songs. All flight-call spectrograms refer to a common time scale 200 ms on each x-axis and a common energy scale of 2 kHz increments on each y-axis with dark reference lines at 6 and 10 kHz. All song spectrograms refer to a common time scale 2500 ms on each x-axis and a common energy scale of 2 kHz increments on each y-axis with dark reference lines at 6 and 10 kHz.

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Methods

We gathered body mass data from Dunning (1993) and the Birds of North America series (BNA, see references for a full list) and bill (culmen) length data (BNA) for 33 species of wood-warblers that occur in the United States east of the Rocky Mountains. These data represent averages of pooled males and females. We used recordings, spectrograms and flight-call metrics (see Table 6.1) from Farnsworth (2001) and Evans and O'Brien (2002) and recordings of songs (Type 1 songs; see following reference) from Borror and Gunn (1985), the Borror Laboratory of Bioacoustics at The Ohio State University, and the Macaulay Library of Natural Sounds at the Cornell Laboratory of Ornithology. We digitized flight-calls and songs (22,050 Hz sampling rate, 512 FFT, 87.5 % overlap) using the sound analysis package Raven (Charif 2003). Because some flight-calls approach 11 kHz (i.e., the Nyquist frequency for our sampling rate), we examined spectrograms of all recordings to confirm that no aliasing occurred during digitization. The age and sex of the vocalizing individuals are not known for any of our samples of flight-calls. The 33 species in our study represent taxa for which genetic data and recordings of flight-calls of known identity are available (Lovette and Bermingham 2001, 2002; Evans and O'Brien 2002). More details about flight-call recordings, including the process of identification and certainty of identification, are available in Evans (1994), Evans and Rosenberg (1999), Farnsworth (2001), and Evans and O'Brien (2002); more details about song recordings are available in Borror and Gunn (1985) and at the Borror Laboratory of Bioacoustics (The Ohio State University) and the Macaulay Library of Natural Sounds (Cornell University). We measured the following values in flight-calls and songs: maximum frequency (CALLMAX, SONGMAX) measured at the top of the highest frequency portion of a note, minimum frequency (CALLMIN, SONGMIN) measured at the

bottom of the lowest frequency portion of a note, and frequency bandwidth (CALLBAND = MAX - MIN, SONGBAND).

We used the method of independent contrasts for nondirectional comparative tests (Felsenstein 1985; also see Tubaro and Mahler 1998 for body size-song frequency applications), generating standardized linear contrasts with CAIC software version 2.6.9 (Purvis and Rumbaut 1995). We identified the evolution of ancestral character states by invoking a model assuming that branch lengths define the timing and occurrence of evolution in characters (Harvey and Purvis 1991, Pagel 1992, Freckleton et al. 2002). The method of independent contrasts produces a new variable (i.e., a contrast) based on differences in measurements of a chosen variable for pairs of sister species. Contrasts are independent because divergences occur after the origin of the species' pair; additionally, dividing by the square root of branch lengths under comparison standardizes these contrasts (Purvis and Rumbaut 1995, Tubaro and Mahler 1998). Standard linear regression models forced through the origin detect any associations between contrasts of different variables (Felsenstein 1985, Purvis and Rumbaut 1995, Tubaro and Mahler 1998).

Table 6.1. Individual bill lengths, body masses, frequency data for flight-calls and songs and associated group means, standard deviations, maxima, minima, and ranges for 33 species of wood-warblers.

Species	Bill length[a,d]	Body mass[b,d]	Call maximum[c,e]	Call minimum[c,e]	Call bandwidth[c,e]	Song maximum[c,f]	Song minimum[c,f]	Song bandwidth[c,f]
Blackpoll warbler	9.95	13.00	9.10	5.90	3.20	9.91	7.93	1.99
Cape May warbler	7.70	11.00	8.80	6.40	2.40	9.31	7.04	2.27
Pine warbler	10.75	11.90	8.50	4.80	3.70	5.60	3.31	2.29
Black-throated blue warbler	9.30	10.50	10.70	6.30	4.40	6.02	3.15	2.87
Black-and-white warbler	11.40	11.00	10.80	6.60	4.20	8.75	5.54	3.22
Kentucky warbler	8.50	14.30	7.10	5.60	1.50	5.42	2.10	3.32
Prairie warbler	9.95	8.00	8.70	5.20	3.50	7.10	3.63	3.47
Bay-breasted warbler	10.00	13.10	10.20	6.20	4.00	9.12	5.58	3.54
Yellow-rumped warbler	9.45	12.60	8.90	5.30	3.60	6.53	2.89	3.64
Black-throated green warbler	9.70	8.80	10.00	6.20	3.80	7.52	3.71	3.82
Magnolia warbler	8.98	8.90	9.10	5.70	3.40	7.00	3.05	3.96

a) mm.
b) g.
c) kHz.
d) N = 33.
e) N = 419.
f) N = 211.

Table 6.1 (Continued).

Species	Bill length[a,d]	Body mass[b,d]	Call maximum[c,e]	Call minimum[c,e]	Call bandwidth[c,e]	Song maximum[c,f]	Song minimum[c,f]	Song bandwidth[c,f]
Yellow-throated warbler	10.35	9.40	7.70	5.30	2.40	7.04	3.07	3.97
Hooded warbler	10.00	10.80	7.30	5.90	1.40	6.60	2.59	4.01
Orange-crowned warbler	11.20	9.00	10.00	5.60	4.40	7.62	3.58	4.04
Wilson's warbler	6.10	7.30	8.80	4.40	4.40	7.27	3.21	4.06
Northern parula	7.30	8.60	9.20	5.30	3.90	7.56	3.35	4.21
Common yellowthroat	10.60	10.30	9.50	3.40	6.10	7.15	2.93	4.22
Palm warbler	10.16	10.30	7.00	3.60	3.40	7.54	3.13	4.42
Worm-eating warbler	11.99	13.00	9.60	6.20	3.40	8.30	3.87	4.43
Mourning warbler	8.65	13.00	8.80	5.30	3.50	6.55	2.02	4.53
Nashville warbler	9.50	8.90	10.00	5.80	4.20	8.26	3.44	4.82
Yellow warbler	7.96	9.80	9.20	5.40	3.80	8.11	3.26	4.85
Northern waterthrush	10.40	17.80	9.40	4.90	4.50	7.36	2.45	4.91
Canada warbler	9.79	10.60	9.20	2.70	6.50	8.03	3.09	4.94
Cerulean warbler	9.59	9.50	8.30	6.00	2.30	7.84	2.84	5.00
Chestnut-sided warbler	9.65	9.80	8.00	5.00	3.00	8.05	3.04	5.01
Swainson's warbler	11.50	18.90	9.10	7.50	1.60	7.68	2.65	5.03
American redstart	8.65	8.50	10.00	5.40	4.60	8.89	3.59	5.30

Table 6.1 (Continued).

Species	Bill length[a,d]	Body mass[b,d]	Call maximum[c,e]	Call minimum[c,e]	Call bandwidth[c,e]	Song maximum[c,f]	Song minimum[c,f]	Song bandwidth[c,f]
Louisiana Waterthrush	13.20	19.80	8.70	6.80	1.90	7.62	2.30	5.32
Blackburnian warbler	10.11	10.00	9.70	6.50	3.20	9.70	3.92	5.78
Prothonotary warbler	14.30	15.00	10.40	5.70	4.70	9.62	3.74	5.88
Ovenbird	11.80	19.40	9.40	6.20	3.20	9.02	2.88	6.14
Tennessee warbler	7.95	10.20	10.20	6.20	4.00	9.45	3.12	6.33
Mean	9.89	11.61	9.13	5.55	3.58	7.80	3.51	4.29
SD	1.65	3.33	0.97	0.98	1.15	1.17	1.28	1.08
Maximum	14.30	19.80	10.80	7.50	6.50	9.91	7.93	6.33
Minimum	6.10	7.30	7.00	2.70	1.40	5.42	2.02	1.99
Range	8.20	12.50	3.80	4.80	5.10	4.49	5.91	4.34

For comparative analyses, we used a phylogenetic hypothesis derived from the mitochondrial sequences for 33 species of wood-warblers reported in Lovette and Bermingham (1999, 2002). The sequence dataset included a total of 3639 nucleotides of protein-coding mitochondrial DNA per taxon (see Lovette and Bermingham 2002 for details). We generated the phylogeny shown here (Figure 6.1) using the Bayesian likelihood approach implemented in the program MRBAYES 2.01 (Huelsenbeck and Ronquist 2001) under the general time-reversible model (nst=6), with site-specific rate variation partitioned by codon. We ran searches for 10,000,000 generations, with topologies and model parameters sampled every 10,000 generations; we discarded samples from the first 2,500,000 generations as burn-in, and we used the remaining 750 topologies to estimate the posterior probabilities of branches.

We modeled the relationship between body mass and frequency characters of flight-calls and songs using the linear contrasts and raw values (i.e., treating each species as an independent data point) for call characters. We compared CALLMAX and SONGMAX, CALLMIN and SONGMIN, and CALLBAND and SONGBAND with body mass. We used the residuals of the frequency data generated by CAIC (Purvis and Rambaut 1995) to remove the effects of body mass for the bill length and frequency character comparisons (following Palacios and Tubaro 2000). We used SAS (SAS Institute 1999) to test for differences between call and song frequencies and to examine the relationships between song and call frequencies. We set our initial significance level to $\alpha = 0.05$ across all analyses; however, we corrected for multiple comparisons in our body mass and bill length analyses using a typical Bonferroni correction (e.g., Miller 1981) with a new critical value for 18 multiple comparisons (adjusted $\alpha = 0.0028$) and a less conservative sequential Bonferroni technique (Holm's Method: see Holm 1979, Rice 1989; assessments use the statement $P_1 \leq \alpha/(1 + k - i)$

where k is the number of comparisons and i is the number of the sequential repetition from 0 to k).

Results

For masses, bill lengths, and song and flight-call data for individual species, as well as mean, standard deviation, maximum, minimum, and range across all species, see Table 6.1.

Comparisons of raw body mass and flight-call frequency revealed no significant relationships between body mass and CALLBAND, CALLMIN, or CALLMAX for the 33 species of wood-warblers (Figure 6.2a, 6.2b, 6.2c; all P-values > 0.0028 and Holm's Method). Species with greater mass had no significant tendency to exhibit larger bandwidths, lower minimum frequencies, or lower maximum frequencies. Comparisons of raw body mass and song frequency data revealed no significant relationships between body mass and SONGBAND, SONGMIN, or SONGMAX for the 33 species of wood-warblers (Figure 6.2a, 6.2b, 6.2c; all P-values > 0.0028 and Holm's Method). Species with greater mass had no significant tendency to exhibit larger bandwidths, lower minimum frequencies, or lower maximum frequencies.

Controlling for phylogenetic effects, pairwise contrasts revealed no significant relationships between body mass and CALLMAX, CALLMIN, or CALLBAND or between body mass and SONGMAX, SONGMIN, or SONGBAND (Figure 6.3a, 6.3b, 6.3c; all P-values > 0.0028 and Holm's Method). Within each comparison of paired species or nodes, the species or nodes with the greater body mass did not necessarily have a larger call or song bandwidth, lower call or song minimum frequency, or lower call or song maximum frequency. We also found no significant relationship between bill length and CALLMAX ($r^2 = 0.02$; $P = 0.5030$), CALLMIN ($r^2 = 0.03$; $P = 0.4227$), or CALLBAND ($r^2 = 0.00$; $P = 0.9604$) for the independent pairwise

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contrasts we performed after correcting for the effects of body mass. The species or

nodes with the greater bill length did not necessarily have a larger bandwidth, lower

minimum frequency, or lower maximum frequency within each pairwise comparison.

Furthermore, we found no significant relationship between bill length and

SONGMAX ($r^2 = 0.00$; $P = 0.8875$), SONGMIN ($r^2 = 0.09$; $P = 0.1355$), or

SONGBAND ($r^2 = 0.11$; $P = 0.0873$) for the independent pairwise contrasts. Greater

bill length did not necessarily correspond to larger bandwidth, lower minimum

frequency, or lower maximum frequency within each pairwise comparison.
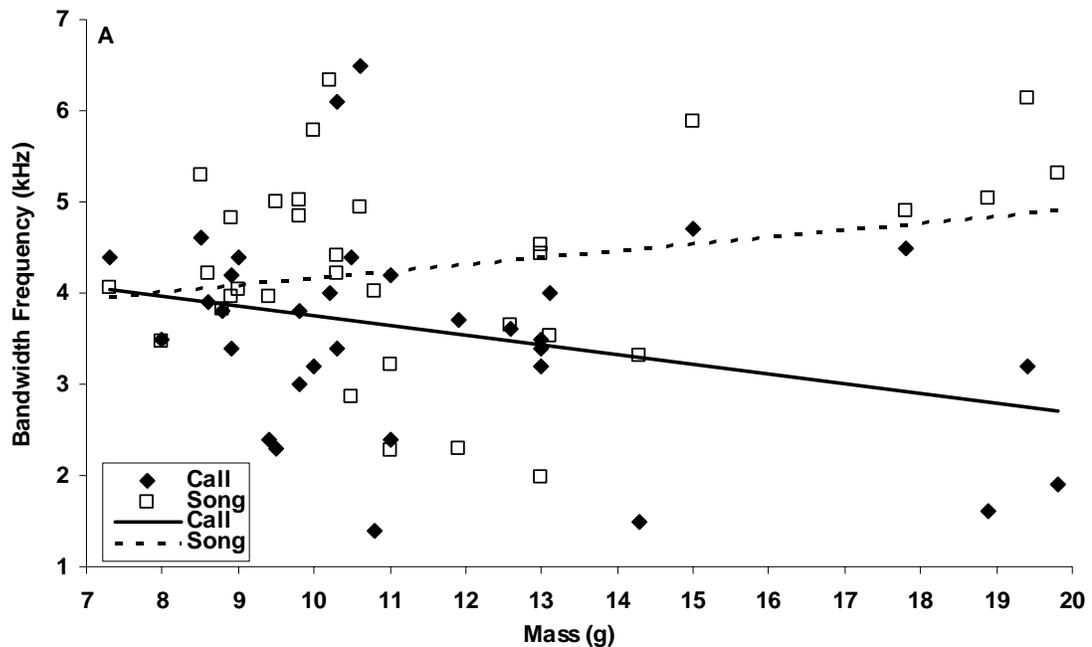
Figure 6.2. Frequency (kHz) of flight-calls and songs on body mass (g) (A)
Bandwidth. Flight-call Regression Line: $y = -0.11x + 4.81$; $r^2 = 0.09$; $P = 0.0825$.
Song Regression Line: $y = 0.08x + 3.41$; $r^2 = 0.06$; $P = 0.1890$ (B) Minimum. Flight-
call Regression Line: $y = 0.10x + 4.36$; $r^2 = 0.12$; $P = 0.0468$. Song Regression Line:
$y = -0.05x + 4.31$; $r^2 = 0.02$; $P = 0.4414$ (C) Maximum. Flight-call Regression Line: $y = -0.003x + 9.17$; $r^2 = 0.00$; $P = 0.9507$. Song Regression Line: $y = 0.02x + 7.54$; $r^2 = 0.00$; $P = 0.7188$.

