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USE AND CHARACTERISTICS OF TWO SINGING MODES IN PINE WARBLERS

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ABSTRACT.—North American wood-warblers (Parulidae) are well known for exhibiting two distinct singing modes: first category song, in which a single song type is sung repeatedly, usually before dawn, and second category song, in which several song types are sung in irregular sequence. Studies suggest that first category song types have higher performance characteristics and that second category song types are shared preferentially among territorial neighbors. Here we present the first formal description of two-category singing in the Pine Warbler (*Setophaga pinus*). Similar to other species in the genus *Setophaga*, Pine Warblers produce second category song before dawn and first category song primarily during daylight hours. First category songs also had significantly higher trill rates, suggesting that they are more challenging to perform. Unlike many congeners, however, Pine Warblers regularly alternate between first and second category singing throughout the day, and first category song types often appear intermixed in second category singing, including singing before dawn. Furthermore, comparisons among territorial males showed that individuals do not share song types more with neighbors than with non-neighbors. Our results suggest that Pine Warblers have two song categories similar to other *Setophaga* warblers, but singing patterns in this species differ from congeners in interesting ways that warrant further investigation. *Received 9 January 2013. Accepted 7 April 2013.*

Key words: communication, *Dendroica*, *Setophaga*, singing modes, song type sharing, vocal performance, wood-warbler.

Many songbirds produce more than one song type, each of which appears to serve dual functions in both mate attraction and interactions with rival males (Collins 2004, Catchpole and Slater 2008). Several groups of songbirds, however, are known to exhibit two distinct modes, or categories, of singing, which differ in their patterns of song presentation and in the contexts in which they are performed (Spector 1992, Kroodsma 1999, Molles and Vehrencamp 1999). For example, in North American wood-warblers (Parulidae) of the genus *Setophaga* (including all former *Dendroica* and *Parula* taxa as well as *Wilsonia citrina*; Chesser et al. 2011), males produce one or a few of their song types in a highly repetitive fashion while long-distance broadcast singing during the day (first category song) and produce other song types with greater variety and at higher rates at dawn and during close-range interactions between territorial males (second category song) (Lemon et al. 1985; Kroodsma et al. 1989; Staicer 1989, 1996; Spector 1991, 1992; Wiley et al. 1994; Byers 1995; Bolsinger 2000). Species in this genus are closely related within a well-defined clade (Lovette et al. 2010, Chesser et al. 2011), based on molecular evidence. However, whether or not all members of this clade exhibit such distinct singing categories is not known (Spector 1992).

Studies have shown that first category and second category songs differ in ways other than just context and mode of presentation. Beebee (2004b), for instance, provided evidence for consistent structural differences between the first and second category songs of Yellow Warblers (*Setophaga petechia*). First category songs have significantly higher performance characteristics, measured as higher trill rates and wider frequency bandwidths, than do second category songs, suggesting that first category song types are more difficult for males to perform and thus might advertise a singer's abilities (Podos 1997, Ballentine et al. 2004). Wood-warbler song categories may differ in other ways as well, such as in note amplitudes and complexity (e.g., Spector 1991, Staicer 1996, Bolsinger 2000). Interestingly, however, the song types used in each category are usually not standardized across males within a species, with the first category song of one male often clearly resembling the second category song of another (Lemon et al. 1985; Staicer 1989; Spector 1991, 1992; Beebee 2004b).

In at least some wood-warbler species, males share significantly more of their second category song types with territorial neighbors than with non-neighbors, whereas first category songs exhibit no such patterns (e.g., Chestnut-sided Warblers, *Setophaga pensylvanica*: Byers 1996; Yellow Warblers: Beebee 2002). Such song type

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sharing could be adaptive if second category songs are used preferentially during territorial interactions between rival males (Spector 1992, Wiley et al. 1994, Byers 1995). Sharing song types with neighbors is known to provide important advantages for communication in some songbirds (reviewed by Catchpole and Slater 2008); however, in wood-warblers there is little evidence that males use their shared and unshared song types differently during territorial interactions (Lemon et al. 1985, Byers 1996). Moreover, playback experiments with Yellow Warblers show that males use both song categories when interacting with both males and females, suggesting that singing modes do not have distinct sex-specific functions (Beebee 2004a). Clearly, more work is needed to understand the evolution of wood-warbler song categories and the functions of these different singing modes in communication.

