Song transmission and auditory perception of distance in wood warblers (Parulinae)

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Abstract. The influence of breeding habitat on the evolution of song structure was examined in four wood warbler species of the sub-family Parulinae. The effects of song degradation on the ability of territorial paruline males to estimate distance by means of acoustic cues was also investigated. Song transmission characteristics of paruline breeding habitats were compared in southeastern Ontario, Canada; songs native to the habitat in which they were broadcast did not degrade less than foreign songs. The response of territorial paruline males to playback of 'near' (undegraded) and 'far' (degraded) conspecific songs broadcast from the same position within the territory at the same amplitude were then compared. Males responded to near songs as they would to a conspecific territorial intruder and with less intensity to far songs, suggesting that males may use cues from song degradation to estimate distance to vocal conspecifics. Our results from transmission and playback experiments are discussed with respect to the ranging hypothesis, which proposes that selection should favour males that structure songs to minimize their degradation, so that songs function to disrupt or intimidate rivals by providing unreliable distance cues.

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It is important for territorial male songbirds to gain information about the location of vocal conspecifics; a singer within the receiver's territory can pose a direct threat to territory tenure and paternity, but a singer outside the territory poses little or no threat at all (McGregor 1991). It is also important for males, separated by a distance, to gather this information using acoustic cues, because visual signalling is often impossible in dense vegetation or under conditions of low light levels at dawn or dusk. Playback experiments have shown that territorial males of some songbird species are able to gather information about distance by means of acoustic cues (reviewed by McGregor 1994). In these experiments, males discriminated between undegraded songs (recorded at close range) and degraded songs (recorded from afar), even though all songs were broadcast to subjects at the same amplitude,

suggesting that distance was estimated using cues from sound degradation (McGregor & Krebs 1984; Naguib 1996a, b; Wiley & Goddard 1996; but see Fotheringham & Ratcliffe 1995).

The acoustic adaptation hypothesis proposes that selection should favour male songbirds that structure their songs to minimize degradation and maximize transmission range in their native breeding habitat (Morton 1970). Males that sing such songs may be at a selective advantage because they could attract conspecific females by song from a larger area. It has also been suggested that males with songs structured to minimize degradation benefit by disrupting and/or intimidating conspecific male receivers that judge these signallers to be closer than they actually are (Morton 1982, 1986). Several studies have provided evidence to support the acoustic adaptation hypothesis by: (1) matching characteristics of song structure to breeding habitat across many passerine species (Morton 1975; Wiley 1991); (2) relating differences in song structure to habitat across populations of a single species (Hunter & Krebs 1979; Handford 1988); or (3) conducting detailed transmission experiments to compare the magnitude of degradation of songs propagated through

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native versus foreign habitats (Gish & Morton 1981). Some researchers, however, have considered predictions from the acoustic adaptation hypothesis to be counterintuitive. For example, although songs structured to maximize transmission range may cost song receivers time and energy (as they respond unnecessarily to songs from afar), they may also cost signallers by attracting predators from a larger area (Wiley & Richards 1982). Songbirds that structure their songs to minimize degradation also make it difficult for neighbours to estimate their location by means of acoustic cues; two territorial neighbours, both singing from within their respective boundaries, may mutually benefit by assessing each other's acoustic distance and consequently reducing the energetic cost of territorial defence (McGregor 1994).

In this study, we used playback techniques to test whether territorial male yellow warblers, *Dendroica petechia*, common yellowthroats, *Geothlypis trichas*, ovenbirds, *Seiurus aurocapillus*, and American redstarts, *Setophaga ruticilla*, can estimate distance using cues from sound degradation. We also performed transmission experiments to test whether songs of the four species are structured to reduce degradation resulting from propagation through native breeding habitat. Studies investigating environmental influences on avian singing behaviour have invariably used only one species; by studying four closely related species, we hoped to provide comparative results that may be more generally applicable to other passerine species. This is the first study in which both acoustic adaptation to the local environment and the behaviour of song receivers were investigated.

METHODS

Study Species and Site

Yellow warblers, common yellowthroats, ovenbirds and American redstarts are all members of the sub-family Parulinae. All four species are abundant during the breeding season (May to July) at our study site near the Queen's University Biological Station (QUBS), Chaffey's Lock, Ontario, Canada (45°N, 76°W). Yellow warblers are found at high densities (10–100 pairs/km²) in wet meadows and marsh edges, as well as at forest borders in shrubby regrowth.