Figure 6.2 (Continued).
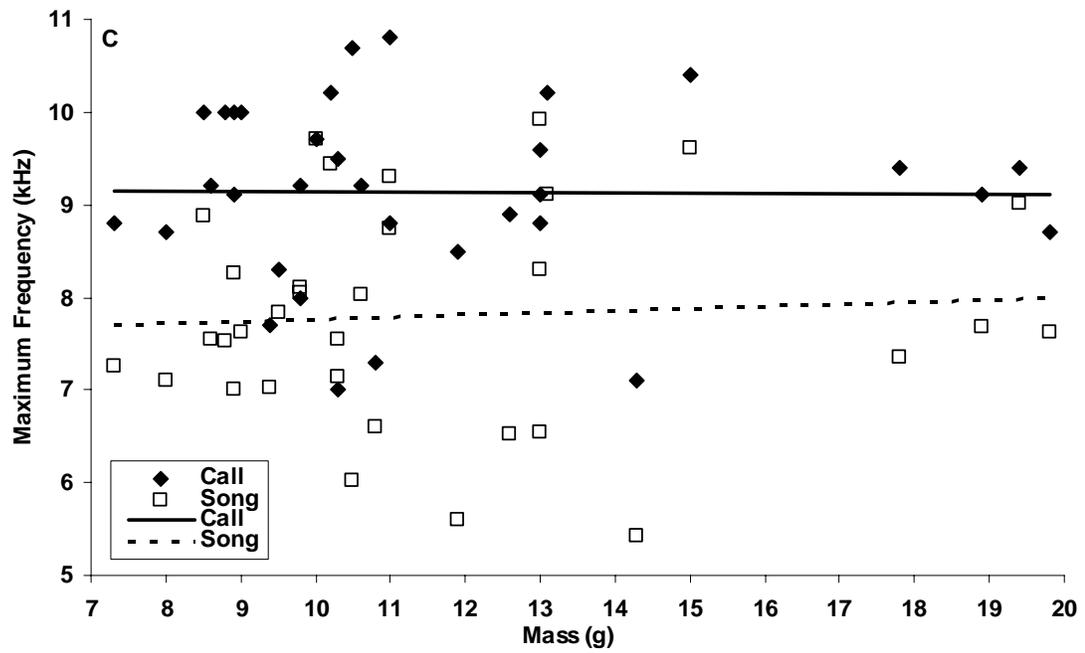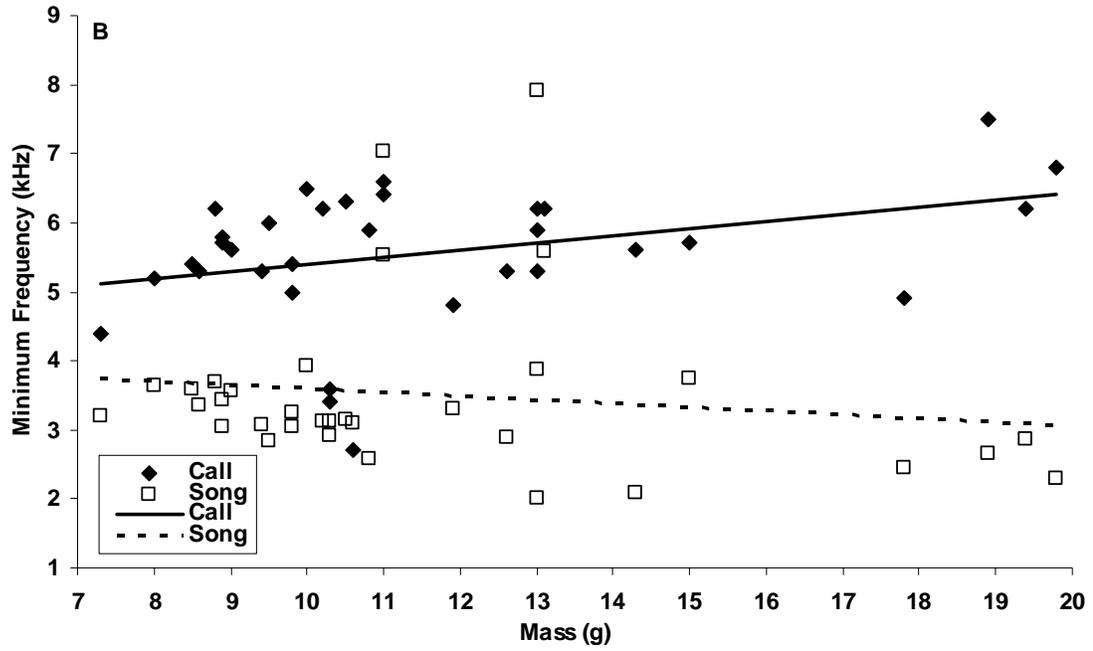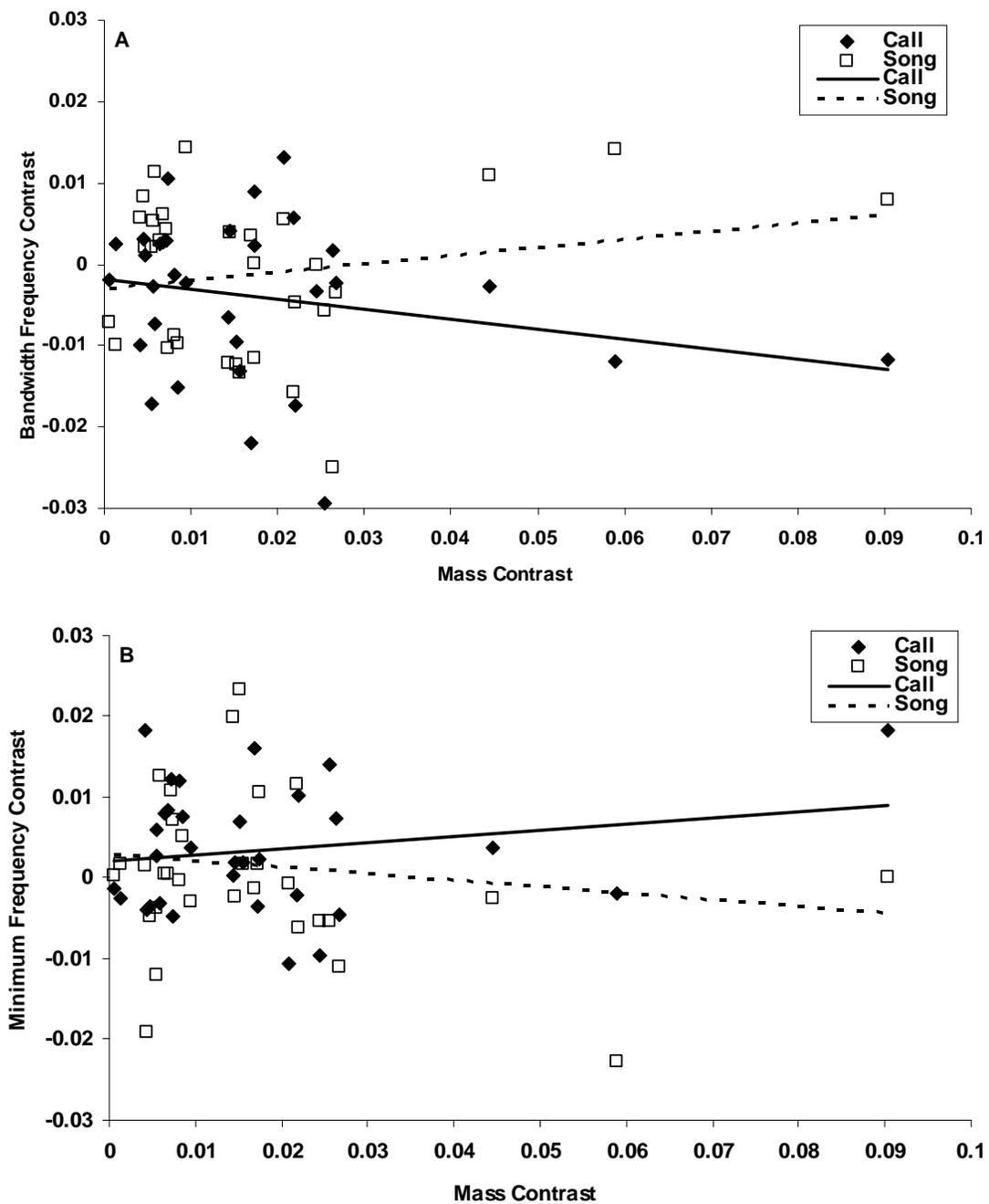
Figure 6.3. Frequency contrasts of flight-calls and songs on body mass contrasts (A) Bandwidth. Flight-call Regression Line: $y = -0.12x - 0.001$; $r^2 = 0.05$; P = 0.3754. Song Regression Line: $y = 0.10x - 0.003$; $r^2 = 0.04$; $P = 0.5951$ (B) Minimum. Flight-call Regression Line: $y = 0.08x + 0.002$; $r^2 = 0.03$; $P = 0.1380$. Song Regression Line: $y = -0.08x + 0.003$; $r^2 = 0.02$; $P = 0.9757$ (C) Maximum. Flight-call Regression Line: $y = -0.05x + 0.0004$; $r^2 = 0.0106$; $P = 0.7574$. Song Regression Line: $y = 0.02x - 0.00009$; $r^2 = 0.00$; $P = 0.5984$.

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Figure 6.3 (Continued).
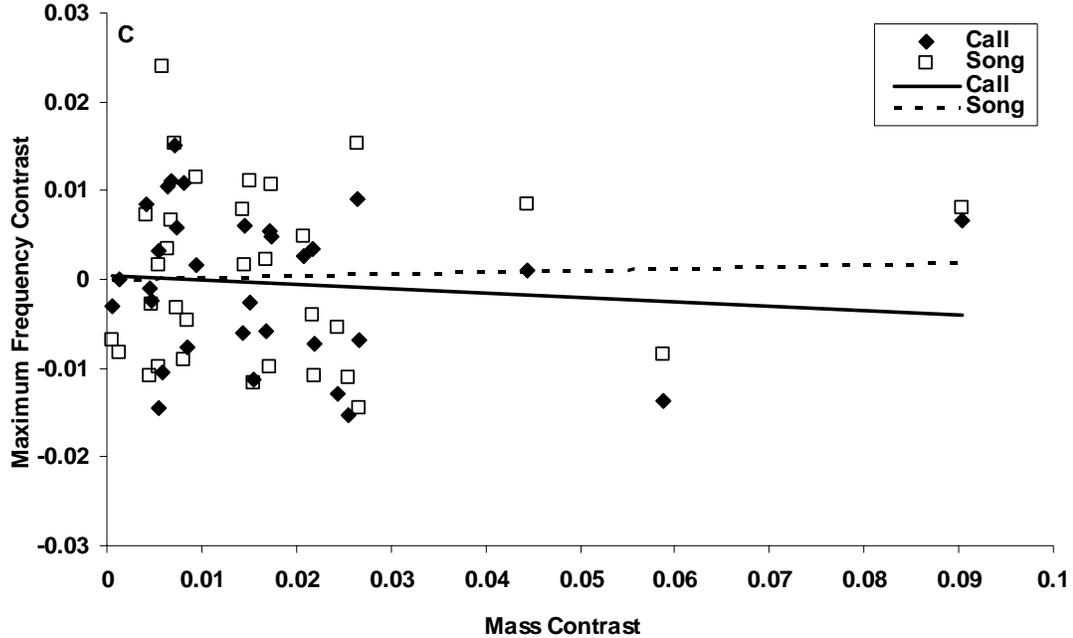
Our analysis showed that flight-call frequencies are significantly different from song frequencies. We found that CALLMAX (Mean, SD = 9.13 ± 0.97 kHz) and CALLMIN (Mean, SD = 5.56 ± 0.98 kHz) are significantly higher in frequency than SONGMAX (Mean, SD = 7.8 ± 1.17 kHz) and SONGMIN (Mean, SD = 3.51 ± 1.28 kHz) for 33 species of wood-warblers, respectively ($P < 0.0001$ for both analyses, see Table 6.2). We also found a significant difference in bandwidth frequency between songs and calls ($P < 0.01$, see Table 6.2), with CALLBAND (Mean, SD = 3.58 ± 1.15 kHz) significantly narrower than SONGBAND (Mean, SD = 4.29 ± 1.08 kHz). Additionally, a significant positive relationship exists between CALLMAX and SONGMAX ($P < 0.01$; Figure 6.4c); however, we found no significant relationships between calls and songs for minimum frequency or bandwidth (Figure 6.4a, 6.4b).

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Table 6.2. Means, standard deviations, and paired *T*-test results for maximum, minimum, and bandwidth frequencies (kHz) for flight-calls and songs of 33 species of wood-warblers.

	Call	Call SD	Song	Song SD	t-statistic	P-value
Maximum Frequency*	9.13	0.97	7.80	1.17	6.86	<0.0001
Minimum Frequency*	5.55	0.98	3.51	1.28	8.25	<0.0001
Bandwidth Frequency*	3.58	1.15	4.29	1.08	-2.72	0.0052

*kHz.
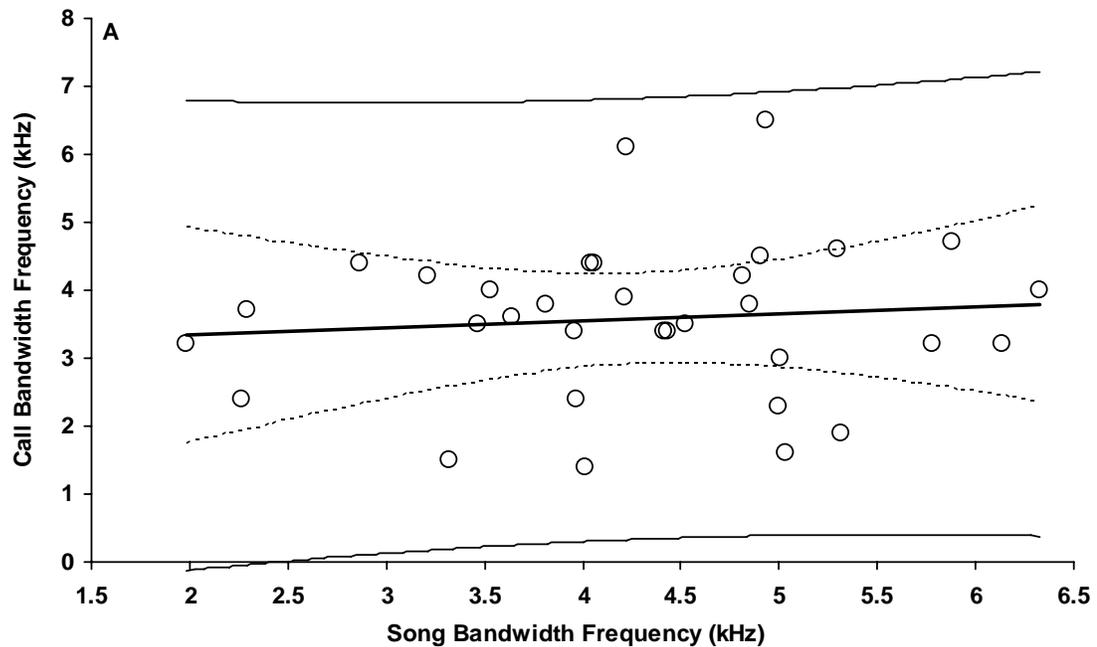
Figure 6.4. Flight-call frequency (kHz) on song frequency (kHz) (A) Bandwidth. Regression Line: y = -0.11x + 3.12; r^2 = 0.01; *P* = 0.5786 (B) Minimum. Regression Line: y = 0.18x + 4.94; r^2 = 0.05; *P* = 0.1993 (C) Maximum. Regression Line: y = 0.39x + 6.09; r^2 = 0.22; *P* = 0.006.