Here we present a quantitative analysis of song characteristics and singing behavior in the Pine Warbler (*Setophaga pinus*). Individual males in this species are known to produce more than one song type (Spector 1992, Rodewald et al. 1999). Yet, whether this species has a two-category song system typical of other *Setophaga* warblers has not been previously investigated. Previous authors have observed Pine Warblers producing two song types in alternation during daytime, suggesting that singing behaviors in this species differ from those of most congeners (Spector 1992). Males also appear to be unusual among wood-warblers in producing ''double'' songs, in which one song type is immediately followed by another with slightly different acoustic features (Rodewald et al. 1999). Pine Warblers are also among the few North American passerines that sing during all months of the year, including during migration (Rodewald et al. 1999). To allow comparison between this species and previously studied wood-warblers, we conducted detailed acoustic analyses of song type usage, vocal performance characteristics, and patterns of song type sharing among territorial males.

METHODS

Song Recording.—We recorded the singing behaviors of 12 male Pine Warblers from 28 June to 30 July 2011. Ten males occupied territories approximately a hectare in size at the University of Michigan Biological Station (UMBS: 45° 33′ N, 84° 42′ W), along the southern shore of Douglas Lake in Cheboygan County, Michigan, and two males had territories at the Chase Osborn Preserve (COP: 46° 21′ N, 84° 8′ W) near Duck Lake on Sugar Island, approximately 100 km to the north along the border of Michigan's upper peninsula and Ontario, Canada (Fig. 1). All territories were in mixed pine-deciduous forest dominated by red pine *Pinus resinosa* and eastern white pine *Pinus strobus*. The breeding status of each male during the sampling period was unknown. We did not color band birds for individual identification; however, only one bird was ever observed singing in each territory and neighboring birds were usually easily distinguishable by their distinct song types (see below). Thus, we are confident that identification of individuals by location was reliable. No females were ever observed singing. We recorded songs during the half hour period before sunrise and throughout the day until 1800 hrs EST. All individuals were recorded over multiple days, and we made an effort to record each individual at different times each day. All digital recordings were made at a sampling rate of 48 kHz and 16 bit depth using a Marantz solid state digital recorder (model PMD670) connected to a Sennheiser directional microphone (model ME67 with K6 power supply). We marked singing locations using a Garmin GPS 60 (Garmin Ltd., Olathe, Kansas, USA). On average, we recorded 112.1 (SE = 22.7) songs per bird (range = 24–282 songs/bird, n = 1,345 songs total) (Table 1).

Song Analysis.—The song of the Pine Warbler consists typically of a rapid, evenly spaced series of nearly identical notes (i.e., a trill), each of which is about 1–2 secs in duration (Fig. 2). We generated sound spectrograms of all recorded songs using Raven Pro 1.4 (Cornell Laboratory of Ornithology, Ithaca, New York, USA; frequency resolution = 135 Hz, time resolution = 10.7 msecs). We then sorted the songs of each male into song types based on note shape and five acoustic measurements: trill rate (notes/sec), mean note duration (msec), lowest frequency, highest frequency, and frequency bandwidth (kHz). Our methods for measuring frequency bandwidths of trills were similar to those used by Podos (1997), in which we used a power spectrum to calculate the difference between the lowest and highest frequencies with amplitudes above −24 dB relative to the peak amplitude. This amplitude threshold excluded most background noise while including most of the frequency characteristics of the bird's song (Cramer and Price 2007). For each