Common yellowthroats breed in wet shrubby areas, often at the edges of lakes or streams as well as in swampy forests (5–10 pairs/km²). Ovenbirds are one of the most abundant forest-dwelling species in our study area (10–100 pairs/km²), breeding in regrowth and mature deciduous and mixed woods. American redstarts breed mostly in regrowth deciduous forests (5–10 pairs/km²), as well as in the subcanopy of mature woods (Martin & Robertson 1994). Territorial males of all four species respond aggressively to playback stimuli (e.g. Weeden & Falls 1959; Ficken & Ficken 1970; Wunderle 1978, 1979; Weary et al. 1994). Although yellow warblers and American redstarts have two modes of singing (MacNally & Lemon 1985; Spector 1991), playback studies have shown that song mode has no effect on male response to playback, at least during the early stages of the breeding season (Ficken & Ficken 1970; Weary et al. 1994). Ovenbirds and common yellowthroats sing only one primary song type during the breeding season (Wunderle 1978, 1979; Lein 1981; Lemon et al. 1987; Ritchison 1995).

Playback Experiments

Song stimuli

We recorded songs from territorial males of each of the four study species at QUBS between 24 April and 2 June 1993. High-quality song recordings were made at distances of 4–8 m from each bird using a Sony Walkman Professional stereo cassette recorder WM-D3 and an Audio-technica 815a unidirectional microphone. Three songs recorded from three individuals of each of the four species were digitized using SoundEdit, a sound analysis package for Macintosh computers (Capps et al. 1989). These songs were filtered (0–2 and 9–16 kHz to 0 dB) to eliminate background noise outside the frequency range of the signals, and the maximum amplitude was standardized between songs. Song replicates were used for each species to minimize concerns regarding the external validity of playback experiments (McGregor et al. 1992).

We broadcast yellow warbler and common yellowthroat songs in an open wet field along the edge of a marsh to create degraded songs for playback. Several yellow warbler and common yellowthroat males defended territories at this transmission site. We broadcast ovenbird and

American redstart songs in regrowth deciduous forest (in which males of both species held territories) for the same purpose. Songs were broadcast using a Sony Walkman Professional stereo cassette recorder WM-D3 and a Sony SRS-77G Active Speaker System on a calm and clear day between 0700 and 1000 hours Eastern Standard Time (EST) on 3 May 1994, when leaves were not yet out on deciduous trees. A Realistic Sound Level Meter 33-2050 at a distance of 5 m from the broadcast speaker measured the loudness of broadcast songs to be 85 ± 5 dB, which approximates the average natural singing amplitude for all four species (J. R. Fotheringham, personal observation). Volume settings on the cassette recorder and the speaker were kept constant during song transmission. We recorded these songs from distances of 10 and 100 m using a Sony Walkman Professional stereo cassette recorder WM-D3 and a Sennheiser MKH 816 microphone. These re-recorded songs were again digitized, filtered to remove background noise outside the frequency range of the signals, and standardized for maximum amplitude using SoundEdit. Songs re-recorded at 10 m were used in playback experiments as 'near' and undegraded song stimuli; those at 100 m were used as 'far' and degraded song stimuli (Fig. 1).

Playback procedure

Conspecific songs were played back to 12 territorial males of each of the four species between 0700 and 1115 hours and between 1700 and 1900 hours EST, 10 May–6 June 1994, at QUBS. We broadcast near and far songs at the same amplitude from the estimated centre of each subject's territory using a Sony Walkman Professional stereo cassette recorder WM-D3 and a Sony SRS-77G Active Speaker System. In all playback experiments, the speaker was 2–4 m above the ground. A Realistic Sound Level Meter 33-2050 at a distance of 5 m from the broadcast speaker measured the loudness of the broadcast songs to be 85 ± 5 dB, and volume settings on the cassette recorder and the playback speaker were kept constant throughout all playback experiments.

We broadcast songs to a chosen test individual in a single playback session that consisted of two trials: one trial for near songs and the other for far songs. Each trial lasted 1 min. During both trials, as well as for 1 min before and after each trial,

behavioural observations were dictated into a Sony ECM-144 Electret Condenser Microphone and a Sony Walkman Professional stereo cassette recorder WM-D3 from a distance greater than 10 m from the broadcast speaker. As an aid for estimating distances, we placed a 20-m measuring tape on the ground with the speaker at its centre. The two playback trials were separated by three minutes. Each subject was tested only once. We used a repeated-measures design to control for variation in behavioural response between subjects. The assignment of songs to trials was block-randomized prior to the experiment to control for order effects and influence of song version.