Figure 6.4 (Continued).
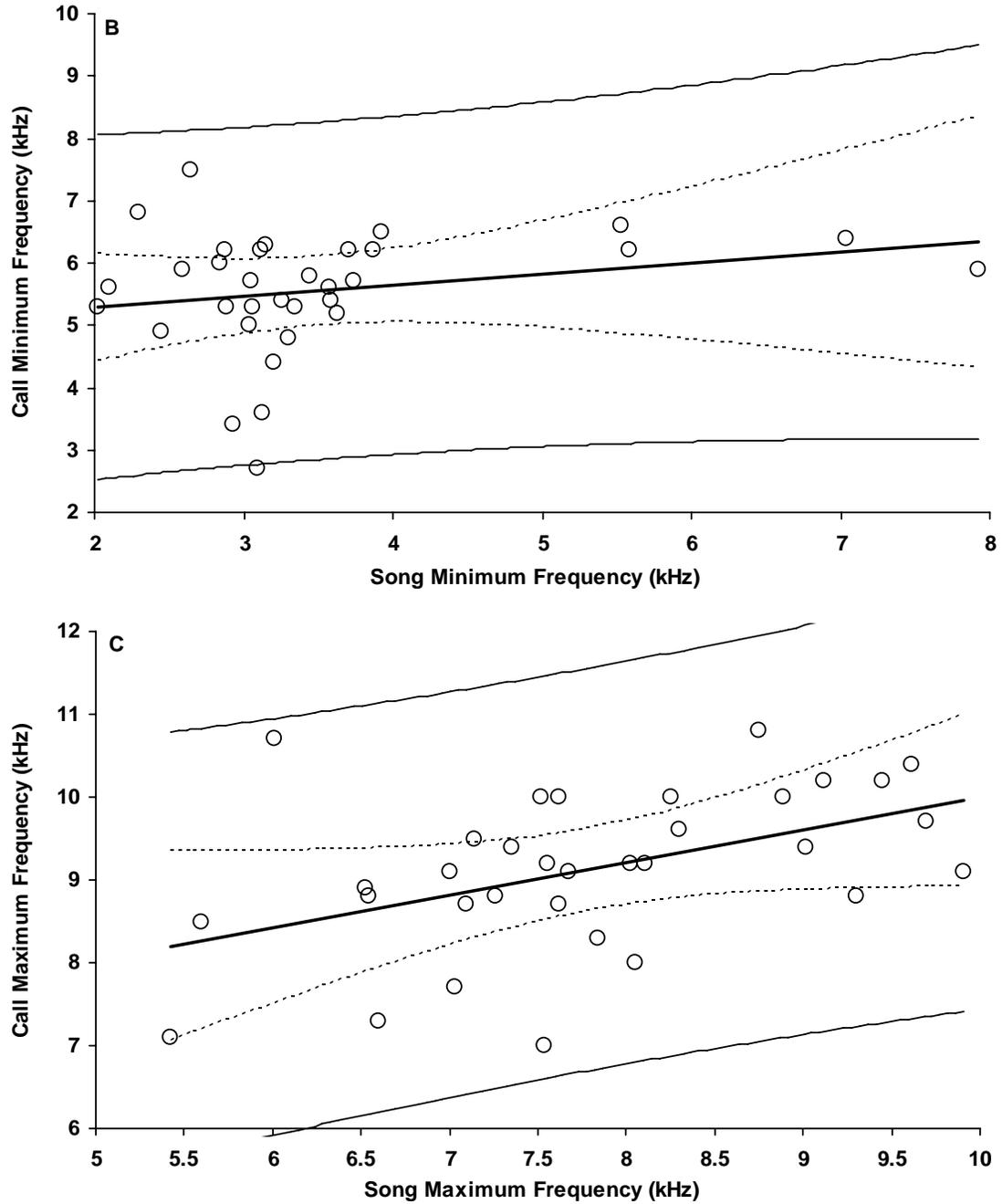
Discussion

In both phylogenetically controlled and uncontrolled analyses we did not find

significant relationships between body mass and flight-call or song frequencies or bill

length and flight-call or song frequencies. Our results are surprising, because for many avian groups changes in frequencies and changes in body mass or bill length are correlated, such as negative relationships between body mass and song frequencies (e.g., Wallschläger 1980) and between bill length and song frequencies (e.g., Palacios and Tubaro 2000). Vocal tract features associated with the production and transmission of a vocalization often are correlated positively with body size (e.g., thicker syringeal membranes associated with larger body mass allow larger birds to produce lower frequency vocalizations). Furthermore, constraints imposed by acoustical short-circuiting at longer wavelengths relax for larger- relative to smaller-bodied birds (see Bradbury and Vehrencamp 1998). However, bird song could escape the constraints of body mass in at least two ways. Ryan and Brenowitz (1985) suggest that the mass of vibrating structures could increase independently of body size, as has occurred in some species of anurans (Ryan 1988). Additionally, changes in suprasyringeal characteristics of the vocal tract such as bill gape correlate with changing song frequencies (Westneat et al. 1993; Podos et al. 1995; Podos 2001).

The 33 species of wood-warblers in this study exhibit small ranges, low coefficients of variation, and low variances for morphological characters when compared to similar studies of other avian taxa (Table 6.3). Previous studies that found significant negative relationships between song frequency and body mass (e.g., Tubaro and Mahler 1998, Palacios and Tubaro 2000) have larger ranges (one order of magnitude: see Table 6.3), higher coefficients of variation, and greater variance (two orders of magnitude: see Table 6.3) for body mass. Additionally, negative relationships between song frequency and bill length (Palacios and Tubaro 2000) that are nearly significant also show greater variation for bill length (Table 6.3). This evaluation suggests that the lack of significant correlation between morphology and vocal (i.e., song and call) frequencies in wood-warblers relates to low morphological

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variation in our sample. Including non-parulid relatives would incorporate a greater range of morphological variation; however, the 33 species of wood-warblers in this study represent almost all the variation within the parulid group for the characters we analyzed (e.g., Dunning 1993, Birds of North America series). Furthermore, maintaining the current scope of our analysis allows us to ask a biologically relevant question when considering such low morphological variation. If body mass and bill length do not strongly influence the frequencies of flight-calls in wood-warblers, what factors do?

Table 6.3. Comparison of species groups, presence of significant relationship trends, sample sizes, means, minima, maxima, ranges, coefficients of variation and variances among four studies of relationships between morphology and vocal frequencies.

Study	Species group	Significant trends	N[c]	Mean	Minimum	Maximum	Range	CV	Variance
Tubaro and Mahler 1998[a,d]	Doves	Yes	44	159.01	30.00	320.00	290.00	0.52	6829.91
Palacios and Tubaro 2000[a,d]	Woodcreepers	Yes	39	54.05	14.30	155.00	140.70	0.60	1066.12
Palacios and Tubaro 2000[b,d]	Woodcreepers	No	39	35.14	12.00	76.00	64.00	0.42	213.02
Farnsworth and Lovette[a,d,e]	Wood-warblers	No	33	11.61	7.30	19.80	12.50	0.29	11.07
Farnsworth and Lovette[b,d,e]	Wood-warblers	No	33	9.89	6.10	14.30	8.20	0.17	2.72

a) Body mass (g).
b) Bill length (cm).
c) Number of species.
d) Song frequencies.
e) Flight-call frequencies.

Major gaps exist in our understanding of flight-calling behavior. No studies have examined the range of distances over which birds use flight-calls for communication, the properties of the timing and control of the formative stages of flight-calls, or the seasonal pattern of flight-call vocalizations. Furthermore, virtually nothing is known about the constraints associated with production of different types of sound during flight. However, although these basic biological, behavioral, and evolutionary data are generally lacking, we can speculate about selection pressures for optimal sound transmission. Optimal sound transmission could play a role in determining species-specific flight-call frequencies. For example, ecological properties of breeding or wintering habitats could cause divergence of flight-call frequencies if warblers use flight-calls often during non-migratory periods. If flight-calls originated as a means of communication near ground-level (i.e., from the ground to tree canopy level), selection could drive divergence among habitats because reverberation, amplitude modulation rate, and the consistency of transmission are important sonic properties defining vocalizations; these properties have been shown to vary with selection pressures among habitats in other taxa (Brown and Hanford 1996, 2000; Badyaev and Leaf 1997; Slabbekoorn and Smith 2002a; Bertelli and Tubaro 2002). Birds living in more open habitats tend to have higher song frequencies and wider bandwidth than those living in more closed habitats (e.g., Morton 1975; Wiley 1991). Ryan and Brenowitz (1985) suggest that properties of ambient noise spectra in different habitats (e.g., the frequencies of wind-generated or insect-generated noise) could force selection for frequencies within specific frequency windows (i.e., quiet regions of the spectra without much ambient noise). Furthermore, if flight-calls are learned behaviors, the influence of vegetation structure and ambient noise spectra could play an important role in the ontogeny of flight-calls (Hansen 1979, Nottebohm 1985). We found a significant relationship between maximum flight-call frequency

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and maximum song frequency both in phylogenetically controlled and uncontrolled analyses and in mass controlled and mass uncontrolled analyses. Therefore, it is possible that limitations in the propagation of frequency maxima are similar for flight-calls and songs.

Selection pressures based on properties of the atmosphere during migration might similarly exist if communication by flight-calls primarily occurs aloft. Our results suggest that a frequency window for communication that differs from song frequency windows might exist for flight-call frequencies. Maximum, minimum, and bandwidth frequencies of flight-calls differ significantly from those frequencies of song, with higher maxima, higher minima, and narrower bandwidths. Additionally, in phylogenetically uncontrolled analysis the slopes of the regression lines for flight-call bandwidth and song bandwidth against body mass are significantly different (PROC MIXED: $F = 4.95$, $P = 0.03$), although this relationship is not significant in phylogenetically controlled analysis (PROC MIXED: $F = 2.79$, $P = 0.10$). It is also possible that ambient noise spectra similar to those discussed by Morton (1975), Ryan and Brenowitz (1985), and Slabbekoorn and Smith (2002b) occur in different atmospheric strata (e.g., as a result of temperature inversions and humidity gradients) and that different spectra require different solutions to communicating within certain altitudinal strata (e.g., different frequency windows generate different frequency calls; choosing optimal strata for communicating based on call frequencies). Flight-calls and songs may also experience different selection pressures related to encoding information in the respective signals: given constraints on production and transmission, warblers may use larger bandwidths with lower maximum and minimum frequencies in songs to encode more detailed information in songs.

Constraints for optimal in-flight communication toward certain frequencies (i.e., higher frequencies in warbler flight-calls) could shape convergent vocalizations

that travel best in specific atmospheric and microclimatic strata or avoid specific ambient noise spectra (e.g., Rundus and Hart 2002, Larom 2002, Slabbekoorn and Smith 2002a, b, Slabbekoorn and Peet 2003). Because signals indicative of longer range communication are lower in frequency (e.g., Larom 2002, Larom et al 1997, Marten and Marler 1977), the pattern of higher frequencies in flight-calls relative to songs suggests that flight-call vocalizations might be used primarily for short distance communication. Additionally, flight-calls and songs differ dramatically in duration (call mean $\pm$ SD: 50.88 $\pm$ 11.90 ms; song mean $\pm$ SD: 1612.73 $\pm$ 465.31 ms); such short durations for flight-calls also suggest that strong constraints (e.g., physiological or environmental) are operating on the evolution of flight-calls.

Testing the aforementioned functional hypotheses will require transmission experiments and detailed atmospheric and microclimatic analyses both near ground-level and above ground in flight strata. In addition to assessing what frequencies travel best in ambient noise, understanding what frequencies are perceived best in ambient noise is probably highly relevant in seeking a more complete understanding of variation in flight-call frequencies. Recent studies show that different species of birds have different detection thresholds for signals in ambient noise (Klump 1996, Langemann et al 1998) as well as different hearing thresholds (e.g., Dooling 1982, Dooling and Saunders 1975, Okanoya and Dooling 1987). Differences in the perceptual abilities, detection thresholds, and hearing abilities among species could play important roles in determining variation in flight-call frequencies.

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CHAPTER SEVEN: THE EVOLUTION OF SIMPLE AVIAN VOCALIZATIONS:
PHYLOGENETIC AND ECOLOGICAL EFFECTS ON INTERSPECIFIC
VARIATION IN FLIGHT-CALLS[*]

Abstract

Many avian vocalizations are highly complex traits that vary substantially within and
among species in acoustic properties and behavioral context, and this complexity of
structure and function has bedeviled phylogenetically informed studies of song
evolution. In comparison to complex songs, flight-calls – short, mostly single-syllable
vocalizations given primarily during sustained flight – are structurally simple
vocalizations with low intraspecific variation and a high likelihood of evolutionary
and behavioral homology among related species. Additionally, the simple structure of
flight-calls is well suited for comparison by techniques such as spectrographic cross-
correlation and ordination methods that are more objective and repeatable than are
most traditional means of comparing animal sounds. We used a multilocus phylogeny
of 47 North American wood-warblers (Aves: Parulidae) to quantify the extent of
phylogenetic signal in flight-call spectrographic characteristics and to remove
phylogenetic effects when testing for associations among flight-call attributes,
behavioral characters related to migration strategies, and ecological habitat variables.
We also employed a quantile regression and null model approach to compare a matrix
of interspecific phylogenetic divergence with indices of the corresponding acoustic
differences derived from spectrographic measurements of flight-calls. Nearly half (17
of 41) of the measurements of flight-call energy distributions and flight-call syllable
structure exhibited significant associations with phylogeny. Controlling for
phylogenetic effects, flight-calls with high acoustic frequencies were significantly

[*] Andrew Farnsworth, Department of Ecology and Evolutionary Biology, Cornell Laboratory of
Ornithology, Cornell University, Ithaca NY 14850; Irby J. Lovette, Evolutionary Biology Program,
Cornell Laboratory of Ornithology, Cornell University, Ithaca NY 14850.

associated with species occupying taller and more open forest canopies. Ecological properties associated with migratory and winter distributions did not exhibit significant correlations with flight-call characteristics. Potential differences exist in the evolutionary histories of structural and signal properties of flight-calls, suggesting that phylogenetic and ecological effects are present in these calls. The evolution of flight-call syllable structure may involve selection for species recognition, whereas adaptation to the acoustic environment likely has influenced the evolution of their spectral and temporal properties.

Introduction

Phylogenetic signal is apparent in the similarity of vocalizations within many groups of birds (Lanyon 1969, Payne 1986, Irwin 1988, 1996, Spector 1992, Martens 1996, Miller 1996, McCracken and Sheldon 1997, Price and Lanyon 2002). Even casual observers know that, in spite of their ecological differences, closely related species of birds often produce more similar vocalizations than do less closely related but ecologically sympatric species. However, comparative studies of interspecific variation in avian vocal signals have lagged behind the more thoroughly explored phylogenetic variation in plumage and other morphological signals (Badyaev and Hill 2003, Burt 2004, Allen and Omland 2004, Lovette 2004, Olson and Owens 2005, Weckstein 2005, Eaton 2006), and studies framing vocal behavior in explicit and robust evolutionary contexts remain rare.

Whereas intraspecific phylogeographic variation in vocal behaviors among populations is well documented (e.g. Wright and Wilkinson 2001, Nelson et al. 2004, Soha et al. 2004, Tack et al. 2005, Wright et al. 2005, Nicholls et al. 2006), past studies of interspecific variation in avian vocal variation have most often tested associations between vocal traits and ecological or morphological variables (Podos 1997, Slabbekoorn and Smith 2002 a,b, Slabbekoorn et al. 2002, Podos et al. 2004,

Podos and Nowicki 2004). For example, many species exhibit variation in the dominant frequency of male songs that parallels across-habitat variation in frequency-specific acoustic attenuation, with this frequency matching a seeming adaptation that broadens the transmission range of these acoustic signals (Morton 1975, Ryan and Brenowitz 1985, Wiley 1991). Nearly all of these previous comparative studies of avian vocalizations have addressed differences in songs (McCracken and Sheldon 1997, Palacios and Tubaro 2000, Mahler and Tubaro 2001, Bertelli and Tubaro 2002, Price and Lanyon 2002, Slabbekoorn and Smith 2002 a,b, Packert et al. 2003, Marler 2004, Seddon 2005), which are the most complex and individually-variable class of avian vocalizations (Peters et al. 1980, Marler and Pickert 1984, Macnally et al. 1986). Complex songs are a particularly challenging target for comparative analyses for two reasons. First, several groups of birds (including the oscine passerine songbirds, the clade comprising approximately 47% of extant avian species diversity; Ames 1971, Raikow 1982, Monroe and Sibley 1993, Barker et al. 2004) have a substantial learned component to their songs, leading to substantial phenotypic plasticity, local dialectical variation, cultural transmission of variation, and generally high rates of change (e.g. Nottebohm 1969, Baker 1975, Baptista 1977, Nelson 1999, Soha et al. 2004, Nichols et al. 2006). Second, the very complexity of these signals makes it difficult to decompose them into discrete characters, to assess the homology of acoustic characters, and to compare these traits among lineages.

