

Song ranging by incubating male Blue-headed Vireos: the importance of song representation in repertoires and implications for song delivery patterns and local/foreign dialect discrimination

Eugene Sillar Morton,^{1,5} Joan Howlett,² Nicole Christine Kopysh,³ and Ioana Chiver⁴

¹Migratory Bird Center, Smithsonian Institution, National Zoological Park, Washington, DC 20008, USA

²3662 Kinter Hill Road, Edinboro, PA, 16412 USA

³Ontario Breeding Bird Atlas, c/o University of Guelph, Blackwood Hall, Guelph, Ontario N1G 2W1, Canada

⁴Department of Biology, York University, Toronto, Ontario M3J 1P3, Canada

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ABSTRACT. Mechanisms used by birds to range their distance from singing conspecifics are being debated. In particular, the idea that an incoming song must be in a bird's repertoire for it to be ranged accurately is controversial, but important to our appreciation of the role ranging plays in song evolution. We tested the relation between ranging accuracy and songs in repertoires in playback experiments to male Blue-headed Vireos (*Vireo solitarius*) whose precise locations were known because they were incubating eggs. Males ranged songs heard while incubating and, when their mates relieved them at the nest, flew directly to the silent playback sites, suggesting that they remembered the locations of simulated intruders. Male vireos approached playback sites of local songs, likely in their own repertoires, more precisely than foreign songs recorded 95–645 km from our study site. Songs included in local and foreign playback tapes differed primarily in frequency modulation, but were similar in other measurements. These results support ranging theory as described by Morton (1986). If the songs within an individual's repertoire are ranged with greater accuracy, we discuss how the stability of neighborhoods becomes a factor as to whether or not selection will favor repertoire sharing in song evolution. As well, singing style is affected by ranging. Because Blue-headed Vireos present their songs in a stereotyped order, a listener can compare ordered sequential changes in signal degradation. Comparing degradation in a sequence of songs adds a temporal element that should result in more accurate ranging of the singer's location.

SINOPSIS. Determinación de la distancia de cantos durante el periodo de incubación en *Vireo solitarius*: la importancia del repertorio de cantos y sus implicaciones en el patrón de exposición y poder discriminar entre cantos locales o dialectos

Los mecanismos utilizados por las aves para determinar la distancia de canto de otros individuos están siendo debatidos. La idea de que la canción debe estar en el repertorio del recipiente para que sea arreglada con exactitud, es controversial, pero importante para poder entender la evolución del canto. Tratamos de probar la relación entre la tasa de exactitud y el repertorio de cantos utilizados. Para estos se expuso, a grabaciones de cantos, a individuos de *Vireo solitarius* cuya localización se sabía con exactitud dado el caso de que dichos individuos estaban incubando. Los machos pudieron dar con la localización del sonido y cuando los hembras los relevaron, volaron directamente hacia el lugar en donde se había puesto la grabación. Esto sugiere que recordaron la localidad desde donde se transmitió el sonido. Los machos se acercaron a las grabaciones de canciones locales (que se encontraban en su propio repertorio), de forma más precisa que las grabaciones de aves extrañas o con otros dialectos. Si los cantos del repertorio de un individuo, son arreglados con gran exactitud, entonces la estabilidad de los cantos de los vecinos va ser un factor, no importa si la selección natural favorece un repertorio compartido, y es una fuente importante de selección en la evolución del canto. Además, el estilo de canto puede ser afectado por su amplitud. El canto en el vireo estudiado es estereotipado y los que escuchan pueden comparar el orden secuencial de una señal degradada. El comparar la degradación en la secuencia de un canto, añade un elemento temporal que debe producir como resultado el poder determinar con exactitud la localización de un ave que canta.

Key words: singing style, song dialects, song familiarity, song neighborhood, spatial memory, territorial defense, *Vireo solitarius*

⁵Current address: Hemlock Hill Field Station, 22318 Teepleville Flats Road, Cambridge Springs, Pennsylvania 16403, USA. Email: mortone@si.edu

Birds have a remarkable ability for ranging (judging the direction and distance to) singing birds that they cannot see. A ranging bird determines a singer's location by assessing both its compass direction and distance. Ranging

permits a bird to make important decisions: a singer outside a bird's territory is ignored whereas one in the territory is attacked (Richards 1981). Thus, ranging ability may be widespread because of the energy saved by responding to songs prudently (Morton 1986, 1996).