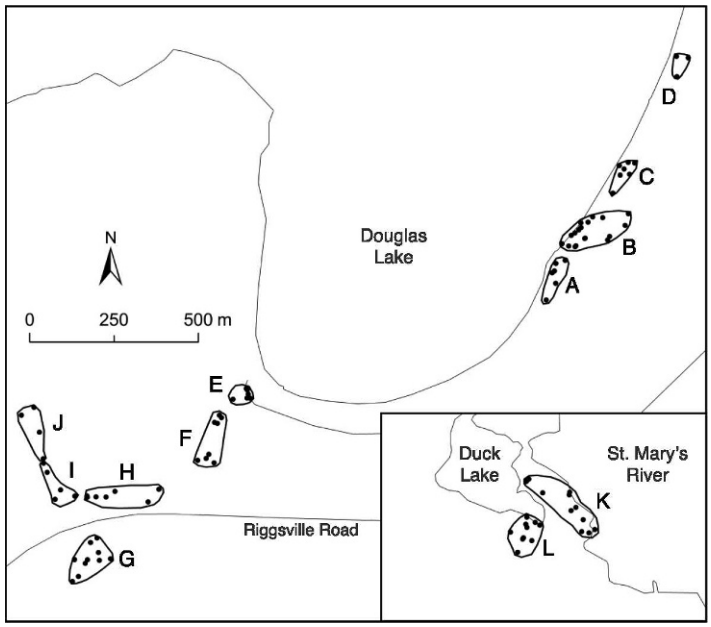

FIG. 1. Singing locations (dots) of Pine Warblers (A–L) recorded at the University of Michigan Biological Station (UMBS) and at the Chase Osborn Preserve (COP, shown in inset). Recording locations were measured using a Garmin GPS 60. Map and scale were produced using ArcGIS 9.3 (ESRI, Redlands, California).

individual bird, we considered songs with identical note shapes and similar acoustic measurements to be the same song type. We later confirmed these initial categorizations using principal components analysis (PCA; James and McCulloch 1990), as described below.

We measured singing modes (scored as ''repeat mode'' or ''mixed mode'' following Wiley et al. 1994) and singing rates (songs/min) from a subset of recordings that included bouts of 10 or more songs ($n = 1{,}221$ songs in 104 bouts). A song type was scored as occurring in repeat mode if it was repeated at least 10 times in succession, whereas songs were scored as occurring in mixed mode if more than one song type appeared in a 10 song series. Typical examples of mixed mode singing included frequently alternating song types, with each song type rarely repeated more than two or three times in succession. Following Spector (1992), we classified song types that were normally presented in repeat mode as first category songs and song types that were presented in alternation with other song types as second category songs. One bird did not provide any recordings longer than 9 songs and so could not be scored ($n = 24$ songs total). Average singing rates were calculated for the period before sunrise, which varied during the course of the study from 0552 to 0620 hrs, and then for roughly 2-hr increments during the morning and 3-hr increments during the afternoon when activity levels were generally lower.

Vocal Performance.—To examine the relative vocal performance levels of song types, we

TABLE 1. Number of song types identified, total number of double songs recorded, and total number of songs recorded from each bird in our study.

	Individual male											
	A	B	C	D	E	F	G	H	I	J	K	L
Identified song types	4	5	3	3	1	5	4	3	3	1	1	4
Double songs	11	39	0	0	0	0	0	16	0	0	0	5
Total songs sampled	189	282	136	24	66	169	116	157	36	25	50	95