The traditional method of dealing with this complexity has been to compare simple and easy to measure components of structural (e.g., minimum, maximum, or median frequency; duration) or syntactical (e.g., note and syllable order and diversity) variation. These simple metrics, however, do not capture much of the complex and sometimes-subtle information encoded in avian songs (e.g. changes in frequency, modulation, amplitude, note structure, syllable order; Kroodsma and Canady 1985,

Kroodsma and Verner 1987, Lambrechts and Dhondt 1990, Goddard and Wiley 1995, Van Buskirk 1997, Molles and Vehrencamp 1999, Portelli 2004). A related methodological issue is that characterizing sounds via the visual inspection of spectrograms may not produce consistent or repeatable measurements across observers (Jones et al. 2001, Rendell and Whitehead 2003). Alternatively, more repeatable and objective methods are available, including spectrographic cross-correlation (Symmes et al. 1979, Clark et al. 1987, Cortopassi and Bradbury 2000, 2006), artificial-intelligence neural network (Placer and Slobodchikoff 2001, 2004), and information-criteria based analysis (Searby and Jouventin 2004, 2005). In addition, sound analysis programs exist that can measure digital representations of sounds (e.g. Raven: Charif et al. 2004; Sound Analysis: Tchernikovski et al. 2000; XBAT: Figueroa 2002). Several studies have compared visual, digital, and artificial intelligence methods (Nowicki and Nelson 1990, Baker and Logue 2003, Deecke and Janik 2006), but the message from such comparisons has not clarified the specifics of which method (or methods) are best (but see Chapter 5). Regardless of methodology, note diversity and syntactical complexity in bird songs can still confound analysis, even using automated and digital approaches.

Here, we investigate the evolution of acoustic signals in a group of 47 North American wood-warbler (Parulidae) species for which we have generated a robust multi-locus phylogeny (Lovette and Bermingham 2002, Lovette and Hochachka 2006). We avoid some of the issues that have previously bedeviled the phylogenetic analysis of avian vocalizations by (1) assaying variation in simple flight-calls rather than complex songs, and (2) employing a diversify of analytical techniques that include both traditional and newly developed quantitative methods for capturing and comparing interspecific variation in acoustic signals. Flight-calls are some of the simplest avian vocalizations. Among small-bodied passerines, flight-calls are

generally short and high in frequency (Evans and O'Brien 2002). Despite their commonly used descriptive name, "flight-calls" are not exclusively associated with flight, rather with a diverse array of behaviors ranging from nocturnal migratory flights to family-group foraging. However, wood-warbler flight-calls comprise a single call-type that appears to be a homologous behavioral trait (deQueiroz and Wimberger 1993), most commonly given during periods of nocturnal migration (Evans and O'Brien 2002). Wood-warbler flight-calls differ significantly from other similarly short calls (such as alarm calls) in that flight-calls are generally much narrower in bandwidth. Although warbler flight-calls exhibit intraspecific variation in several spectral and temporal properties, variation at the interspecific level is substantially greater (Chapter 4).

We use several complementary methods to quantify differences among the flight-calls of warbler species and to test hypotheses about the association of flight-call attributes with ecological and morphological traits. We first compare calls using spectrographic cross-correlation and energy-distribution measurements from spectrograms in conjunction with statistical ordination techniques. These comparisons allow us to characterize both the syntactical properties of sounds (cross correlation, typically used to study vocal behaviors and variation among individuals and populations; Gaunt et al. 1994, Baker and Logue 2003, Cortopassi and Bradbury 2006); and the structural properties of sounds (energy-distribution measurements, typical used to study ecological and environmental relationships aspects of vocal behavior ()). Few studies have used both types of characters simultaneously (e.g., Baptista and Morton 1982, Anderson and Conner 1985), despite the possibility that choosing a single character type may not represent a comprehensive view of acoustic divergence (for example, one that depends on genes and habitat; Slabbekoorn and Smith 2002 b). We then compare acoustic and genetic distances using randomization

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methods and independent contrast analysis to explore whether genetic distance and acoustic distance are significantly related. We test the null hypothesis that acoustic and genetic distances are not significantly autocorrelated; rejecting this hypothesis would indicate the presence of phylogenetic signal in interspecific flight-call variation. We also test null hypotheses involving the comparison of both syllabic and structural measurements of flight-calls against one another and against ecological characters. Wood-warblers have been the focus of much ornithological attention, and a wealth of ecological and phylogenetic information about them is available (e.g. Chapman 1907, MacArthur 1958, Lovette and Bermingham 2002, Lovette and Hochachka 2006). Rejecting any of these hypotheses would indicate significant correlation to ecological characters, potentially separating and clarifying the roles of phylogeny and ecology in shaping these vocalizations.

Methods

Flight-call recordings

Our sample of 47 species represents all regularly occurring migrant warblers in North America. We supplemented published recordings (Evans and O-Brien 2002) of 38 Eastern species with our own recordings of an additional 9 species from free-flying wild and captive birds in the western United States (Lanzone and Farnsworth in preparation, Chapter 4). Birds produce flight-calls most commonly during nocturnal migration, so we analyzed only those calls recorded from free-flying birds when direct visual individual confirmation was possible or from captive birds held in specially designed acoustic cones to ensure that all calls were correctly identified. Several publications provide detailed summaries of these recording methods (Evans and O'Brien 2002, Larkin et al. 2002, Farnsworth et al. 2004, Farnsworth 2005, Lanzone and Farnsworth in preparation).

We recorded flight-calls at 22,050 kHz, as 16-bit .wav files using a pressure zone microphone for recording captive birds (Evans and Mellinger 1999, Evans and Rosenberg 2000, Farnsworth et al. 2004) and a shotgun microphone for recording free-flying birds (Sennheiser MKH-70, www.sennheiser.com). We used only those published vocalizations with sampling rates and accuracies consistent with those of our own field recordings (see Evans and O'Brien 2002 for rate and accuracy data). We computed all spectrograms with identical parameters (Hamming window, 87.5% overlap, 256-point FFT, 256-point frame length) using Raven 1.2.1 (Charif et al. 2004) and editing flight-call spectrograms such that flight-call samples contained approximately 20-40 ms initial and terminal portions of ambient noise that were not part of the call. We filtered frequencies below 1 kHz and excluded any flight-calls if spectrograms contained noise that interfered with the call signal. We measured acoustic features of flight-calls using a spectrographic cross-correlation algorithm (SPCC, Cortopassi unpublished) and XBAT 0.6.3 (www.xbat.org; Figueroa 2002).

Analysis of spectrographic properties of flight-calls

We required single values from each species to compare the typical flight-call parameters with ecological and genetic characters. However, each species was represented by a set of flight-calls that differed slightly from one another, owing to differences in the recording environment and inter-individual call variation. Therefore, we used correlation matrices to identify a typical "template" flight-call that best captured the variation in the intraspecific samples for each species. This approach allowed us to select the single flight-call per species that was most representative of our entire sample of that species' flight-calls.

We identified these template flight-calls by using an SPCC algorithm (Cortopassi unpublished data; for a similar program application, see Cortopassi and Bradbury 2000, 2006) that calculates peak correlation coefficients for all pair-wise

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correlations of flight-calls and generates a matrix of these values. The algorithm

convolves the two spectrogram matrices over each other in both time and frequency to

compute their fit (Clark et al. 1987, Cortopassi and Bradbury 2000; also see ambiguity

functions, Woodward 1953, Angelari 1970). As such, SPCC incorporates spatial and

temporal elements of spectrograms in a repeatable and objective way to generate a

matrix of similarity values (correlations) for each pair of signals in an ensemble, rather

than using a suite of more subjective individual measures of time and frequency to

characterize a signal (Clark et al. 1987, Cortopassi and Bradbury 2000, Baker and

Logue 2004). Whereas some previous applications of SPCC convolved only on a

single scale (e.g. time scale, Cortopassi and Bradbury 2000), convolution on both

scales was necessary in our analyses because flight-call similarity across individuals

and species may shift in both time and frequency (i.e., a pair of flight-calls may show

displacement on the time axis and the frequency axis or differences in both of these

dimensions).

The SPCC program checks that all samples have the same sampling rate.

Before computing the spectrograms for a pair of samples, the program equalizes the

length of the shorter sample duration sample to match the longer sample duration, a

process called zero-padding (Qi 1992, Cortopassi and Bradbury 2000, Lucero and

Koenig 2000). For all correlation calculations, we used the given spectrographic

frequency and filter resolution of the Hamming window and frequency convolution of

± 1000 Hz for frequencies (based on previous visual inspection confirming that calls

did not vary in center and bandwidth frequency by more than this amount). These

settings account for variation in the duration and frequency of a flight-call signal, and

they are necessary to align the time-frequency spectrograms of two sounds. SPCC of

each species' flight-calls yielded 47 different species-specific matrices from which the

algorithm extracted the peak pair-wise correlation coefficients for each flight-call. We

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chose the flight-call for each species with the highest correlation coefficient, or the flight-call that correlated most highly with other calls. Using these methods, we generated a sample of 47 flight-call recordings, one flight-call "template" for each of the 47 species.

We also recorded measurements from the spectrograms of the 47 flight-calls we chose in the aforementioned analysis with an automatic feature extraction process implemented in XBAT (www.xbat.org; Figueroa 2002) that used the given spectrographic frequency and filter resolution of the Hamming window. This set of measurements was a subset of and based upon those available in ACUSTAT (Fristrup and Watkins 1992, 1993). The measurement process is a simple procedure that involves selecting a signal of interest (in this case, a flight-call) by drawing a box around a flight-call onscreen using the cursor. This box represents the bounds within which the feature extraction process occurred, extracting measurements automatically and logging these in a data file. For these analyses, each spectrogram's amplitude-time envelope (aggregate power as a function of time) and power spectrum envelope (power as a function of frequency) were treated conceptually as probability density functions in the time and frequency dimensions, respectively (see Chapter 5).

We used 50% of the total flight-call signal energy in the amplitude-time and power spectrum envelopes to measure statistical quartiles and inter-quartile ranges, where "median" (Me) is the 50th percentile, "initial" (P1) is the 25th percentile, "terminal" (P2) is the 75th percentile, "inter-percentile range" (W) encompasses 50% of the signal energy distribution, and "skewness" is (Me-P1)/W. We use the highest and lowest values that bound the top 50% of the probability distribution of the amplitude-time or power spectrum envelope to calculate the spread (highest minus lowest) in the distribution, which is then used to calculate "skewness" in the amplitude-time or power spectrum envelope. We also use equivalent width to

describe amplitude-time (equivalent-duration) and power spectrum (equivalent bandwidth) data (see Chapter 5).

XBAT extracted measurements to quantify a signal's compactness by sorting the amplitude-time and power spectrum envelopes, referred to as concentration measures (see Chapter 5). The value of concentration in relation to interpercentile range reveals how densely or loosely the signal's energy is distributed. Details of this procedure are available from the Cornell Laboratory of Ornithology Bioacoustic Research Program (Cortopassi, www.birds.cornell.edu/brp/research/algorithms/RSM.html.)

There were 28 measurements taken: 16 from the amplitude-time and power spectrum envelopes and 12 concentration measures derived from sorted probability density functions of the time-varying features in the spectral frames, 9 from the amplitude-time envelope and 3 from the power spectrum envelope. The following are brief descriptions for each of these 28 ACUSTAT measurements (see also Table 7.1)..

1) Median, equivalent-duration and skewness of the amplitude-time envelope (MeENV, EqENV, and SkENV, in seconds);

2) Median, equivalent-bandwidth and skewness of the power spectrum envelope (MePS, EqPS, and SkPS, in Hz);

3) Median, equivalent-width and skewness of the discrete Fourier transform of the amplitude-time envelope, computing the frequency spectrum of the amplitude-time envelope and measuring from that (MeENVM, EqENVM, and SkENVM, in Hz);

4) Median, equivalent-width and skewness of the discrete Fourier transform of the median frequency contour from the amplitude-time envelope weighted by ¼ power of the amplitude-time envelope (MeAFM, EqAFM, and SkAFM in Hz);

5) Attack fraction (ATTACKFR, unitless), fraction of data blocks that have higher energy than the previous block, similar to the musical definition of a crescendo;

6) Up-sweep fraction (UPSWFR, unitless), fraction of data blocks that have higher frequency (based on the peak frequency contour) that the previous block;

7) Up-sweep mean (UPSWM, in Hz), average slope of the peak frequency contour;

8) Sweep magnitude (SWMAG, in Hz), sum of the absolute value of the derivative of the peak frequency contour;

9) Median, spread and skewness of the median-frequency contour (MeFMED, EqFMED, and SkFMED, in Hz), where FMED is the vector of the median-frequency values in each spectral frame of the power spectrum (Chapter 5);

10) Median, spread and skewness of the frequency-concentration contour (MeFCC, EqFCC, and SkFCC, in Hz), where FCC is the vector of the number of bins needed to accumulate 50% of the total energy in the sorted energy distribution for each spectral frame;

11) Median, spread and skewness of the equivalent-bandwidth contour (MeEBC, EqEBC, and SkEBC, in Hz), where EBC is the vector of equivalent-bandwidth values for each spectral frame;

12) Median, spread and skewness of the frequency-skewness contour (MeFSKEW, EqFSKEW, and SkFSKEW in Hz), where FSKEW is the vector of skewness values for each spectral frame;

We performed analyses with these variables in addition to principal components (next section) because we wanted to maintain all original variation in measurements; some percentage of this variation (in our case, approximately 25%, next section) is lost during principal component analysis.

Eigenvalue-based dissimilarity values for flight-call measurements

We used the same SPCC algorithm to generate an interspecific correlation matrix for the 47 flight-call template spectrograms (Cortopassi, unpublished data, Cortopassi and Bradbury 2000). Following the same methods that we used for generating the flight-call templates, we cross-correlated the flight-calls of 47 species to produce peak pairwise correlation coefficients. We also used the SPCC algorithm to perform principal coordinate analysis on the interspecific correlation matrix to extract ordinated, independent measures similar to axes produced by principal component analysis (Gower 1966, Neff and Marcus 1980, Gower 1987, Legendre and Legendre 1998, Everitt and Dunn 2001, Cortopassi and Bradbury 2000, Baker 2004). Principal coordinate analysis, in conjunction with SPCC, produces a reduced set of independent measures, albeit latent measures (unlike principal component analysis in which original relationships are retained, principal coordinates usually lack associations with known variables), useful for visual groupings of sounds and for measuring

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associations with contextual (e.g. biological and behavioral) variables. We retained principal coordinates using a stopping-rule with which we evaluated plots of consecutive eigenvalues ("scree-plots") to determine the number of axes to retain – extract the number of eigenvalues with the largest values associated with the steepest slope of the line of plotted eigenvalues (Gauch 1982, Cliff 1988, Fava and Velicer 1992, Jackson 1993, Peres-Neto et al. 2003). We extracted 5 principal coordinates (PCOs) that represent approximately 93% of the original variation among flight-call cross-correlations (Table 7.2). We also performed a principal component analysis on our raw energy-distribution variable database to reduce the complexity. Many highly correlated (and hence semi-redundant) energy distribution measurements were recorded from each of the 47 flight-call spectrogram templates (Chapter 5, Chapter 4). We used the entire suite of these measurements to ordinate a series of new eigenvalue axes that maintained the original relationships among all variables. We used the same "scree plot" stopping rule to retain principal components. We extracted 5 principal components (PCAs) that represent approximately 75% of the original variation among the sound measurements and defined PCAs by the variables with absolute values of factor loadings greater than 0.71 (Table 7.2).