There is little disagreement that ranging involves assessment of features of song that change, or degrade, with distance (Richards 1981, Morton 1982, Naguib 1998, Naguib and Wiley 2001). To monitor degradation, birds compare the structure of the song or call at its source with the degraded version received after propagation through natural habitat. Morton (1982, 1986) proposed that such a comparison is afforded by referral to a song represented in the neural song control system that serves as an internal standard. Obviously, songs a bird sings are in its neural vocal motor system, but songs not sung by a bird may also be in its neural vocal motor system because some birds store more songs than they use (Marler and Peters 1982, Nelson and Marler 1994). As a result, playback experiments based on the assumption that song repertoires only include songs actually used by males are conservative in differentiating the ability of birds to accurately range songs in, or not in, repertoires.

Several studies have revealed that songs in a bird's repertoire are ranged more accurately than conspecific songs that are not performed (McGregor et al. 1983, McGregor and Falls 1984, McGregor and Krebs 1984, Shy and Morton 1986). Birds responded to degraded songs less aggressively, as though uttered by nonthreatening singers off their territory, only if these songs were in their own repertoires. For songs not in their repertoires, they responded similarly to degraded and nondegraded versions, suggesting they were unable to range these songs (e.g., McGregor et al. 1983, Shy and Morton 1986).

Naguib and Wiley (2001) criticized these studies and suggested that general features of degradation are sufficient for ranging. Degraded songs might simply be more difficult to detect or have less salience for conspecific listeners and thus elicit low response levels relative to undegraded signals. Birds might respond less vigorously to degraded stimuli because they are uninteresting, not because the bird uses them as a distance cue. These authors also point out methodological problems in ranging studies,

particularly the use of prolonged (1–3 min) playbacks of the song stimuli that would permit a responding bird to triangulate as it approaches a speaker rather than ranging it and then approaching (Naguib 1996, Naguib and Wiley 2001). As a result of these criticisms, ranging and its evolutionary implications for singing behavior (Morton 1986) are controversial and generally ignored (Catchpole and Slater 1995, Morton 1998).

Here, we describe a study of ranging by male Blue-headed Vireos (*Vireo solitarius*) that adds a new dimension to interpreting ranging experiments. Male and female Blue-headed Vireos share incubation duties so a male's precise location is known when he is on the nest (Morton et al. 1998). Male incubation also permits the strength of response to a signal to be measured in a unique manner. Normally, incubating males do not leave the nest until their mate arrives to replace them (Morton et al. 1998). Therefore, leaving a nest unattended to respond to playback constitutes a very strong response. Singing from, but remaining on, the nest or neither leaving nor singing would constitute successively weaker responses. When an incubating male leaves the nest, his accuracy in finding the playback location can be tested after a playback has ended and can be assessed in relation to the time since it last heard the playback. Finally, the ability of males to range local songs and foreign songs can be compared because of song variation among populations of Blue-headed Vireo (Martindale 1980).

METHODS

Study area and species. Blue-headed Vireos occur in mixed coniferous/deciduous forests in eastern North America (James 1998). Playback experiments were conducted from 25 May to 13 July 2000 and 2003 at the Hemlock Hill Biological Research Area in northwestern Pennsylvania, USA (41° N, 79° W). The 180-ha forest is composed of mature beech, maple, oak, ash, and hemlock trees (Howlett and Stutchbury 1996, Morton 2005). Nests were located by following nest-building pairs. Nests ($N = 14$) were located 1.5–7 m above the ground (mean = 3.9 ± 0.58 [SE] m). Playback experiments began once a pair began incubation (Fig. 1). Pair members replace one another on a nest approximately every 30 min, covering the eggs 57.3 ± 0.9 min/h under normal situations (Morton



Fig. 1. A Blue-headed Vireo incubating four eggs. The nest is decorated with spider webbing, bark, and often, paper from wasp nests. Decorating nests continues after laying begins as part of the nest exchange behavior of Blue-headed Vireos and probably other species in the subgenus *Vireo* characterized by eye rings and wing bars (Hamilton 1958) that all feature male incubation. Vireos without eye rings and wing bars (subgenus *Vireosylva*) lack male incubation and nests, constructed by females alone, are functional, but not ornate. Photograph by Tim Morton on 15 June 2005 at the Hemlock Hill Field Station, Cambridge Springs, PA.