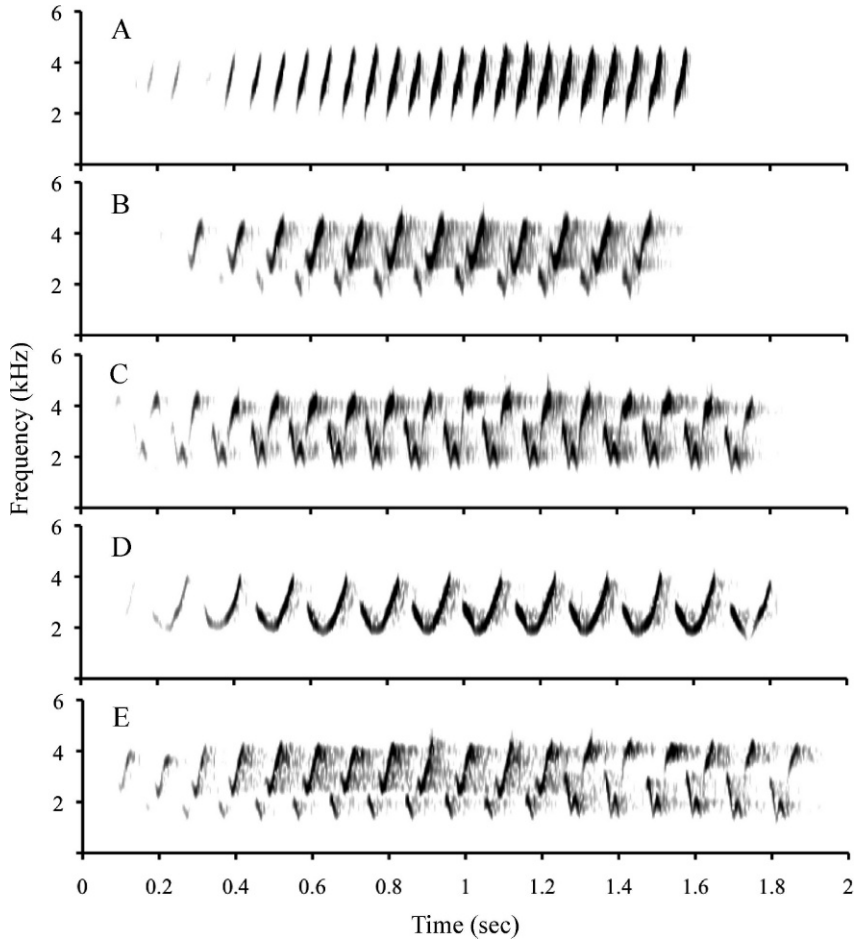

FIG. 2. A typical song type repertoire of one male Pine Warbler (n = 189 songs recorded). Four song types are shown (A–D), as well as an example of ''double'' song (E) in which the trills of two song types (in this case B and C) are concatenated. Song A was scored as this male's first category song type.

plotted their frequency bandwidths against trill rates. Following Podos (1997), we calculated a performance limit for our population by sorting our trill rate measurements into seven bins, each with 3 notes/sec, and then selecting the song type with the broadest frequency bandwidth in each bin for linear regression. Our bin size of 3 notes/sec maximized the number of song types included in the regression while minimizing the inclusion of lower performance songs (also see Cramer and Price 2007). Given that the upper-bound regression was significant (see Results), we then determined the relative performance level of each song type by measuring the orthogonal distance between each song type's measurements and this upper-bound regression line (Ballentine et al. 2004, Beebee 2004b, Cramer and Price 2007). Songs close to the performance limit were considered high performance songs, whereas songs farther from the performance limit were considered lower performance songs. We used these orthogonal deviation measurements to compare the mean vocal performance characteristics of first category and second category song types using an independent samples t-test. Not all of these song type measurements were statistically independent, because most males produced multiple song types. Thus, to control for potential variation among males, we further used a paired-samples t-test to compare the vocal performance characteristics of each male's first category song to the mean characteristics of his second category song types

TABLE 2. Mean (± SE) song characteristics of Pine Warblers recorded at the University of Michigan Biological Station (UMBS) and at Chase Osborn Preserve (COP). Measurements from the two locations did not differ.

	Both populations	UMBS	COP	
	$n = 168$	$n = 143$	$n = 25$	*t*-tests
Measurement	Mean ± SE	Mean ± SE	Mean ± SE	*P*
Trill rate (notes/sec)	14.87 ± 0.51	15.11 ± 0.59	13.49 ± 0.81	0.113
Note length (msec)	56.7 ± 3.2	57.1 ± 3.7	54.7 ± 4.5	0.792
Low freq. (kHz)	2.99 ± 0.02	2.99 ± 0.03	2.97 ± 0.05	0.718
High freq. (kHz)	5.33 ± 0.03	5.30 ± 0.03	5.44 ± 0.09	0.106
Freq. bandwidth (kHz)	2.34 ± 0.03	2.31 ± 0.04	2.47 ± 0.09	0.105

(Beebee 2004b). All comparisons were two-tailed, and all statistical analyses were conducted using SPSS (version 18; IBM, Armonk, New York).

Song Type Sharing.—To assess song type sharing between individuals, we took measurements from five clear examples of each song type and compared these among all recorded males. Some song types exhibited obviously unique acoustic characteristics, based on visual inspection of note shapes in spectrograms (Fig. 2) and comparisons of acoustic measurements. Other song types, however, showed some similarities in their notes and measurements and were therefore placed into seven groups for further statistical analyses. For each of these seven song groupings, we used principal components analysis to compare the five measured song features among males. The majority of variation in these datasets was explained by one or two of the first two principal components (see online supplement). Using the eigenvalues from these analyses, we plotted values for the first two principal components and then plotted 95% confidence ellipses around the points for each bird, using the package ''ellipse'' (Murdock and Chow 2007) in the R statistical program (R Foundation for Statistical Computing, Vienna, Austria). We considered birds with overlapping ellipses to have the same song types and those whose ellipses did not overlap to have different song types.