From PCO and PCA axes we calculated Euclidean distance matrices (PROC DISTANCE; SAS Institute 1999), yielding a 47 species-by-47 species matrix containing 1081 pair-wise values for each set of ordinated axes with each species pair represented by a single distance measurement. These distance matrices represent dissimilarity values, indicating how far apart are the species in each pair-wise value. These dissimilarity matrices represent "acoustic distance" in the same sense as genetic dissimilarities represent "genetic distance (see section on genetic data)."

Table 7.1. XBAT measurements of aggregate time and frequency distributions recorded from each flight-call spectrogram summarized from Fristrup and Watkins (1992,1993) and Figueroa (2002) documentation.

Measurement	Analogous ACUSTAT Measurement	Description	Estimates
1) Amplitude Time Envelope (ENV, in sec)	Energy Envelope (ENV)	Amplitude time envelope from the aggregate energy envelope	Median (Me), Equivalent Duration (EQD), Skewness (Sk)
2) Power Spectrum Envelope (PS, in Hz)	Frequency Bandwidth (TS)	Power spectrum envelope from the aggregate power spectrum	Median (Me), Equivalent Bandwidth (EQB), Skewness (Sk)
3) Frequency Spectrum of Amplitude Time Envelope (ENVM, in Hz)	Amplitude Modulation (AM)	Discrete Fourier transform of the amplitude-time envelope, computing the frequency spectrum of the amplitude-time envelope and measuring from that	Median (Me), Equivalent Bandwidth (EQB), Skewness (Sk)
4) Median Frequency Contour Spectrum of Amplitude Time Envelope (AFM, in Hz)	Amplitude-Frequency Modulation (AFM)	Discrete Fourier transform of the median frequency contour from the amplitude-time envelope weighted by ¼ power of the amplitude-time envelope	Median (Me), Equivalent Bandwidth (EQB), Skewness (Sk)
5) Attack Fraction (ATTACKFR, unitless)	Attack Fraction (ATTACKFR)	Fraction of data blocks that have higher energy than the previous block	
6) Up-sweep Fraction (UPSWP, unitless)	Up-sweep Fraction (UPSWFR)	Fraction of data blocks that have higher frequency (peak frequency contour) that the previous block	
7) Up-sweep Mean (UPSWM, in Hz)	Up-sweep Mean (UPSWM)	Average slope of the peak frequency contour	
8) Sweep Magnitude (SWMAG, in Hz)	Sweep Magnitude (SWMAG)	Sum of the absolute value of the derivative of the peak frequency contour	
9) Median Frequency Contour (FMED, in Hz)	Median Frequency Contour (FMED)	The vector of the median-frequency values in each spectral frame of the power spectrum	Median (Me), Spread (Sp), Skewness (Sk)
10) Frequency Concentration Contour (FCC, in Hz)	Frequency Concentration Contour (CONC)	The vector of the number of bins needed to accumulate 50% of the total energy in the sorted energy distribution for each spectral frame	Median (Me), Spread (Sp), Skewness (Sk)
11) Equivalent Bandwidth Contour (EBC, in Hz)	Equivalent Bandwidth Contour (MODW)	The vector of equivalent-bandwidth values for each spectral frame	Median (Me), Spread (Sp), Skewness (Sk)
12) Frequency Skewness Contour (FSKEW, in Hz)	Frequency Asymmetry Contour (FASYM)	The vector of skewness values for each spectral frame	Median (Me), Spread (Sp), Skewness (Sk)

Parenthetical notation represents the abbreviations used in XBAT. Estimates refer to order statistics used to describe measurements.   Measures and estimates (for example FMED and ME = FMEDME) describe the acoustic characteristics of flight-calls measured

Table 7.2. Eigenvalue-based measurements derived from principal coordinate (PCO) and principal component (PCA) analysis.

Analysis	Variable	Factor1	Factor2	Factor3	Factor4	Factor5
PCO	Proportion of Variance Explained	57%	18%	10%	5%	3%
	Cumulative Variance Explained			93%		
PCA	Proportion of Variance Explained	26%	18%	14%	9%	7%
	Cumulative Variance Explained			74%		
PCA	Amplitude Frequency Modulation Median					0.916
	Amplitude Frequency Modulation Mode Width					0.7954
	Amplitude Modulation Median				0.8701	
	Amplitude Modulation Mode Width				0.8805	
	Frequency Concentration Contour Median	0.876				
	Frequency Concentration Contour Spread	0.848				
	Energy Envelope Asymmetry			0.7816		
	Energy Envelope Median				-0.8084	
	Energy Envelope Mode Width			0.8045		
	Median Frequency Contour Median		0.95			
	Equivalent Bandwidth Contour Median	0.85				
	Equivalent Bandwidth Contour Spread	0.787				
	Sweep Magnitude	0.857				
	Median Frequency		0.97			

PCO factors show the axes extracted from a flight-call SPCC matrix, the percentage of variance explained by each axis, and the cumulative percentage of variance explained by all axes. PCA factors show the axes extracted from a flight-call energy-distribution measurement matrix, the variance explained by each axis, and the cumulative percentage of variance explained by all axes.

Additional measurements of flight-call spectrograms

We also recorded some traditional temporal and spectral measurements from flight-call spectrograms using visual inspection. Many studies using spectrograms as a basis for assessing differences in sounds record duration and frequency measurements based on visual inspection. Despite an inherent subjectivity to visual inspection, convergent patterns in the ways that observers classify similarity suggest that some consistency may exist in visual methods (Cortopassi and Bradbury, Jones et al. 2001, Rendell and Whitehead 2003). For 33 species, we used previously published data on maximum, minimum and bandwidth frequencies and duration (Farnsworth and Lovette 2005). We recorded these measurements for the additional 14 species in our sample that were not available from this study by inspecting spectrograms visually and recording the measurements following a previous published methodology (methods: p. 338, Farnsworth and Lovette 2005).

In addition to the suite of aforementioned continuous measurements from visual inspection, we recorded discrete, qualitative measurements of flight-call spectrograms to describe additional features that continuous, energy distribution measurements may not have captured. Although SPCC uses many discernible structural elements, it is not clear whether SPCC assesses all possible elements for discerning differences in flight-calls. The visual approach using discrete measurements may better approximate the SPCC approach than it approximates the energy-distribution approach. As such, these measurements are more similar to syllable structure of flight-calls (spectrographic "shape" from SPCC) than they are similar to spectral and temporal properties. However, SPCC does not identify what features compose the measurements that correlate among calls; nor do energy-distribution measurements capture this variation in syllables. We defined four characters to describe syllable structure (Table 7.3). Sweep describes in five

categories the slope of the frequency energy as depicted by spectrogram (for example, is the call rising or falling in pitch?). Modulation describes in three basic categories the oscillation of the frequency track (for example, is the call buzzy or pure tone?). Inflection describes a similar measurement to modulation only in terms of three categories of number of inflection points (for example, does the call have many inflection points or few?). Finally, type describes the basic shape of the call (for example, is it v-shaped or is it m-shaped?).

Ecological Data

We compiled ancillary information on ecological characteristics that may be related to variation in flight-call acoustic properties. These characteristics included previously published data, supplemented where necessary with additional observations of the authors (Table 7.3). We converted all ecological characteristics into continuous, quantitative measures. We used five variables derived by Van Buskirk (1997) that describe vegetation and moisture levels in preferred or most frequent warbler breeding habitats (supplemental information: Curson et al. 1994, Dunn and Garrett 1997, Gill and Poole 2004). The variables describing vegetation density, height, and type are: canopy density and canopy height, describing the thickness and height of tree canopy; understory density, describing the thickness of undergrowth and near-ground vegetation; and tree type, describing the primary leaf type of trees in warbler breeding habitat. The variable moisture describes the wetness of the habitat, including habitats with standing water (streams, bogs).

Table 7.3. Categories and coding for additional qualitative flight-call measurements and ecological characters.

Coding	Sweep	Modulation	Inflection	Moisture	Understory Density	Canopy Density	Canopy Height	Tree Type	Migration System	Migration Strategy	Winter Distribution
0	Both	Fine	Many	Dry	Dense	Dense	Low	Deciduous	East	All	Primarily Central American
1	Ascending	Coarse	Intermediate	Intermediate	Intermediate	Intermediate	Intermediate	Mixed	West	Florida-West Indies	Primarily Caribbean
2	Descending	Heavy	Few	Moist	Open	Open	Tall	Coniferous	Both	Trans-gulf	South America
3	Flat	n/a	n/a	Stream/Bog	n/a	n/a	n/a	n/a	n/a	Circum-gulf	North American north of Isthmus of Tehuantepec
4	Variable	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	All

Flight-call measurements: sweep, the slope of the frequency of the flight-call defined in the broad manner one would describe the slope of a regression line (e.g. is the call rising in pitch?); modulation, the general degree of frequency modulation visible in the flight-call spectrogram (e.g. is the call buzzy?); inflection, the number of apparent slope changes (e.g. does the call have many inflection points?); type classifies each flight-call by its strident characters into shape categories (e.g. what is the overall pattern of the flight-call spectrogram?).

Ecological characters: habitat – moisture is a description of the wetness of a given habitat; understory density is the thickness of vegetation in the understory; canopy density is the thickness of vegetation at the highest parts of the canopy; canopy height is the height of the tallest parts of the canopy; tree type is a description of the leaf-fall tendencies of the primary trees in the preferred habitat; migratory traits: migration system is the basic geographic distribution pattern of the species migration routes; migration strategy is the choice of migration route and a general proxy for geographic location of movements; winter distribution is the center of abundance for species' non-breeding distributions.

We used four variables to describe preferred migration routes, based on current range maps (Gill and Poole 2004) and personal observations (AF). We defined these variables for warblers as follows: species migrating through Florida and the West Indies, species crossing the Gulf of Mexico, species migrating around the Gulf of Mexico, and species using all these routes. We also used three variables to describe the continental distribution of primary migratory movements of warblers (i.e., in what part of the continent does this species occur; Sibley 2000, Gill and Poole 2004): east of the Rocky Mountains, west of the Rocky Mountains, and both sides of the Rocky Mountains. Finally, we used five variables to describe primary wintering areas based on centers of abundance (Christmas Bird Count data: www.audubon.org/bird/cbc) and current distributions (Hilty and Brown 1986, Ridgely and Tudor 1994, Howell and Webb 1995, AOU 1998, Raffaele et al. 1998, Ridgely and Greenfield 2001, Hilty 2004). We defined these wintering areas as Central American, Caribbean, South American, North American (north of the Isthmus of Tehuantepec), and a distribution encompassing all of the above areas.

Phylogenetic Hypotheses and Comparative Methods

We generated a matrix of pairwise genetic distances for 47 species of wood-warbler species based on complete sequences of five mitochondrial genes (4116 nucleotides/ taxa): cytochrome oxidase I and II, NAH dehydrogenase II, and ATPase 6 and 8 (GenBank AY650182-AY650224; Lovette and Bermingham 2002, Lovette and Hochachka 2006). We assumed that mitochondrial DNA is accurate for representing relationships among warbler species and that introgression has not biased this representation. Evidence supports these assumptions, namely long species-specific mitochondrial lineages (Lovette and Bermingham 1999, 2002) and high congruence between mitochondrial gene trees and tree generated independently using nuclear genes (Lovette unpublished data). The distance matrix represents a large and

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comprehensive compilation of mitochondrial genes that is significantly longer than mitochondrial alignments used in many species-level phylogenies among birds (see additional details, for example, in Lovette 2004, Lovette and Hochachka 2006).

Although maximum likelihood methods are suitable for generating pair-wise distances for wood-warbler genetic data, we chose the more conservative method of generating distances using an ultrametric tree (accounting for possible non-constant mitochondrial divergence; Lovette and Hochachka 2006). By summing the branch lengths connecting each pair of termini (taxa), such a tree satisfies the following assumptions: all distances are positive; a distance between two points can be zero only if the points are the same; distances are symmetrical; no shortcuts exist in the tree (for example, the distance between points a-c cannot be longer than the sum of distances between points a-b and points b-c); and distance a-b cannot be larger than their distance to a third point (for example, the maximum of distances a-c and b-c). We derived the ultrametric tree using the following steps: importing a Bayesian topology as a constraint tree in PAUP* 4.0 (Swofford 2002); using an heuristic search algorithm to produce a clocklike topology; and conducting a maximum likelihood analysis using mean general time reversible (GTR)-g+I parameters derived from the Bayesian Markov chain Monte Carlo (MCMC) analysis (Lovette and Hochachka 2006). With the same long mitochondrial sequences we also reconstructed phylogenetic relationships, using MrBayes 3.0b4 (Huelsenbeck and Ronquist 2001) to generate analyses with a Bayesian MCMC approach under the GTR-g+I model of sequence evolution. We ran this approach for 5×10^6 generations, sampling every 2500 generations; we discarded the initial 1000 samples as burn-in (Huelsenbeck and Ronquist 2001).

Phylogenetic analysis using linear contrasts and quantile regression

The primary rationale for the use of phylogenetically based statistical methods is that phylogenetic signal, the tendency of genetically related organisms to resemble each other, is nearly ubiquitous (Felsenstein 1985, Pagel 1992, Jones and Purvis 1997, Blomberg et al. 2003, Hansen and Orzack 2005). As such, testing and subsequently controlling for phylogenetic signal is crucial to the outcome of a comparative study (Abouheif 1999, Blomberg et al. 2003, Rheindt et al. 2004). We imported a set of 2006 Bayesian phylogenies into Mesquite 1.11 (Maddison and Maddison 2006). We tested for phylogenetic signal in discrete characters against a null model in which the analysis software shuffled these characters randomly among taxa while holding the tree topology constant and then comparing the distribution of the number of state changes for observed versus randomized trees (Maddison and Slatkin 1991; after Farris 1970, Fitch 1971). In this approach, the smaller the actual number of changes relative to the number of changes expected in a random distribution, the more likely is a trait to be constrained by its phylogenetic history (Maddison and Slatkin 1991). We used Mesquite 1.11 (Maddison and Maddison 2006) to generate distributions of this difference by running 10000 iterations of the randomization. We also tested for phylogenetic signal (phylogenetic non-independence) by performing tests for serial independence (continuous characters; TFSI) and runs tests (discrete characters; RT) using the software package Phylogenetic Independence (PI, Abouheif 1999, Reeve and Abouheif 2003; also see Rheindt et al. 2004). TFSI and RT generate data to test the null hypothesis that a trait is not significantly associated with its phylogenetic history.

We performed independent contrasts for all characters that showed significant phylogenetic signal, using raw, non-contrasted data for characters that did not exhibit significant signal (Felsenstein 1985, Hansen and Orzack 2005). We used Mesquite

1.11 (Maddison and Maddison 2006) to generate linear contrasts. However, this approach allowed straightforward comparisons between pairs of traits that both showed either phylogenetic autocorrelation or lack thereof. Comparisons between one phylogenetically autocorrelated trait and one non-phylogenetically autocorrelated trait were more complex (Blomberg et al. 2003, Rheindt et al. 2004), requiring comparisons of linear contrasts using the resolved phylogenetic hypothesis for characters with phylogenetic signal and linear contrasts using a star phylogeny (completely unresolved tree) for characters that did not exhibit phylogenetic signal (Blomberg et al. 2003). We performed such comparisons of contrasts in Mesquite, but we used a MATLAB algorithm (PHYSIG; Blomberg et al. 2003) to generate the contrasts from the star phylogeny and then imported these into Mesquite.

We used several diagnostic plots to confirm that our analyses met the statistical assumptions inherent in performing evolutionary pairwise contrasts. These tests indicate whether the pattern of change is consistent with the Brownian-motion model of Felsenstein (1985), or if the approximate branch lengths are systematically biased (Diaz-Uriate & Garland 1996). We regressed absolute values of contrasts on the estimated nodal values to test for slopes significantly different from zero, indicative of a need to transform data. We also regressed the absolute values of standardized contrasts on age of the node and square root of the expected variance. In addition, because predicted values of the dependent variable are directly proportional to contrasts in the predictor variable, we regressed absolute values of the residuals against standardized contrasts in the independent variable. For all contrasts, we found no significant relationships across all diagnostic tests, suggesting that our data met statistical assumptions for pair-wise contrasts and did not require additional transformation.