et al. 1998). Each male Blue-headed Vireo sings 6–22 different songs, one after another, at a rate of 20–30/min and forming a first-order Markov chain where individual song types are delivered in a stereotyped sequence (e.g., A-B-C-D-A-B-C-D and so on; Martindale 1980, James 1981). Within populations, males share most songs, but each bird has a slightly different repertoire of additional songs (James 1981). The song repertoires of male Blue-headed Vireos at one location are more similar to each other than to songs of males in other areas (Martindale 1980), but such local similarity does not equate with dialects because some songs can be found in widely separate populations (James 1998). Males repeat the same series of songs several times before

switching, randomly, “to other highly probable strings as they cycle through their repertoires in a quasi-periodic fashion” (Martindale 1980). The songs of male Blue-headed Vireos in western Pennsylvania have some distinctive properties, such as the presence of a highly modulated (buzzy) song (James 1981).

Playback song characteristics. Birds were recorded with a Nagra IV tape recorder (tape speed of 38.1 cm/s; Nagravision SA, Cheseaux, Switzerland) and a Sennheiser MKH 104 microphone (Sennheiser Electronic Corporation, Old Lyme, CT) mounted in a parabolic reflector. Tapes were made from songs of local males (recorded in previous years and no longer present) and songs of males recorded 95–645 km from our study site (foreign songs) in the Adirondack region and Ithaca, NY, and near Warren, PA. The foreign tapes were the highest quality exemplars available from the Macaulay Library of Natural Sounds (Cornell Laboratory of Ornithology, Ithaca, New York, NY) were recorded using either a Nagra III or Nagra IV tape recorder (tape speed of 38.1 cm/s) and a Sennheiser MKH microphone mounted in a 76.2 cm parabolic reflector. Both local and foreign songs were screened for reverberations and all tapes were high quality, essentially free of reverberation, as determined by spectrographic analysis (AvisoftSASLabPro; Specht 2000).

All songs included in each 3-min playback tape were analyzed with the built-in frequency and time cursors using the Avisoft program. Details of measurements of the songs used in playback are provided in Table 1 and compared statistically in Table 2 using Mann-Whitney tests (SPSS ver.12 SPSS, Chicago, IL). The number of songs and their durations, minimum and maximum frequencies, and frequency ranges, were averaged for each playback tape. The total number of songs on the tapes of local ($N = 3$) and foreign ($N = 3$) songs was 195 and 268, respectively. Spectrographic analysis revealed that the three foreign tapes contained 12, 15, and 17 song types, and the three local tapes contained 13, 16, and 20 song types, respectively. The average time between consecutive songs provided a measure of song delivery rate. During aggressive encounters, males deliver songs rapidly whereas males normally deliver songs at intervals of 1–2 s (Martindale 1980). Only natural sequences of song from unprovoked males were used.

Table 1. Characteristics of songs used in six 3-min playback tapes.

Playback tape	Number of songs	Length of song (s)	Minimum frequency (Hz)	Maximum frequency (Hz)	Frequency range (Hz)	Time between songs (s)
1	62	0.369 ± 0.006	2357 ± 547	5675 ± 514	3318 ± 743	1.9 ± 1.0
2	63	0.328 ± 0.006	2025 ± 488	5917 ± 522	3892 ± 646	1.9 ± 0.7
3	70	0.333 ± 0.053	2330 ± 446	5218 ± 650	2888 ± 947	2.0 ± 0.8
4	73	0.407 ± 0.088	1969 ± 253	6049 ± 600	4080 ± 656	1.8 ± 0.6
5	99	0.383 ± 0.101	2160 ± 398	6594 ± 577	4433 ± 825	1.4 ± 0.3
6	96	0.416 ± 0.128	2189 ± 336	5668 ± 751	3479 ± 739	1.5 ± 0.5

Tapes 1–3 were from local birds and 4–6 from more distant locations (foreign songs). Values are means ± 1 SD for all songs on each tape.

The large number of songs presented to our subjects helped avoid the possibility of pseudoreplication effects (Hopp and Morton 1998: 332–334). We were limited by the number of high-quality foreign tapes available. Many excellent recordings contained aggressive fast song, probably because playback of conspecific songs had been used by the recording individual to bring the singing bird closer. Also, in ranging studies, the variability in degradation inevitable in natural recordings introduces an uncontrolled variable central to the hypothesis under investigation. In this case, a compromise is to use several exemplars, to help avoid pseudoreplication, but to restrict exemplars to maintain a standard level of degradation.