To determine if song sharing was more or less common between birds with adjacent territories (neighbors), we compared levels of song type sharing between neighbors to those between non-neighboring birds. We considered birds neighbors if they were observed singing at locations within 100 m of each other. For each pair of birds, we calculated an index of repertoire sharing (RS) using the formula $RS = Z/[(X + Y) - Z]$, in which X and Y represent the number of song types identified in each bird and Z represents the number of song types shared by the two birds (Hultsch and Todt 1981). This index potentially varied between 0, in which no songs are shared, and 1, in which all song types are shared, and it accounted for the fact that different males had different numbers of identified song types. We compared overall levels of song type sharing as well as sharing of first category and second category song types using independent samples *t*-tests. We further compared mean levels of sharing with neighbors and with non-neighbors by each male using a paired-samples *t*-test.

RESULTS

Singing Characteristics.—In our sample of 1,345 songs from 12 Pine Warblers, we initially identified 37 song types. Song repertoire sizes varied from 1–5 song types per male (mean = 3.08, SE = 0.42 song types) (Table 1). However, repertoire size was significantly influenced by number of songs sampled (ANOVA; $F_{1,10} = 11.33$, $P = 0.007$), indicating that our samples of at least some individuals were not large enough to accurately represent complete song type repertoires. Mean song characteristics at our two study locations, UMBS and COP, were not significantly different (in *t*-tests: $P > 0.1$) (Table 2).

Birds sang throughout the day, often while foraging 10–20 m above the ground in stands of red or white pine. Singers rarely stayed on one perch for long, typically moving from branch to branch at regular intervals between every few songs. We occasionally observed males singing while holding insect prey in their bills. Males and females were rarely seen together in the morning; whereas, they were often seen foraging near each other in the mid and late afternoon. Neighboring males appeared to counter-sing regularly, especially early in the morning, usually in alternation

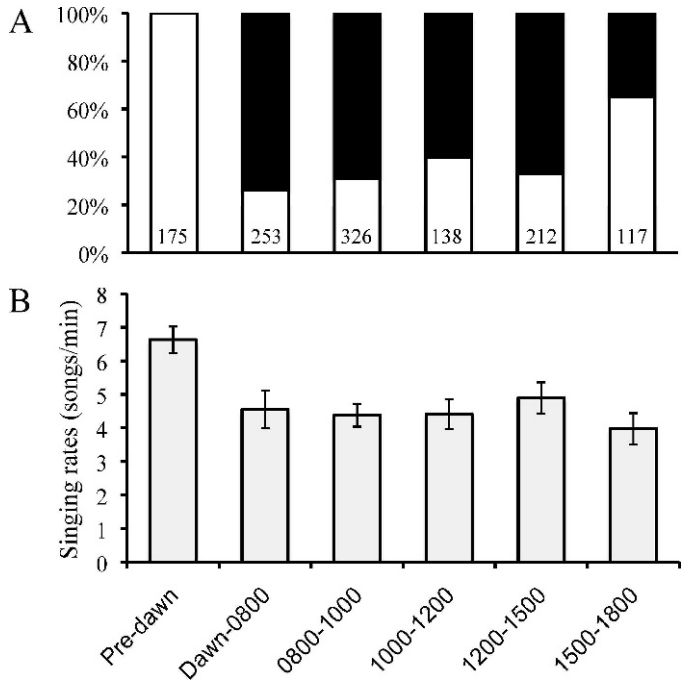

FIG. 3. (A) Proportions of time spent singing in repeat mode (black) and mixed mode (white) during each time period, with numbers of recorded songs shown at the base of each column. All songs produced before dawn were presented in mixed mode, whereas singing after dawn and during much of the day included mostly repeat mode singing. (B) Mean (± SE) singing rates (songs/min) during each time period, which were higher during pre-dawn singing than during the rest of the day.

but sometimes one male's song would overlap the song of a neighbor.

Songs recorded before dawn were always produced in mixed mode. Singing after dawn and during the rest of the day included mostly repeat mode, intermixed with bouts of mixed-mode singing (Fig. 3A). Birds appeared to sing with more variety later in the afternoon. Average singing rates were also significantly higher during the period before dawn (6.63 ± 0.39 songs/min) than during other times of day (4.48 ± 0.20 songs/min; *t*-test: $t_{86} = 4.74$, $P < 0.001$) (Fig. 3B).