We also explored the relationships between genetic distance and acoustic distance using linear quantile regression that describe the entire distribution of response variables at all predictor variable values (Koenker and Bassett 1978, Cade and Noon 2003, Lovette and Hochachka 2006). Standard linear regressions describing changes only in mean responses with a single, best-fit line may miss some relationships involving only a subset of taxon pairs (Cade and Noon 2003, Lovette and Hochachka 2006), and the mean relationship between acoustic and genetic dissimilarity could vary little even if some of the most dissimilar species pairs show strongly non-random correlations. We examined changes in the 5%, 50% (median) and 95% quantiles of acoustic measures as a function of genetic distance. The 5% quantile refers to the 95th percentile of acoustic dissimilarity, while the 95% quantile refers to the 5th percentile of acoustic dissimilarity – thus the 5% quantile examines the most acoustically dissimilar species-pairs and the 95% quantile examines the least acoustically dissimilar species-pairs. The 50% quantile (median) examines whether pervasive changes in acoustic dissimilarity exist along the entire distribution of genetic distances. Changes in each quantile represent changes across the entire distribution of genetic distance. These changes, however, do not imply that only 5% and 95% of the species-pairs varied with genetic distance. Rather, species-pairs that are most and least acoustically similar are more likely to exhibit such a relationship.

Relating acoustic dissimilarity to local ecological overlap and genetic distance

In addition to the previously described analysis of specific acoustic, genetic, and ecological characters, we also explored relationships that are more general between ecological overlap and acoustic dissimilarity. For these analyses, we used a slightly different method for quantifying acoustic dissimilarity. We counted the number of least squares mean energy-distribution measurements (generated in PROC MIXED, SAS Institute 2006) that differed significantly between flight-calls of 13 regionally

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sympatric species-pairs (data from a previous analysis, Chapter 4). We chose only 13

species-pairs because we wanted to explore the species-pairs representing sister-taxa

(two tips on the phylogeny connected by a single node). We tabulated the number of

significantly different mean values from 28 energy-distribution measurements for each

species-pair, and this sum became our measure of acoustic dissimilarity (Table 7.4).

A larger number represents a higher number of significantly different measures

between two members of a species-pair, indicating that the two species have flight-

calls that are more dissimilar. We related this number to a measure of ecological

overlap defined by probability of local co-occurrence. We used probability

dissimilarity data from a previous study that examined the relationship between

phylogeny and current species co-occurrences (see Lovette and Hochachka 200x for

additional and extensive detail). These data were generated from Breeding Bird

Survey (BBS) transects (Sauer et al. 2003) for quantifying co-occurrence in local

sympatry at a fine spatial scale (transects are approximately 40 km in length). Two

species co-occur if they are detected at the same BBS transect point. Probabilities

ranged from 0 to 1, 0 representing complete co-occurrence and 1 representing no co-

occurrence (Table 7.4). We plotted probability of local co-occurrence against acoustic

dissimilarity as defined by the number of significantly different measurements

between members of a species-pair.   We also plotted genetic dissimilarity (as defined

in the previous section) against this new measure of acoustic dissimilarity.

Critical values for multiple comparisons

We corrected for multiple comparisons using two different methods. A typical

Bonferroni correction for 41 dependent variables across 8 independent variables

would result in a critical value of $P = 0.0002$. However, Bonferroni correction may be

overly conservative (Westfall and Young 1993, Benjamini and Hochberg 1995,

Benjamini and Yekeulti 2001), so we used a less conservative method for multiple

comparison correction (after Holm 1979; applied in Farnsworth and Lovette 2005),

resulting in a critical value of P = 0.002 after accounting for sequential replications.

Any critical value 0.002 < P < 0.05 we consider a non-significant trend.

Table 7.4. Genetic distances and probabilities of local co-occurrence for 13 regionally
sympatric species of warblers.

Species Pair	Genetic Distance	Probability of Local Co-Occurrence	Differences
MGWA-MOWA	0.024	1	0
HEWA-TOWA	0.01	1	1
BWWA-GWWA	0.044	0.82609	3
BTYW-GRWA	0.014	0.95082	4
COYE-KEWA	0.092	0.94134	4
PIWA-YTWA	0.074	0.91304	5
LOWA-NOWA	0.078	1	5
PROW-SWWA	0.156	0.93711	5
BLPW-YEWA	0.052	0.76254	12
BBWA-BLBW	0.08	0.89944	15
LUWA-VIWA	0.016	0.97297	16
BTBW-MAWA	0.098	0.77702	18
CMWA-NOPA	0.1	0.83893	18

Correcting for morphology

We examined relationships between flight-call variables and body mass and bill length

to determine whether any corrections for these morphological measurements were

necessary. Although such correction is often important for song (body mass and song

frequencies often show negative correlations (Wallschläger 1980), we previously

showed this correction was not necessary for warbler flight-calls. However, this

species sample is larger, and we needed to determine whether the additional species

affected the need for correction. We used previously published data on body mass and

bill length from 33 species (Farnsworth and Lovette 2005 for data and sources) and we

gathered information for the additional 14 species from Dunning (1993) and the Birds

of North America series (Gill and Poole 2004). Although body mass exhibited significant phylogenetic autocorrelation ($P < 0.0001$), indicating a need to correct for phylogeny in all analyses considering body mass, bill length exhibited only a trend toward phylogenetic autocorrelation, suggesting that correcting for phylogeny might be necessary ($P = 0.04$). However, all relationships between morphological and acoustic measurements showed only trends (all positive except PC4). Therefore, we present results uncorrected for body mass and bill length.

Results

We tested whether flight-call, habitat, and migration behavior variables were non-randomly distributed across the phylogeny of these 47 wood-warbler species. Although many flight-call variables showed no apparent phylogenetic association, a subset of these measures contained phylogenetic signal, as 4 of 5 PCAs and 7 of 28 measurements from the flight-call energy distributions correlated significantly with phylogeny; likewise, 2 of 4 measurements derived from visual inspection and an additional 7 energy-distribution measurements exhibited trends toward phylogenetic autocorrelation (Table 7.5). All categorical descriptors of flight-calls exhibited significant phylogenetic correlation in runs tests (Table 7.5). Additionally, we found support for phylogenetic autocorrelation in runs tests for two of five habitat associations and two of three migration-related characters (Table 7.5). These results suggest that correcting for phylogeny is necessary for all of these flight-call measurements with significant phylogenetic correlations as well as for analyses modeling tree type, understory density, migration system, and migration strategy.

Table 7.5. Significant and near-significant phylogenetic autocorrelation between acoustic and ecological characters. Acoustic measurements are abbreviation consistent with Tables 1 and 2.

Acoustic Measurement	Phylogeny	Tree Type[B]	Understory Density[B]	Canopy Density	Canopy Height	Moisture	Migration System[A]	Migration Route[A]	Winter Distribution	Body Mass[A]	Bill Length[B]
SkAFM	No	No	No	No	No	No	No	No	No	No	No
MeAFM	No	No	No	No	No	No	No	No	No	No	No
EqAFM	No	No	No	No	No	No	No	No	No	No	No
SkENVM	No	No	No	Trend (-)	No	No	No	No	No	Trend (+)	No
MeENVM	Trend	No	No	No	No	Trend (-)	No	No	No	No	No
EqENVM	Trend	No	No	No	No	No	No	No	No	No	No
ATTACKFR	No	No	No	No	No	No	No	No	No	No	No
SkFCC	Trend	No	No	No	No	No	No	No	No	No	No
MeFCC	Trend	No	No	No	No	No	No	No	No	No	No
SpFCC	No	No	No	No	No	No	No	No	No	No	No
SkENV	No	No	No	No	No	No	No	No	No	No	No
MeENV	No	No	No	No	No	No	No	No	No	No	No
EqENV	Trend	No	No	No	No	No	No	No	No	No	No
SkFSKEW	Yes	No	No	No	No	No	No	No	No	Trend (+)	No
MeFSKEW	Yes	No	No	No	No	No	No	No	No	No	No
SpFSKEW	Yes	No	No	No	No	No	No	No	No	No	No
SkFMED	No	No	No	No	No	No	No	No	No	No	No
MeFMED	Trend	No	Trend (+)	No	Yes	Trend (+)	No	No	No	No	No
SpFMED	No	No	No	No	No	Trend (+)	No	No	No	No	No

* Signficant, [A] significant with phylogeny, P<=0.002
^ Trend, [B] trend with phylogeny, 0.002 < P < 0.05
[C] P<=0.002, but not an ordinal or interval character

Table 7.5 (Continued).

Acoustic Measurement	Phylogeny	Tree Type[B]	Understory Density[B]	Canopy Density	Canopy Height	Moisture	Migration System[A]	Migration Route[A]	Winter Distribution	Body Mass[A]	Bill Length[B]
SkEBC	No	No	No	No	No	No	No	No	Yes	No	No
MeEBC	Yes	No	No	No	No	No	No	No	No	No	No
SpEBC	No	No	No	No	No	No	No	No	No	No	No
SWMAG	Yes	No	No	No	Trend (+)	No	No	No	No	No	No
SkPS	Yes	No	No	Trend (-)	No	No	No	No	No	No	No
MePS	Trend	No	Trend (+)	No	Yes	Trend (+)	No	No	No	Trend (+)	No
EqPS	Yes	No	No	No	Trend (+)	No	No	No	No	No	No
UPSWFR	Trend	No	Trend (-)	No	No	No	No	No	No	Trend (+)	No
UPSWM	No	No	No	No	No	No	No	No	No	No	No
F1*	Yes	No	No	Trend (-)	No	No	No	No	No	No	No
F2*	Yes	No	Trend (+)	No	Yes	No	No	No	No	No	Trend (+)
F3*	Yes	No	No	No	No	No	No	No	No	No	No
F4*	Yes	No	No	No	No	No	No	No	No	Trend (-)	No
F5	No	No	No	No	No	No	No	No	No	No	No
Minimum Frequency*	Yes	No	Trend (+)	Trend (-)	Trend (+)	No	No	No	No	Trend (+)	No
Maximum Frequency^	Trend	No	No	No	No	No	No	No	No	No	No
Bandwidth Frequency^	Trend	No	No	No	No	No	No	No	No	No	No
Duration*	Yes	No	No	No	No	No	No	No	No	No	No
Type[C]	Yes	No	No	No	No	No	No	No	No	No	No
Sweep*	Yes	No	No	No	No	No	No	No	No	No	No
Modulation*	Yes	No	No	No	No	No	No	No	No	No	No
Inflection*	Yes	No	No	No	Trend (-)	No	No	No	No	No	No

Phylogenetically controlled analyses

We compared linear contrasts of flight-call spectrographic properties with contrasts of habitat or migration characters when both sets of characters showed evidence of phylogenetic effects. Linear contrasts of several measurements of flight-call frequency and duration showed near-significant correlations with linear contrasts of understory density (Table 7.5). Minimum frequency exhibited a positive trend with understory density (r = 0.3, P = 0.04), suggesting higher minimum frequencies associated with more open habitats. Median frequency (MePS, r = 0.4, P = 0.007) and median frequency contour (MeFMED, r = 0.35, P = 0.013) also exhibited near-significant positive trends with understory density, suggesting that higher median frequency might be associated with more open habitat. Similarly, PC2 ("peak and median frequencies") exhibited a positive trend (r = 0.3, P = 0.03), supporting the apparent association between median frequency and understory density. Upsweep fraction showed a negative trend with understory density (UPSWFR, r = -0.4, P = 0.005), suggesting that flight-calls with less frequency sweep (a lower fraction of increasing frequencies across the duration of the call) may be related to less open habitat. We found no significant correlations between any flight-call measurements and tree type, or between contrasts of migration characters and acoustic characters (Table 7.5).

Phylogenetically uncontrolled analysis

We used uncontrasted approaches for comparing flight-call variables with habitat or migration characters when both sets of characters showed no evidence of phylogenetic effects. We found only one highly significant correlations among this set of acoustic and ecological characters between skewness of equivalent bandwidth contour – a measure how much the compactness of a flight-call's frequency is skewed toward median frequency – and winter distribution (SkEBC, r = 0.6, P < 0.0001). However,

two of four ecological characters exhibited near-significant trends. Canopy density and skewness of amplitude time envelope frequency spectrum showed a negative trend (SkENVM, r = -0.33, P = 0.02) as did canopy density and skewness of power spectrum (SkPS, r = -0.31, P = 0.04). Flight-calls that have more energy distributed earlier in the duration of the signal may be associated with thicker canopy. Moisture and spread of median frequency contour showed a positive trend (SpFMED, r = 0.37, P = 0.01). Flight-calls that have wider median frequency contours may be associated with more moist habitats.

Phylogenetically mixed analysis

We used linear contrasts from the resolved phylogeny for characters with phylogenetic signal and linear contrasts from the unresolved phylogeny for characters that did not exhibit phylogenetic signal when comparing flight-call variables with habitat or migration characters when one character showed evidence of phylogenetic effects and one character showed no evidence of phylogenetic effects. Among mixed phylogenetically correlated and uncorrelated characters, three relationships are significant and 10 trends are near significant. We found significant positive correlations between canopy height and PC2 ("peak and median frequency" axis, r = 0.44, P = 0.0002), median frequency (MePS, r = 0.46, P = 0.001) and median frequency contour (MeFMED, r = 0.44, P = 0.002). We found positive trends between canopy height and sweep magnitude (SWMAG, r = 0.31, P = 0.03), equivalent bandwidth of the power spectrum (EqbPS, r = 0.32, P = 0.03), and minimum frequency (r = 0.38, P = 0.009), as well as a negative trend canopy height and inflection (r = -0.38, P = 0.03). Canopy density exhibited negative trends with PC1 ("signal compactness and sweep magnitude" axis, P = 0.04) and with minimum frequency (r = -0.4, P = 0.006). Moisture exhibited positive trends with median frequency (MePS, r = 0.34, P = 0.02) and median frequency contour (MeFMED, r =

0.29, P = 0.047) and a negative trend with PC4 ("amplitude modulation/duration" axis; r = -0.36, P = 0.05) and with median of amplitude time envelope frequency spectrum (MeENVM, r = -0.34, P = 0.02).