Playback protocol. Blue-headed Vireos are relatively tame and the birds ignored our activity and equipment (Morton et al. 1998). Before each trial, a camcorder (Sony Digital 8 Handycam, Sony Corporation, Tokyo, Japan) was placed 5–10 m from the nest and focused on the incubating bird. Experiments began once the focal male was determined to be the incubating. Three-minute tapes were used in the playback experiments. Our goal was to conduct

eight playback experiments with each focal male ($N = 14$) using randomly selected tapes of local ($N = 3$) and foreign ($N = 3$) songs played over a speaker located either 50 or 100 m from the nest. However, we actually conducted 62 experiments because nest predation prematurely ended the incubation period at several nests. The order of presentation was random, with the caveat that each male was presented with all stimulus types. The compass direction of the speaker from the nest was randomly chosen, but the speaker was always in the focal male's territory. Males were subjected to only two playback experiments per day separated by 2–3 h.

Playbacks were made via a Sony TC-D5 Pro II tape recorder (Sony Corporation, Tokyo, Japan) through a SME-AFS Amplified Playback Field Speaker (Saul Mineroff Electronics, Elmont, New York, NY) with a frequency range of 100 Hz–12 kHz, placed 1 m above ground and facing the nest. Speaker gain was held constant to produce a playback of 90 dB at 1.0 m from the speaker. Each playback lasted 3 min and was repeated every 5–10 min until the male left the nest. If a male left during playback, the playback was stopped and time

Table 2. Results of pair-wise tests (Mann-Whitney) for differences in the five measurements between playback tapes 1–6 from Table 1.

	1	2	3	4	5	6
1		D,Mf,Mxf,F,T	D,Mf,Mxf,F,T	D,Mf,Mxf,F,T	D,Mf,Mxf,F,T	D,Mf,Mxf,F,T
2			D,Mf,Mxf,F,T	D,Mf,Mxf,F,T	D,Mf,Mxf,F,T	D,Mf,Mxf,F,T
3				D,Mf,Mxf,F,T	D,Mf,Mxf,F,T	D,Mf,Mxf,F,T
4					D,Mf,Mxf,F,T	D,Mf,Mxf,F,T
5						D,Mf,Mxf,F,T

Playback tapes 1–3 were from local birds whereas 4–6 are from distant locations. Variables differing significantly ($P < 0.01$) are in bold.

D = duration of song; Mf = minimum frequency; Mxf = maximum frequency; F = frequency range; T = time in seconds between songs.

from the end of playback to departure from nest was scored as zero. One observer watched the nest and the male's initial flight direction and location and a second or third observer operated the playback and observed the male if he approached that location. Each person used a two-way radio to transmit all observations to a radio receiver attached to the video camera. The camera recorded the radioed observations by two or three observers of the male's behavior when he left the nest and provided a time line for each trial. Observers tracked the male's location by sight and vocalizations and noted his location and direction from the playback and height until he moved away from the playback location. The compass direction from the nest to the first place the male landed after leaving the nest and the closest he approached the playback location were then measured. It was difficult to calculate exact compass directions due to forest vegetation so we scored responses as directly toward the playback (within 10°) or not toward the playback site (anything greater than 10°).

One of us (JH) extracted the data from the videotapes. We separated behavioral measures into those on or leaving the nest and after having left the nest. These measures are not correlated with one another so we compared each in terms of responses to local and foreign song playbacks rather than resorting to a principal components measure. We used parametric *t*-tests on song characteristics and nonparametric tests on responses to playbacks because we wished to use distribution-free tests for the behavioral data (Siegel 1956). We compare the same males' responses to both foreign and local songs so the data are not entirely independent. To be conservative, data were subjected to two-tailed Wilcoxon matched-pairs signed-ranks tests (SPSS) even though we predicted a stronger response to local songs. Values are presented as mean \pm 1 SD.