Most Pine Warblers in our population had just one song type that they repeated for long stretches of time during daylight hours. We designated this song type as each male's first category song (Spector 1992). Other song types were only presented in alternation with other song types and were designated as second category songs. One male did not fit this pattern and had two song types that were sung in repeat mode on different occasions, both of which we scored as his first category songs. First category song types were sometimes included in bouts sung in mixed mode (19.1 ± 5.8% of the time), including singing bouts before dawn. Second category song types, in contrast, were never sung in repeat mode. Of the five most poorly sampled males (24–66 recorded songs, Table 1), three produced only one song type each in our recordings, which we scored as first category song, and one male had no recordings of 10 or more songs and thus could not be scored.

Occasionally (5.28% of songs recorded), a bird combined two of its song types into one continuous song, as noted by Rodewald et al. (1999), in which one trilled syllable was immediately followed by another at a slightly different frequency and rate (Fig. 2E). Four males exhibited such double songs (Table 1), which we scored as examples of mixed-mode singing, and three of these males produced multiple types of double songs using more than one combination of song types. Double songs occurred during all time periods, including before dawn, and could include either first or second category song types.

Approximately 30% of the examples we recorded included a first category song type.

Vocal Performance.—Frequency bandwidths of song types were significantly negatively related to trill rate in a linear regression (ANOVA: $F_{1,35} = 24.7$, $r^2 = 0.41$, $P < 0.001$), and the upper-bound regression line estimating the performance maximum for the population had a significantly negative slope ($y = -0.079x + 3.88$; $F_{1,5} = 69.6$, $r^2 = 0.93$, $P < 0.001$) (Fig. 4A). First category song types had significantly faster trill rates than did second category songs (*t*-test: $t_{35} = 2.64$, $P = 0.012$), but frequency bandwidths did not differ ($t_{35} = -0.625$, $P = 0.54$). Moreover, first category song types appeared closer on average to the upper performance limit than did second category songs (Fig. 4B), and this difference in orthogonal distance from the upper-bound line was nearly significant ($t_{35} = -1.879$, $P = 0.069$). A paired-samples *t*-test using a smaller sample of males exhibiting both song categories ($n = 8$) found no significant difference in the performance characteristics of each male's first and second category song types ($t_7 = -0.654$, $P = 0.53$). However, first category song types nearly always exhibited the highest trill rate in each male's repertoire (mean ± SE = 17.25 ± 1.66 notes/sec for first category song and 11.62 ± 0.83 notes/sec for second category song; $t_7 = 3.416$, $P = 0.011$).

Song Type Sharing.—Pair-wise comparisons between recorded males revealed that all males shared at least one song type with another male in the population, but no two males shared more than one song type. Of the 37 song types initially identified, many were shared among males and only 26 were structurally distinct across the population according to PCA. Males shared song types with 1–5 other males (mean = 2.5, SE = 0.4), including two song types that were shared between the UMBS and COP populations. Average levels of repertoire sharing between neighbors (RS = 0.067 ± 0.28) and non-neighbors (RS = 0.068 ± 0.26) did not differ overall ($t_{64} = -0.015$, $P = 0.99$) or in a paired-samples test ($t_{10} = 5.86$, $P = 0.57$) (Fig. 5). Furthermore, the mean proportion of first category songs that were shared between birds (33.3%) was not significantly different from the proportion of second category songs that were shared (36.1%; *G*-test: $G = 0.396$, df = 1, $P = 0.53$). In five cases, a song type used by one male as first category song was used by another as a second category song, and three males used the same song type as their first category song.