Ecological and genetic relationships and significant acoustic differences

We tested whether 13 sympatric warbler species-pairs (26 sympatric species out of 47 total species) showed significant correlations between similarities in flight-call characteristics and genetic and ecological similarities. We used probability of local co-occurrence as a measure of ecological similarity and number of significantly different energy-distribution measurements of flight-calls between species-pairs as a measure of acoustic similarity. We found a negative trend between ecological overlap and total number of significantly different flight-call measurements among species-pairs (Table 7.4, Figure 7.1; y = -0.01x + 0.99; r = -0.57, P = 0.04). Species-pairs with higher probabilities of local co-occurrence tended to have more significantly different flight-call properties (i.e. a larger number). We did not find a relationship between genetic distance and number of different measurements (y = 0.004x + 0.04; r = 0.37, P > 0.05. The number of significantly different flight-call properties between members of a species-pair therefore does not depend on how closely related are the two members of the pair. However, the slope of this non-significant relationship is positive suggesting that less closely related species might have more differences in flight-call measurements.
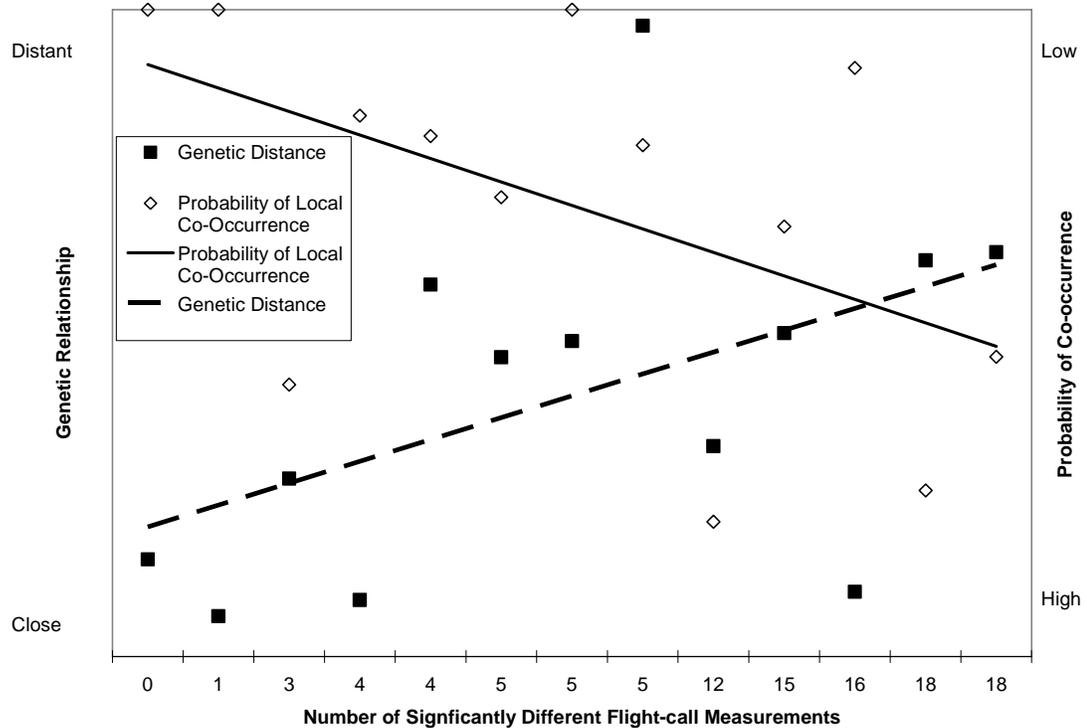
Figure 7.1. Relationships between the number of significantly different measurements and ecological overlap and genetic distance among species-pairs.

Quantile regression

We explored whether genetic distance and acoustic distance are significantly related using linear quantile regression. The quantile regressions of PCO and PCA acoustic distances on genetic distance supported a pattern of concordant dissimilarity in these flight-calls properties and genetic distances, with less closely related species-pairs being less similar in their flight-calls. Median quantiles for actual PCO and actual PCA distributions indicated that these significant relationships were pervasive across the entire distribution (PCO: $y = 0.47x + 0.21$, $r = 0.13$, $P < 0.0001$; PCA: $y = 3.64x + 2.38$, $r = 0.12$, $P < 0.0001$), whereas random PCO and random PCA distributions indicated a relationship no different than one expected by chance (PCO: $y = 0.08x + 0.36$, $r = 0.01$, $P > 0.05$; PCA: $y = 1.51x + 3.23$, $r = 0.03$, $P > 0.05$). However, we

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found that the slopes of these relationships, in particular their strength in terms of significance and their direction, varied across genetic distances (Figure 7.2a, 7.2c).

The highest PCO values for the slope estimates of these genetic and acoustic relationships occurred above the 70th (below the 30% quantile) and below the 5th (above the 95% quantile) percentiles of the acoustic distance distributions (Figure 7.2a; $P < 0.0001$). These patterns suggest that species-pairs with flight-calls that are either highly similar or highly dissimilar show stronger relationships with genetic distance. The same pattern is apparent for PCA distributions, particularly for highly dissimilar flight-calls (Figure 7.2c). However, a slope value significantly less than zero is apparent below the 5th percentile (above the 95% quantile). This suggests that the species-pairs that are least dissimilar acoustically exhibit a relationship with genetic distance that is opposite of the aforementioned patterns: species-pairs with more similar flight-calls are less closely related. Random distributions of acoustic dissimilarity (PCO and PCA) against genetic distance produced no significant relationships (Figure 7.2b, d; all $P > 0.5$), suggesting that the pattern we found in actual acoustic dissimilarity data did not occur by chance. Regression lines fitting actual distributions of PCO and PCA dissimilarities against genetic distances have significantly smaller intercepts ($P < 0.0001$) than regression lines for random distributions of PCO and PCA dissimilarities (Figures 7.3, 7.4 respectively). This pattern supports our results from the analysis of phylogenetic signal in flight-calls, suggesting that across all genetic distances flight-call measurements are generally more similar than expected by chance.
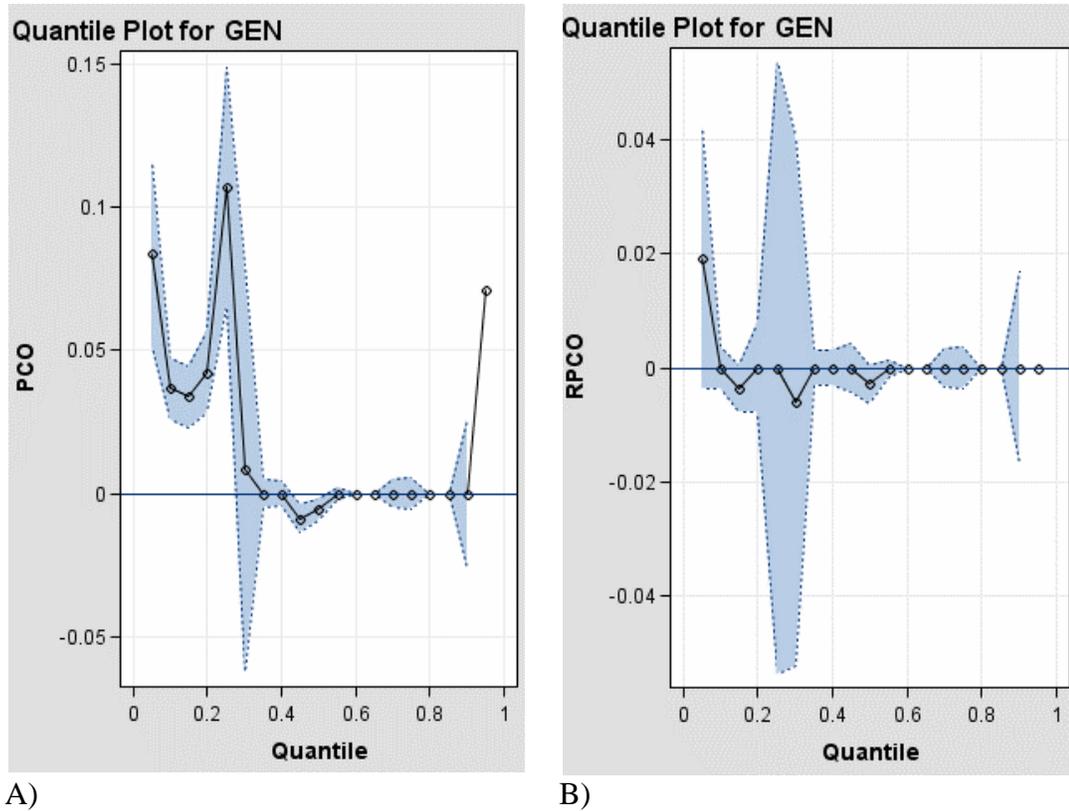
Figure 7.2. Quantile regression plots of quantile intervals from 5% to 95% in 5% intervals for acoustic distance (Ordinate axis) against genetic distance (Abscissa axis). A) Actual principal coordinate (PCO) distribution. B) Random PCO distribution. C) Actual principal component (PCA) distribution. D). Random PCA distribution.

Figure 7.2 (Continued).
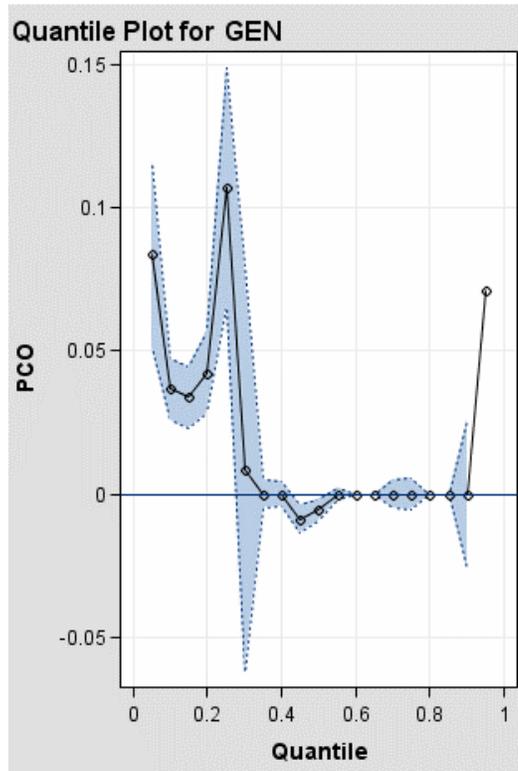
C)
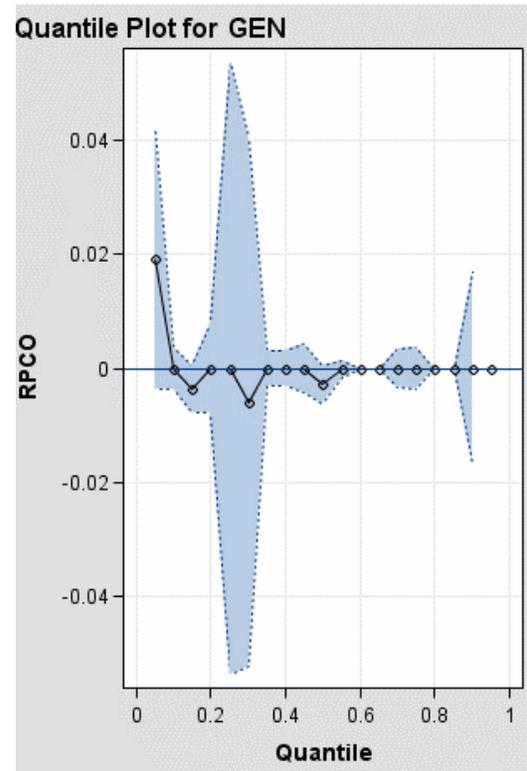
D)
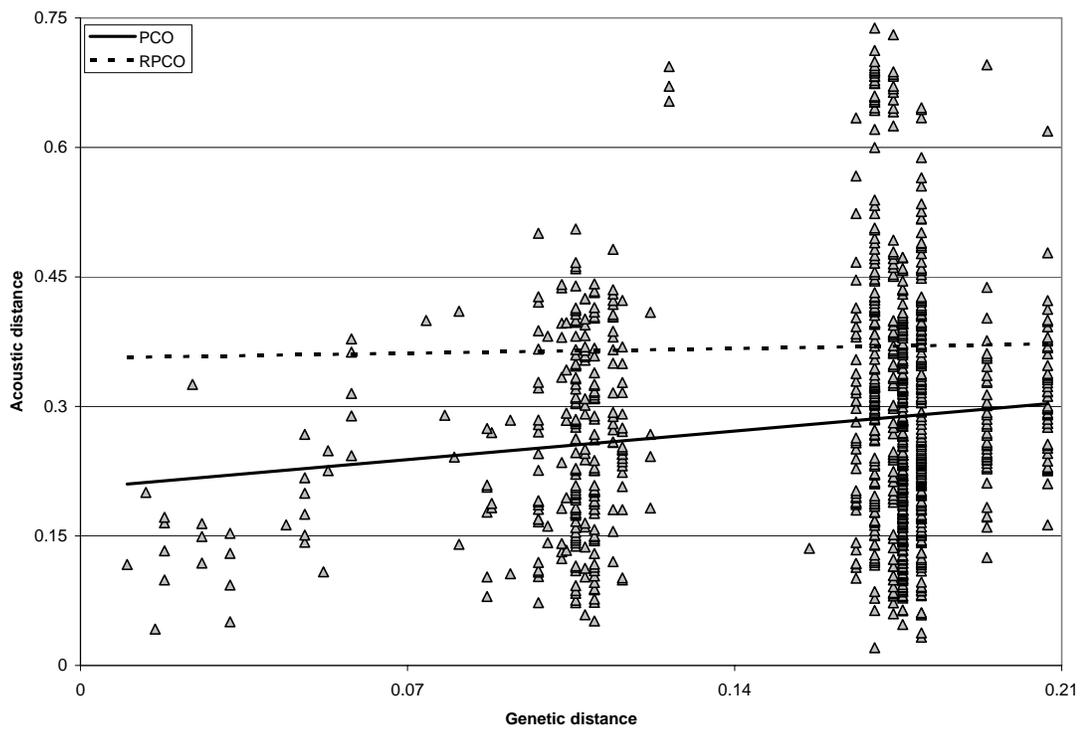
Figure 7.3. Quantile regression plots of the median (50% quantile) values for actual (solid line) and random (dashed line) distributions of PCOs against genetic distance.
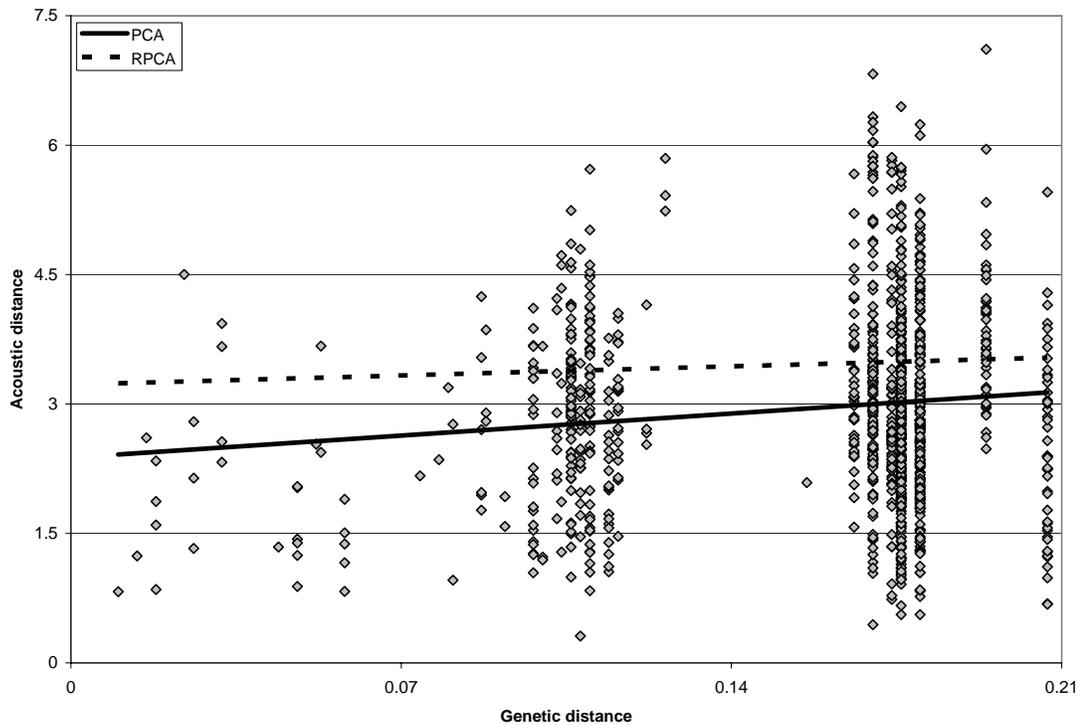
Figure 7.4. Quantile regression plots of the median (50% quantile) values for actual (solid line) and random (dashed line) distributions of PCAs against genetic distance.