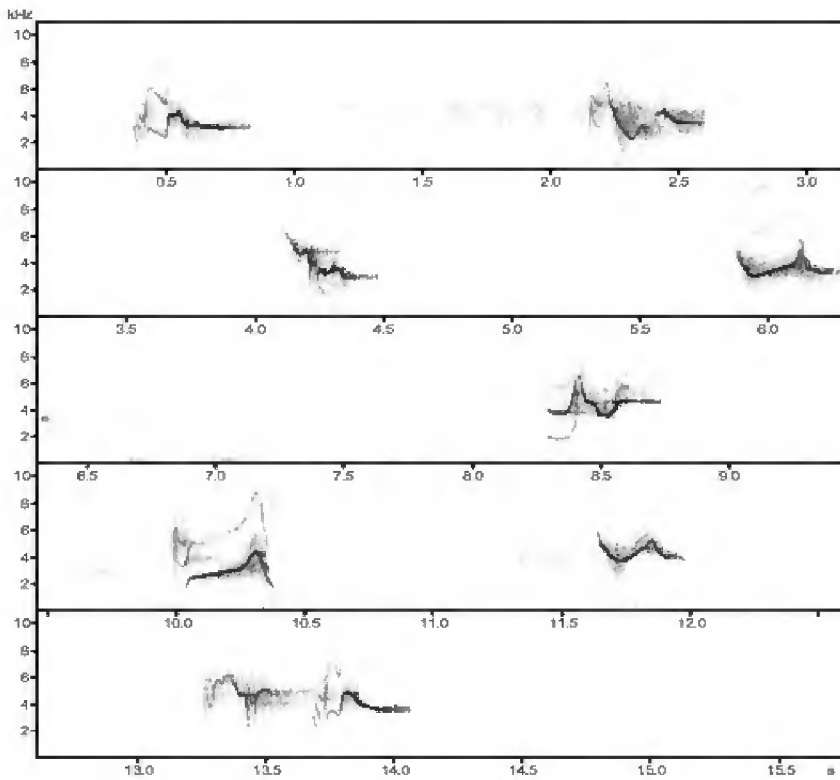
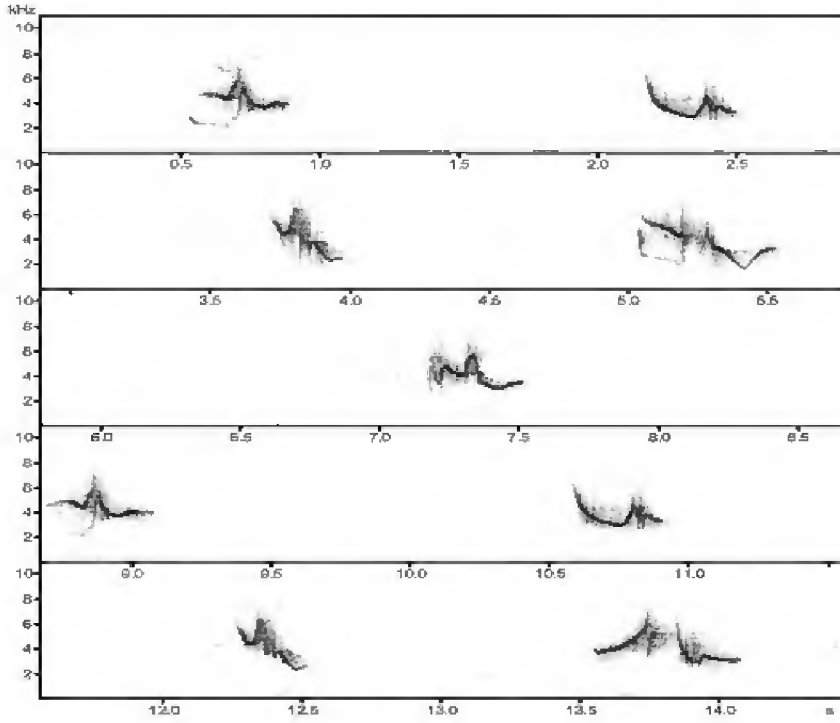
RESULTS

A sample of local and foreign songs illustrating differences in frequency modulation is provided

in Figure 2. The songs included in the local and foreign playback tapes differed significantly in mean song duration ($t = -5.15$, $P = 0.0001$), minimum ($t = 2.01$, $P = 0.05$) and maximum ($t = -8.36$, $P = 0.0001$) frequencies, frequency range ($t = -7.55$, $P = 0.0001$), and timing between songs ($t = 3.64$, $P = 0.0001$, $df = 2$ for these independent samples *t*-tests). Foreign songs were longer, higher, and lower in frequency, and were delivered more rapidly than local songs. However, these overall comparisons were not consistent as shown by paired comparisons that more accurately represent what the focal birds were hearing than the overall means for the six playback tapes combined (Table 2). There was no consistent difference in these general parameters between individual playback tapes regardless of whether they were from foreign or local vireos. For example, songs included on our local songs playback tape 1 differed significantly from those included on our local songs playback tape 2 in mean duration, maximum and minimum frequencies, and frequency range, but did not differ from the songs included on our foreign song playback tape 6 in any of these measurements (Table 2).