During the playback trials, songs were broadcast at rates simulating those observed in the wild; yellow warbler songs were broadcast every 8 s (J. R. Fotheringham, unpublished data), common yellowthroat songs were broadcast at 10-s intervals (Wunderle 1978, 1979), ovenbird songs were broadcast every 10 s (Ficken & Ficken 1970), and American redstart songs were broadcast every 6 s (MacNally & Lemon 1985).

### Behavioural categories and analysis

The behavioural responses of subjects for each of the four species were compared using Wilcoxon signed-ranks tests (two-tailed) in five categories: number of flights towards the playback speaker, latency to first flight towards the speaker in seconds, number of songs, closest approach to speaker in metres and minimum perch height in metres above the ground.

Territorial male songbirds typically sing from high perches to vocal rivals outside their territory, but directly approach and physically displace vocal territory intruders (e.g. Richards 1981; Shackleton et al. 1992; Dabelsteen et al. 1993; McGregor 1994). If territorial paruline males can estimate distance by means of song degradation cues, we predicted that playback subjects would make more flights towards the speaker, take less time to respond, sing less, approach the speaker more closely and perch closer to the ground in response to near songs (relative to far songs).

Transmission Experiments

Sites

We conducted song transmission experiments between 0700 and 1100 hours and between 1600 and 2100 hours EST, 7–12 June 1994. To choose
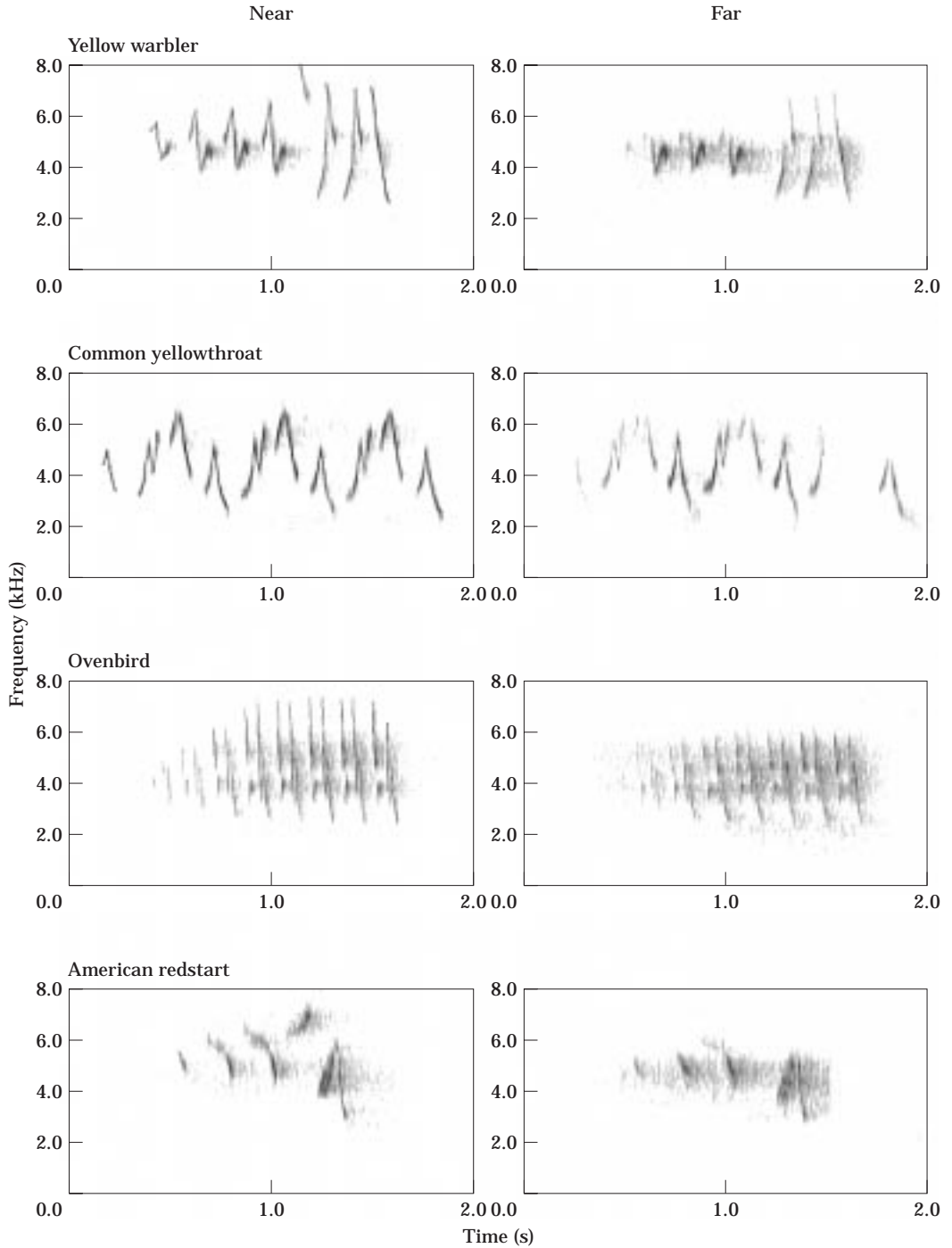
Figure 1. Sonagrams of 'near' and 'far' songs used as playback stimuli presented to territorial male yellow warblers, common yellowthroats, ovenbirds and American redstarts. One of three song versions used in the playback experiments is shown for each species.