Discussion

Cross-taxon comparisons of acoustic signals

Although the diversity and complexity of avian vocalizations is remarkable, several fundamental patterns likely govern the evolution of this diversity. Divergence in signals may occur via several processes including as a by-product of adaptation (either morphological or environmental) and as a means to facilitate species recognition. Bird song generally diversifies as a product of selection against hybridization (species recognition; e.g. Emlen 1972, Sorenson et al. 2003, Qvarnstrom et al. 2006) or in different foraging niches and habitats as a product of selection for optimal morphology and efficient sound transmission (acoustic adaptation; e.g. Wiley 1991, Slabbekoorn and Smith 2002, Podos et al. 2004). However, there is much less evidence to support the pathways by which more simple vocalizations such as calls diverge. We

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investigated the roles of ecology and phylogeny in shaping such a simple type of vocalization, warbler flight-calls. Because these calls are much simpler than songs, we applied two distinct approaches to capture interspecific variation in flight-calls. By cross-correlating flight-call spectrograms, we assessed similarities in syllable structure (focusing on the role of phylogeny), whereas by recording energy-distribution measurements, we assessed the spectral and temporal properties of these sounds (focusing on the role of evolution). Based on our results we suggest that warbler flight-calls follow a path to divergence that is slightly different from the path songs follow.

Phylogenetic effects on flight-call vocalizations

Phylogenetic effects are widespread in avian vocalizations (e.g. Lanyon 1969, Payne 1986, Spector 1992, Irwin 1996, Martens 1996, McCracken and Sheldon 1997, Price and Lanyon 2002, Packert et al. 2003), but some rapidly evolving vocal traits may diverge so quickly that phylogenetic effects are minimal in comparisons among species or more ancient lineages (Rheindt et al. 2004). This is particularly true for vocalizations that have a large learned component, such as the many local and regional song dialects of *Zonotrichia* sparrows (family Emberizidae: Nottebohm 1969, Baker 1975, Baptista 1977, Trainer 1983, Tubaro and Segura 1994, Nelson 1998, Soha et al. 2004), blackbirds (family Icteridae: Avery 1977, Trainer 1989, Ologhlen 1995), and finches (family Fringillidae: Mundinger 1975). In contrast, warbler flight-calls exhibited substantial phylogenetic signal both in syllable structure and, more surprisingly, in some energy distribution measurements (Table 7.5). Several studies have identified syllable structure as likely to show phylogenetic signal, informative of evolutionary patterns and processes as well as taxonomic relationships (Helbig et al. 1996, McCracken and Sheldon 1997, Price and Lanyon 2002, Packert et al. 2004, Lei

et al. 2005). However, this study is one of first to identify explicit phylogenetic effects in spectral and temporal properties.

All syllable structure measurements showed highly significant phylogenetic autocorrelation. These measurements describe qualities of the shape of flight-call spectrograms, including their frequency slope, modulation, number of inflection points, and overall syllable type. Many spectral and temporal measurements of flight-call spectrograms also showed highly significant relationships with phylogeny. These measurements describe the energy distribution of flight-calls using repeatable and robust statistics, and they include compactness of frequency bandwidth (EqbPS, MeEBC), skewness of frequency (MeFSKEW, SpFSKEW, SkFSKEW, SkPS) and frequency sweep (SWMAG). In addition, several spectral and temporal measurements showed trends towards phylogenetic autocorrelation, including additional measures of frequency concentration (MeFCC, SkFCC), duration compactness (MeENVM, EqbENVM, EqdENV), median frequency (MePS, MeFMED), and upsweep fraction (UPSWFR). The principal component scores that are a composite of these variables showed similar patterns, as four of the five PCs showed highly significant correlations with phylogeny. The only non-significant PC (PC5) represented the only suite of measurements for which we found no phylogenetic autocorrelation (AFM). We also found highly significant phylogenetic autocorrelation in minimum frequency and duration, more traditional measurements of sound made by visual inspection and employed in many studies before the advent of more advanced digital analysis techniques.

Phylogenetic signal in flight-call syllable structure may stem from similar adaptations among related taxa or the effects of phylogenetic inertia, a tendency to resist current or past adaptive pressures (Derricksen and Ricklefs 1988, Hansen and Orzack 2005). Some properties of calls with significant phylogenetic autocorrelation

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may reflect the similar behaviors or syringeal structure of related warbler species as opposed to their shared environmental and habitat affinities, whereas vocal characters that do not exhibit significant phylogenetic autocorrelation may be evolving more rapidly than syllable structure, potentially obscuring some of the patterns of phylogenetic signal (Rheindt et al. 2004). Although syringeal structure probably does not differ substantially among these warblers, the need to recognize conspecifics is likely strong. Syllabic characters may represent an evolutionarily conserved mechanism for such recognition. However, the reason that some spectral and temporal properties of flight-calls show phylogenetic effects is less clear. Such characters do not correlate generally with phylogeny (but see Rheindt et al. 2004); rather, these properties are often subject to ecological convergence and more dependent on vegetation structure (McCracken and Sheldon 1997). In fact, sound penetration through vegetation is largely a frequency dependent feature (Morton 1975, Wiley 1991, Brown and Hanford 1996, 2000). Yet, we found several phylogenetically autocorrelated frequency measurements and several phylogenetically-non-autocorrelated non-frequency measurements (for example, ENVM, ENV, duration; see Table 7.5). Given these findings, we agree with Rheindt et al. (2004) that relationships between spectral and temporal properties and phylogeny may need to be reevaluated.

The relationships between genetic distance and acoustic distance using linear quantile regression show general agreement with our results from phylogenetic signal analysis. Acoustic distances are smaller than expected by chance across the entire distribution of genetic distances, indicating that general measures of acoustic relatedness, whether syllabic (PCO data) or spectral and temporal (PCA data), show significant phylogenetic signal. Quantile regression plots suggest that species-pairs that are more closely related (smaller genetic distances) are more similar acoustically

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(Figure 7.2a, 7.2c), despite a single instance where the opposite may be true (Figure 7.2c). However, these relationships leave a substantial percentage of variance between acoustic and genetic distances unexplained (Figures 7.3, 7.4).

Associations between flight-calls and non-acoustic traits

Numerous near-significant trends and several highly significant correlations between spectrographic measurements of warbler flight-calls and habitat suggest that ecology plays a role in shaping flight-calls of warblers (Table 7.5, Figure 7.1). Moreover, flight-calls exhibit patterns of habitat-related transmission properties similar to the patterns exhibited by songs. These results, taken in concert, provide support for the acoustic adaptation hypothesis as one factor in the diversification of flight-calls and in the diversification of bird vocalizations generally.

Higher median frequencies showed near-significant associations with taller and more open canopies and more moist habitats. These spectral properties of flight-calls, therefore, exhibit some patterns of environmental correlations similar to those correlations found for song properties suggesting higher frequency and more modulated signals associate with habitats that are more open (Morton 1975, Ryan and Brenowitz 1985, Wiley 1991, Brown and Hanford 1996, 2000, Seddon 2005, Tubaro and Litjmaer 2006). Near-significant trends also suggest such concordance between song and call relationships with their environment. PC1 (signal compactness and sweep magnitude axis) showed a negative trend with canopy density, suggesting that longer duration flight-calls with fewer changes in frequency sweep tended to associate with denser canopy. Again, following the pattern apparent in songs, flight-calls with longer duration and narrower bandwidth correlated with denser forest. Furthermore, increased inflection values, indicating more frequency modulated signals, tended to associate with more open canopy. This pattern, too, mirrors the correlation between more modulated and buzzy vocalizations and open habitats exhibited by bird songs

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(Wiley 1991, Brown and Hanford 1996, 2000). These patterns of acoustic and environmental correlation have important implications for signal propagation and differences in propagation among habitats. Although highly significant relationships between flight-calls and ecological characters were not universal, the similarity of these patterns to those seen in previous studies of songs suggests that broad patterns between spectral and temporal properties of sounds and environment exist. Migration strategies such as route traveled and geographic distribution of migration did not show any significant or near-significant relationships with acoustic characteristics. Although both of these ecological characters showed significant phylogenetic autocorrelations, there are no meaningful relationships apparent with vocal behaviors. Although winter distribution did not show any phylogenetic autocorrelation, the same pattern of no significant relationships generally applied to analyses comparing winter distribution with the exception of one highly significant positive correlation (SkEBC, measuring the degree of skew in the compactness of a flight-call's frequency toward median frequency). High values for SkEBC, indicative of flight-calls with bandwidths skewed toward higher frequencies, correlated significantly with winter distributions in North America. This correlation may represent a relationship between signal frequency bandwidth and vegetation structure indirectly, perhaps a function of more open habitat types found in these temperate distributions.

Because warblers use flight-calls extensively during migratory periods and to a lesser extent during non-breeding wintering periods (Farnsworth 200_), association between acoustic properties and these geographic behavioral strategies is plausible. Therefore, the lack of correlations between flight-calls and these characteristics is somewhat surprising, considering current hypotheses about the function of flight-calls (Thake 1981, 1983). Migratory traits for which we did not account may play a more important role in communication than simply the strategies and geographic patterns of

migration, particularly flocking preferences (for example, during migratory stopover) and migration timing (for example, early migrants versus late migrants).

Acoustic Character Displacement

Character displacement generally refers to a pattern among similar species with partially overlapping distributions of higher trait divergence in areas of high local co-occurrence and more intense competition for a resource, and of trait convergence in areas of low or no local co-occurrence and less intense or no competition for resources. We found intriguing possible evidence for character displacement in warbler flight calls: among sympatric warbler species-pairs, those pairs with higher probability of local co-occurrence exhibited a trend toward less similar flight-calls (higher number of significantly different properties). Locally sympatric species may have more different flight-calls than those of species that are not locally sympatric. These results suggest weak support for character displacement in flight-calls. Species in direct contact (local sympatry) may require divergent flight-calls to communicate in an otherwise similar active space. These results may also support the species recognition hypothesis, suggesting that flight-calls may be an important means of species-recognitions in certain contexts outside the typical breeding season and territorial context.

We cannot confirm this hypothesis, because we have only a single allopatric species-pair for which we have acoustic and ecological overlap data (Mourning and MacGillivray's Warblers) and an additional allopatric species-pair for which we have only acoustic data (Red-faced Warbler, Canada Warbler). Interestingly, the Mourning-MacGillivray's species-pair shows no significant differences in flight-call characteristics. However, a much larger sample of flight-calls in allopatry is required to understand whether regionally sympatric species in local sympatry are more different from the same pair in allopatry. Additionally, much more information about

the resource, communication space, and its limits and characteristics over time and space is needed. Additional information about the genetic basis for this variation is required to confirm that variation is not simply a result of phenotypic plasticity.

Unlike some other vocalizations (for example, territorial song: Packert et al. 2004), the number of differences in vocal characters did not correlate significantly with genetic distances among species-pairs for warbler flight-calls (Figure 7.1). However, a positive relationship between genetic distance and degree of difference in vocalization may exist, suggested by the near-significant positive trend for more closely related species-pairs (smaller genetic distances) to have fewer significant differences in flight-calls.

A phylogenetic perspective on flight-call function

A suite of phylogenetic, ecological, and atmospheric factors probably shapes warbler flight-call properties, and these relationships may provide insight into the function of these simple vocalizations. Hamilton (1962) proposed that flight-calls might function to stimulate conspecifics to continue flying or to maintain flock organizations, an idea met with general agreement in subsequent studies (Graber 1968, Griffin 1969). Additional hypotheses of function include that calls may be useful for spacing (Graber 1968) or echolocation (Griffin 1969). Furthermore, Thake (1981, 1983) theorized that these calls might improve orientation abilities, by allowing a bird with knowledge of flight-call properties to identify the position and direction of movement of conspecifics during nocturnal flights. However, these interpretations considered flight-calls only in the migratory context. Recent studies have shown that flight-calls occur in other contexts of warblers' annual cycles, with migratory periods simply representing the highest instances of the behavior (Farnsworth 200_). Any discussion of function, therefore, likely requires consideration of these additional contexts.

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Relationships with ecological characters highlight the primary importance of spectral and temporal properties of flight-calls. That these significant and near-significant relationships exist, and relationships between flight-calls and migration strategies do not, implies a role for ecology not previously defined for flight-call function. Communicating during family foraging or while traveling with intra- and interspecific flocks is probably related to these ecological factors. However, because flight-calls are high in frequency and short in duration, they may be useful only over limited distances. If this were true, flight-calls would be limited to certain types of communication. This assumes that high frequency, short duration sounds degrade quickly under many conditions and that information transmitted by such signals may not be intelligible over any substantial distance (Bradbury and Vehrencamp 1998). Given ecologic and propagation constraints as well as diverse behavioral contexts, flight-calls may function as a short-distance communication signal that aids species recognition and flock cohesion. Whether these calls are localizable and therefore representative of some orientation, location, or spatial-relation function is unknown. High frequency, narrow bandwidth calls generally do not make useful beacons to identify a bird's location (Marler 1955). However, signals with frequency modulation sweeps may provide substantial information necessary for localizing a sound source. Many bat vocalizations exhibit such frequency sweeps, and flight-calls of many of the species in our study exhibit such patterns (after Griffin 1969).

In the context of diverse breeding ecology, phylogenetically informative properties of flight-calls may best communicate information. Yet in the context of offspring traveling with and attempting to locate parents, different properties for recognizing correctly species and individual may be important for juveniles communicating with parents. Flight-calls exhibit clear differences among species and enough differences among individuals to suggest that individual recognition is

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possible (at least for some frequency properties; Chapter 4, Chapter 5). Individuality

may be an important attribute in contexts as varied as parent-offspring foraging flocks,

nocturnal migration, and intra- and interspecific winter foraging. Frequency and

amplitude modulations may themselves encode species- or individual-specific

information about a vocal warbler. Furthermore, communication outside of certain

spectral and temporal resolutions, with flight-calls being higher in frequency and

shorter than certain predators can detect, may prove useful for avoiding predation

(Klump et al. 1996, Langemann et al. 1998, Gill and Sealy 2004). As such, features

that relate directly and indirectly to warbler life history may constrain both

phylogenetically- and individually-informative properties of flight-calls.

Clearly, a substantial gap remains in our knowledge of the types of information

that flight-calls might transmit. If syllable structure is constrained by phylogeny,

flight-calls may be constrained to evolve in a limited number of ways dependent on

their function, environmental selection pressures, and the information they encode.

Whereas detailed examination of syllable structure hints that such patterns exist,

understanding patterns of syringeal usage may clarify the existence of such avenues

for evolution. The fact that these calls are so short yet have substantial rapid

frequency and probably amplitude modulation is a distinctive feature among avian

calls. Studies of the mechanisms for producing rapid amplitude and frequency

modulations are necessary, particularly in relation to the energetic costs of flight-call

production, the mechanisms by which warblers produce such sounds, and potential

variation in fitness associated with flight-call production and reception.

Both phylogenetic and ecological characters correlate to warbler flight-call

syllable structure and spectral and temporal properties, these patterns supporting

hypotheses of diversification as a function of species recognition and acoustic

adaptation, respectively. Additionally, morphological characters do not constrain

warbler flight-call frequencies and duration (for example, body mass and bill size) in phylogenetically controlled and uncontrolled analysis (Farnsworth and Lovette 2005), these patterns not supporting the hypothesis of diversification as a function of selection for optimal morphology. Both of our approaches to sound analysis (cross-correlation and multiple objective measurements) show concordant patterns of phylogenetic autocorrelation. However, energy-distribution measurements exhibit more relationships with ecological characters, suggesting a closer relationship among ecological, spectral, and temporal properties than between ecological and syllable structure properties. Understanding the true role of ecological factors in shaping flight-calls requires ontogenetic information. If flight-calls are learned, additional variation across populations may exist that relate to habitat-dependent acoustic environments. Such divergence based on learning may account for some unexplained variation in acoustic and genetic relationships in flight-calls. In addition, heritability of variation in syllabic, spectral and temporal properties is a crucial but presently unknown feature important to understanding flight-call acoustic and genetic relationships. A learned vocalization that exhibits substantial phylogenetic signal may provide insight into the mechanisms of vocal evolution, species recognition, and the roles of ontogeny and phylogeny in shaping these short vocalizations.

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