During some playback experiments, focal males did not respond. Instead, they flew to the forest canopy and began foraging, as they normally do when relieved by mates after a long incubation bout. Male vireos responded significantly more often ($\chi^2_1 = 9.03$, $P < 0.01$) to playback of local songs (30 of 32 experiments) than to playback of foreign songs (18 of 29 experiments). We also found no difference in the tendency of males to respond to foreign songs played from 50 m or 100 m ($\chi^2_1 = 2.5$, $P < 0.1$), even though songs played back from 100 m would be more degraded when they reached the incubating male vireos. The more time that transpired between when a bird had last heard a foreign song playback and when it left its nest the less likely it was to respond to the playback (Mann-Whitney *U*-test, $N = 29$, $Z = -2.64$, $P = 0.01$). We now present data only from trials where focal males responded to playback.

Fig. 2. Spectrograms of a sequence of Blue-headed Vireo songs from a local male (upper) and a foreign male (bottom) used in the playback experiments. In each sequence, songs are repeated in a chain-like fashion before the bird switches to another sequence. The local male repeats his sequence of five songs at 8.5 s whereas the foreign male example shows a longer sequence of eight songs before beginning to repeat the sequence after 13.5 s. The timing between songs is typical of the song rate during broadcast singing bouts.



Responses of males on their nests. Male Blue-headed Vireos left their nests before their mate arrived to relieve them more often (Wilcoxon Signed-Rank Test, $Z = -2.83$, $P < 0.001$) in response to playback of local songs (8 of 14 males) than to playback of foreign songs (none of 14 males). Thirteen males sang from the nest in response to playback of local songs, whereas only eight sang in response to playback of foreign songs ($Z = -2.45$, $P < 0.01$). When they left nests, males flew directly toward the speaker location more often in response to playback of local songs (24 of 30 trials) than to playback of foreign songs (10 of 19 trials; $Z = -1.89$, $P < 0.05$).

Ability to range playback locations. Males approached the playback locations by landing and then resuming flight. This approach pattern was measured for responses to playback at 50 and 100 m from nest sites. The distance from the playback locations to the point where approaching males first stopped was 20.6 ± 9.5 m in response to local songs and 23.8 ± 9.5 m in response to foreign songs for playback sites 50 m from nest sites and, for playback sites 100 m from nest sites, these distances were 38.1 ± 13.0 m and 34.0 ± 18.4 m, respectively. Approach distances in response to playback at 50 and 100 m from nest sites did not differ ($Z = -0.54$, $P = 0.59$, $N = 14$) so these data were combined.

We found no differences in response to playback of local and foreign songs in either the time it took for males to leave nests after playbacks began or the time between when a bird last heard a playback until it departed from the nest (Table 3). In addition, there was no correlation

between when a male had last heard a song and its closest approach to the speaker site for playback of either local ($r = -0.30$, $P = 0.43$, $N = 7$) or foreign ($r = -0.45$, $P = 0.31$, $N = 9$) songs. We also found no difference in the total time birds spent responding to foreign or local songs after departing nests (Table 3). However, after leaving nests, males approached the silent speaker significantly more closely (closest approach) in response to playback of local songs than in response to foreign songs (Table 3).

DISCUSSION

Comparing ranging of local and foreign songs. Song ranging allows males to respond prudently to rivals by using behaviors and energy appropriate to the situation (Mathevon and Aubin 1997). Male Blue-headed Vireos approached the locations where speakers, now silent, had played back undegraded conspecific songs. Responding males flew directly toward the silent playback sites thus assessing both distance and direction in their ranging. The birds treated both playback types as salient, but differed in their ability to locate them. The lack of differences in responses, except for their ability to find the source of the playback (closest approach) suggests that male Blue-headed Vireos were equally motivated by the two playback types.

Songs recorded from local males, most of which were in the repertoires of our focal males (James 1981, ESM unpubl. data), were ranged more accurately. While incubating, males responded more strongly to local songs and, when they left the nest, approached the speaker more

Table 3. Responses of male Blue-headed Vireos ($N = 14$) to playbacks of local and foreign songs after incubation bouts.