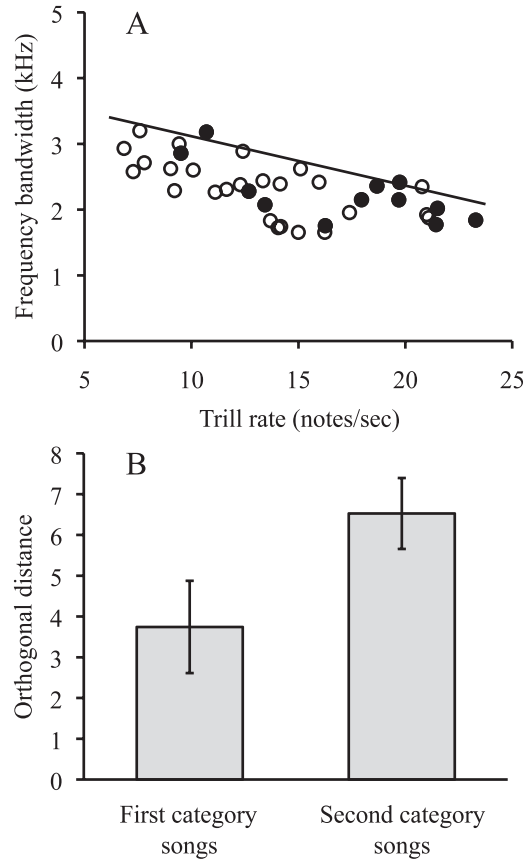

FIG. 4. (A) Frequency bandwidth versus trill rate for all song types recorded in the study ($n = 37$). An upper-bound regression line estimates the performance maximum for the population. First category songs (black filled circles) had significantly higher trill rates than did second category songs (white filled circles). (B) Mean (± SE) orthogonal distances from the upper-bound regression suggest that first category song types were performed closer to the performance maximum (i.e., had higher performance levels) than were second category song types.

DISCUSSION

In several respects, the singing patterns of Pine Warblers resemble those of other *Setophaga* wood-warblers. Like previously studied congeners, Pine Warblers exhibit a two-category song system in which one song type is typically repeated for long periods of time with high stereotypy (first category song) and other song types are mixed in irregular sequence during singing bouts (second category song) (Spector 1992). Songs before dawn were always sung in mixed mode, and pre-dawn singing occurred at significantly higher rates than did singing during

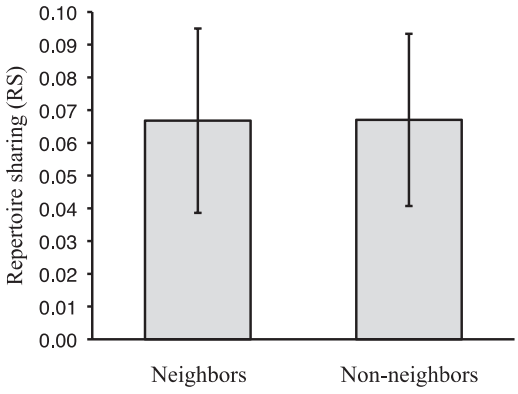

FIG. 5. Mean (± SE) levels of repertoire sharing between neighboring (n = 10) and non-neighboring (n = 56) males.

the rest of the day. Furthermore, and perhaps most interestingly, first category song types exhibited higher performance characteristics (e.g., higher trill rates) than did second category songs, suggesting that first category song types are generally more challenging to perform (Ballentine et al. 2004, Beebee 2004b). Nevertheless, as has been shown in several other wood-warbler species (Lemon et al. 1985; Staicer 1989; Spector 1991, 1992; Beebee 2002, 2004b), the particular song types used in each category were not standardized across males in our population. First category song types of some males were nearly identical to the second category song types of other males. Our results are consistent with Beebee's (2004b) suggestion that individual males subdivide their repertoires into two distinct singing categories in order to highlight a particularly well-performed song type.

Pine Warblers also exhibit several interesting differences from other wood-warblers, as noted by previous authors. For instance, Spector (1992) noted that Pine Warblers regularly produce more than one song type in alternation during daytime singing, unlike most congeners. Our study confirms this observation by showing that >25% of song bouts throughout the day included multiple song types produced in mixed mode (Fig. 3A). However, we should note that our study was conducted relatively late in the breeding season, and other wood-warbler species are known to produce first category songs less frequently after mating (e.g., Spector 1991); consequently, it is possible that the high levels of second category singing we observed in our population do not reflect typical singing patterns during breeding. Future investigations should confirm whether frequent second category singing during daylight is indeed typical of Pine Warblers throughout the year, as implied by previous authors (Spector 1992, Rodewald et al. 1999), or occurs only during the later part of the breeding season.

Unlike other wood-warblers, Pine Warblers regularly included their first category song types in bouts sung in mixed mode (<20% of the time), including singing bouts before dawn. Of the nine males in our study from which we recorded more than one song type, all were observed mixing their first and second category song types during singing bouts. For comparison, Spector (1991) reported only a single Yellow Warbler (out of 17 study subjects) that interspersed its first category song with second category song types during predawn singing bouts. Pine Warblers are also unusual in producing double songs, in which two song types are concatenated into one continuous song. As in other examples of mixed-mode singing in this species, double songs sometimes included a mixture of first and second category song types. Whether or not these combined songs have a specialized function in communication remains to be investigated.