Variable	Local songs	Foreign songs	Z^a	P
Time from playback start to nest departure (min)	13.6 ± 11.9	13.2 ± 7.9	-0.03	0.96
Time from playback end to nest departure (min)	1.0 ± 1.7	2.2 ± 2.6	-1.35	0.12
Time to first stop (s)	38.6 ± 35.9	41.9 ± 37.6	-0.15	0.88
Time to closest approach (s)	193 ± 214.5	116 ± 195.5	-1.41	0.16
Distance flown to first stop (m)	33.0 ± 19.8	41.2 ± 18.7	-1.66	0.10
Closest approach to speaker (m)	13.8 ± 8.8	34.1 ± 16.4	-2.92	0.001
Total time responding after departing nest (min)	7.6 ± 6.2	5.7 ± 4.1	-1.17	0.24

Values are presented as mean \pm 1 SD.

^aWilcoxon signed-ranks tests.

closely in response to playback of local songs. In the absence of confounding variables, we suggest that it was the increased ability of the birds to range songs in their own repertoire, rather than a response to general features of song degradation, that underlies the difference in accuracy. With the exception of frequency modulation, the foreign and local songs were similar. This similarity suggests that ranging by Blue-headed Vireos requires songs to be very similar to one in a bird's memory before it can be ranged. Studies of the neurophysiologic basis of degradation assessment mechanisms are still lacking (Morton 1986).

Incubating male Blue-headed Vireos ranged the source of song playbacks from their nests. They must have remembered these locations because they immediately flew to them. The length of time they were able to remember playback locations was not determined because we repeated playbacks every 5–10 min until males left the nest. Males remembered playback locations for an average of 2.5 min after last hearing the playback. One male flew immediately to the playback site 6.2 min after the last playback had ended. Anecdotal evidence also suggests that an incubating male can remember more than one location. Uncertain that our first playback during another study (Chiver et al. 2007) was on a focal male's territory, we moved the speaker location 50 m between the first and second playbacks. When this male left his nest, he first visited the most recent playback site and then flew to the first playback site. Thus, males may be able to range multiple locations and track intruders while they incubate, reducing the need to leave nests during an incubation bout to defend territory.

Our results support those of other studies that show birds range songs in their repertoires more accurately than songs not in their repertoires (McGregor et al. 1983, McGregor and Falls 1984, McGregor and Krebs 1984, Shy and Morton 1986). The sounds used for playbacks in these studies were degraded by playback and rerecording through natural habitat or by propagation through natural habitat without prior degradation (e.g., Shy and Morton 1986; this study). In contrast, experiments using playback of songs degraded artificially in a large room or attic fail to support Morton's (1982, 1986) hypothesis that degradation is measured by referral to a song represented in the neural song control

system used as an internal standard (Wiley and Godard 1996, Naguib and Wiley 2001). Why might signals, degraded artificially in this manner, pose a problem? Perception of degradation involves precise time assessment, and birds may be able to resolve sounds separated by as little as 1–2 ms (Dooling 1982). If this ability is common in songbirds, it may allow them to detect differences in reverberation pathway lengths. A song in nature begins generating echoes near its source as well as from points increasingly nearer to the listener, producing a complex mix of time-delayed echoes. Although echoes off walls in a room introduce reverberation, such signals used in playback studies in the field do not include the differences in pathway lengths of natural reverberations. Also, in nature, the increase in reverberation with distance is counteracted by disappearance of low amplitude reverberation due to attenuation (Fotheringham et al. 1997). This suggests that both changes in energy distribution in sound frequency and changes in reverberation pathway lengths must be assessed by a bird for accurate ranging to occur. In the absence of these stimuli, as in a signal degraded in a room, it is likely birds could still differentiate between clear and degraded songs, as demonstrated in a laboratory study (Morton et al. 1986), but it is unlikely they could range them. If so, responses to songs in, or not in, a bird's repertoire would be statistically indistinguishable. However, to conclude that all songs can be ranged regardless of what birds have memorized seems premature.

Wiley and Godard (1996) assumed that the single song type repertoire characteristic of male Kentucky Warblers (*Oporornis formosus*) precluded them from using memorized songs in ranging because each male has its own version. However, Kentucky Warblers have an unusual song. Males change the energy distribution in their songs to match that of rivals. They can accomplish this by shifting the frequency range of their entire song up or down and by changing the distribution of energy within their song, putting more emphasis on higher or lower components to match the frequencies containing the highest amplitude in a rival's song. Morton and Young (1986) described this ability and concluded Kentucky Warblers may appear to have a single song repertoire but their single song functions like a multisong repertoire. By changing the energy allocation of its song, a Kentucky Warbler can match the song of a rival male in the

same way that males in species with many songs match rivals by switching songs. They predicted that this ability would preclude the need for a repertoire of songs in other species sharing the singing ability of Kentucky Warblers. This suggestion has been confirmed for Black-capped Chickadees (Horn et al. 1992) and several other species (reviewed in Christie et al. 2004). This "plastic" way of forming songs, as opposed to categorical perception, is not common.

Ranging in relation to song delivery patterns. A repertoire of categorically perceived songs is by far the most common singing style in songbirds. The manner in which categorical songs are delivered might be influenced by the benefits of selection derived from ranging. The entire song is perceived as a category so, in species with categorical song discrimination, even small differences in song features are perceived as distinct songs (Falls et al. 1988, Weary et al. 1990, Weary and Krebs 1992, Searcy et al. 1999). Searcy et al. (2003) further suggested that geographic discrimination of song by Song Sparrows (*Melospiza melodia*) is not accomplished by recognition of individual notes within songs, but by entire songs. Neurophysiologic studies support a mechanistic basis for song recognition and categorization (Margoliash 1983, Margoliash and Konishi 1985, Mooney et al. 2001).

The stereotyped delivery of categorical song types by Blue-headed Vireos (Martindale 1980) could add a temporal feature to ranging where the degradation of several songs in a fixed sequence could be compared. Each song in the sequence will have a different structure associated with unique degradation properties. A listener could compare degradation changes over a sequence of songs with those same sequences in its own memory. For a ranging bird, this would be like "reading" a sentence rather than listening to individual words. There are other species with stereotyped or Markov-chain singing styles where this hypothesis could be tested (e.g., Dobson and Lemon 1977, Dobson and Lemon 1979, Kroodsma 1979, Martin 1990, Lemon et al. 2000). Because ranging is the more general phenomenon, occurring before the evolution of song learning (Morton 1986, Morton and Derrickson 1996), ranging may have affected both categorical perception as well as singing patterns in species that learn songs.

Ranging and foreign/local discrimination. Ranging affects song structure in two ways. Degradation of songs may be reduced as singers learn those songs better adapted to local habitat acoustics (Hansen 1979, Hunter and Krebs 1979, Gish and Morton 1981) and use them to sound closer to perceivers that have the signals in memory. But, regardless of how well they propagate, the sharing of signals has important functional consequences due to the way ranging works. Shared songs are, by definition, in the neural vocal pathways of all birds sharing the songs. As a consequence of sharing, listeners have accurate cues to a singer's location. The functional consequence of singing shared songs is that these are more threatening to rivals than unshared songs because the location of the "song matcher" is more precise (Krebs et al. 1981), particularly when territorial boundaries are known (Morton 1986).

Such is the case in stable populations. Sharing songs is favored by selection in stable populations because territorial boundaries are well known to the participants when individuals interact over long periods of time (over several breeding seasons). In interactions over well-known territorial boundaries, birds repel rivals best by singing songs they share with them (e.g., in both their repertoires) because their individual locations in relation to these familiar boundaries is important (Owings and Morton 1998: 151, Fig. 3.13). When population turnover is low and climatic conditions favor sedentary behavior, single song repertoires, all shared, often result (Morton 1986). Song sharing, whether or not associated with any acoustic adaptation to habitat, is the most widespread aspect of singing behavior predicted by ranging theory. The close positive relation between neighborhood stability and song sharing is well documented (reviewed in Rogers 2004). As was pointed out earlier (Morton 1982, 1986), the functional reason for the evolution of this relationship is the dependency of ranging on songs in the song neural control network, as we illustrated here with the Blue-headed Vireo. Morton (1986: 75–76) specifically predicted that: "Listeners in dialect species should respond strongly only to songs they are able to range. Songs from other dialects. . . . should evoke weak responses since dialect species use song only for threat. . . ." This prediction has been supported in dialect

discrimination studies (e.g., Nelson and Soha 2004). Dialects and matched counter-singing are functionally related because they share the same origin. Both rely on distance assessment through ranging. Ranging and dialect discrimination studies are complimentary and differ only in their level of analysis. Foreign/local dialect discrimination focuses on the population level whereas ranging represents a mechanism operating at the level of individual selection and provides a functional interpretation for why and how song discrimination occurs.

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