In general, the two-mode song system of Pine Warblers appears to lack the clear distinction between song categories typical of most other *Setophaga* wood-warblers (Spector 1992). Yet, in Pine Warblers these song categories nevertheless exhibited consistently different acoustic characteristics, as in other taxa (Spector 1991, Staicer 1996, Beebee 2004b). First category songs had significantly higher trill rates than did second category songs. Furthermore, in comparisons to a performance maximum for the population estimated by plotting trill rates against frequency bandwidths, first category songs were generally closer to this upper limit (Fig. 4), although not significantly so (P = 0.069). In a similar comparison of vocal performance levels in Yellow Warblers, Beebee (2004b) showed that first category song types were significantly closer to a performance maximum than were second category song types when inter-individual variation was controlled for using paired-samples comparisons (n = 33). Our paired-samples analysis using a much smaller sample of Pine Warblers (n = 8) showed no significant differences in this measure of vocal performance. Yet, within each male's repertoire, first category song types nearly always exhibited the highest trill

rates. Trill rates could be an especially salient indicator of vocal performance in Pine Warblers, unlike frequency characteristics which can degrade during transmission and thus might provide less reliable information in long distance communication (Wiley and Richards 1982).

Pine Warblers also differ from previously studied taxa in their patterns of song type sharing among males. Unlike Yellow Warblers (Beebee 2002) and Chestnut-sided Warblers (Byers 1996), which preferentially share second category song types with close neighbors, Pine Warblers do not appear to share song types with neighbors over non-neighboring males. Indeed, our subjects shared song types between the two study populations, approximately 100 km apart, just as often as they did between adjacent territories, and levels of sharing did not differ between first and second category songs. In other wood-warbler species, second category song is thought to be used primarily during territorial interactions (Spector 1992, Wiley et al. 1994, Byers 1995), and it has been suggested that song type sharing allows complex communication between neighboring males (Beebee 2002, Catchpole and Slater 2008). Yet, studies suggest that male wood-warblers do not use their shared and unshared songs differently during territorial interactions (Lemon et al. 1985, Byers 1996), and playback experiments show that males often use first rather than second category song when responding to potential territorial intruders (Beebee 2004a). Thus, an alternative explanation for song type sharing is that it is simply a consequence of how males learn their songs (Spector 1992, Beebee 2002), with males preferentially learning some of their second category song types from neighbors following natal dispersal. Therefore, song sharing might have no relevance to how males use their songs to interact with other males (Beebee 2004a).

If general patterns of song type sharing in wood-warblers are explained by learning rather than their functional significance in communication, the absence of any clear relationship between song sharing and geographic distance in our Michigan population of Pine Warblers would suggest that these birds have different vocal learning patterns than most congeners. This might make sense, as Pine Warblers are among the few songbirds that sing year-round, including during migration (Rodewald et al. 1999), so young birds are presumably frequently exposed to song types from wide geographic areas. Some more southerly populations of Pine Warblers are known to be non-migratory (Rodewald et al. 1999), and it would be interesting to compare the patterns of song type sharing in our population to those of year-round resident birds. Levels of song sharing with immediate neighbors, as well as song repertoire sizes, might be greater in resident populations (Ewert and Kroodsma 1994).

Although the two song categories of wood-warblers may not have distinct sex-specific functions as previously thought (Beebee 2004a), differences in their acoustic characteristics and patterns of use nonetheless suggest that they play different roles in communication. For instance, the higher performance characteristics of first category songs might reflect the role that these song types play as assessment signals (Beebee 2004b), unlike second category singing which may have functions in mediating interactions between territorial males. Assessment signals presumably could be directed at either male or female receivers, which is consistent with previous findings that males tend to use their first category songs in the contexts of both attracting females and repelling perceived male intruders (e.g., Spector 1991, 1992; Wiley et al. 1994; Bolsinger 2000; Beebee 2004a). Song categories may also have evolved as specializations for communication over different distances and under different levels of noise (Wiley et al. 1994). Repeating a signal with high redundancy and stereotypy, as in first category singing, is a common adaptation for overcoming signal degradation and background noise when communicating over long distances (Wiley and Richards 1982, Wiley 1994). Repetition of a signal allows listeners more opportunities for detecting and assessing signal features (Byers 2007, Price 2013). In contrast, there should be relatively little selection for such redundancy in signals used at closer range and between familiar individuals, such as territorial neighbors. Future studies should investigate these possibilities in Pine Warblers and in other wood-warbler taxa, perhaps using playback experiments (Beebee 2004a). Our descriptive analysis presented here provides an important step towards understanding the evolution and function of two-category song systems.

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