sites for transmission experiments that represented native breeding habitats for each of the four species, we randomly selected three of the 12 territories in which successful playback experiments were carried out for each species (i.e. for each of the four paruline species, three representative habitats were used as transmission sites). Transmission experiments were carried out during calm and clear weather conditions, when leaves were out on deciduous trees (this allowed for measurement of maximum effects of degradation for all species' songs, due to denser vegetation). The terrain was relatively flat at all 12 selected sites.
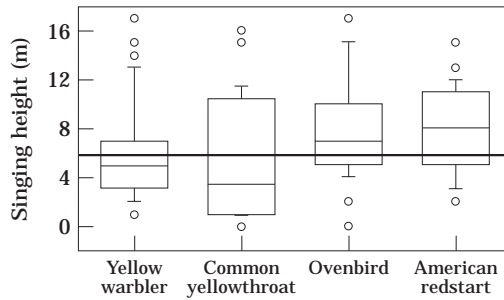
Songs

Natural songs were recorded from males of each of the four species between 24 April and 2 June 1993 (as described above). Two songs from each of three individuals of each of the four species were digitized, filtered to eliminate background noise outside the frequency range of the signals, and standardized for maximum amplitude using SoundEdit. All 24 songs were broadcast at each transmission site (i.e. songs both native and foreign to each habitat were broadcast).

We broadcast 10 replicates of each of the 24 songs at all 12 transmission sites using a Sony Walkman Professional cassette recorder WM-D3 and a Sony SRS-77G Active Speaker System at a height of 6 m. This height falls within the inter-quartile range of natural song perch heights for males of all four species, as observed within the first minute prior to playback trials (Fig. 2). The broadcast amplitude was measured at 85 ± 5 dB using a Realistic Sound Level Meter 33-2050 at 5 m from the speaker. We recorded songs at 10, 25, 50, 75 and 100 m from the speaker using a Sony Walkman Professional cassette recorder WM-D3 and a Sennheiser MKH816 microphone, also at a height of 6 m. In sum, 10 samples of two songs from each of three individuals of four species were broadcast and recorded from each of five distances at 12 transmission sites.

Analysis

The quantity and quality of bird songs are affected as they travel through an environment. The quantity of sound decreases over distance; sound amplitude falls as a result of geometrical

Figure 2. Natural singing heights observed for territorial male yellow warblers, common yellowthroats, ovenbirds and American redstarts during the first minute prior to playback trials. In transmission experiments, songs were broadcast and recorded from a height of 6 m (thick black line), which falls within the inter-quartile range of the singing heights for each species. Horizontal lines in box plots represent 10th, 25th, 50th 75th and 90th percentiles from bottom to top and all data points outside this range are shown ($N=12$ birds of each species).

spreading and general absorption of sound energy. This is called sound attenuation (Morton 1975; Wiley & Richards 1978, 1982). The quality of a signal also decreases over distance; it is distorted by reverberations, frequency-dependent attenuation and irregular amplitude fluctuations. Reverberations are echoes caused by the reflection of sound energy off solid surfaces (e.g. the ground or vegetation), frequency-dependent attenuation results from the selective absorption and scattering of higher frequencies, and irregular fluctuations of amplitude are caused by variation in wind speed or the movements of vegetation in the path of sound transmission. Qualitative changes in song structure are collectively referred to as sound degradation (e.g. Morton 1975, 1986; Wiley & Richards 1982; McGregor 1994). Sound degradation, as opposed to sound attenuation, should be used by birds to estimate distance because, although the degree of sound degradation is predictable over distance in any environment, sound attenuation depends on atmospheric conditions, ambient noise and the behaviour of the singer (Richards 1981; Morton 1982; Wiley & Richards 1982; McGregor 1994).

We analysed songs using a KAY Elemetrics DSP Sona-Graph Model 5500 to determine whether songs of different species degrade differently in different habitats. We measured duration, maximum frequency and frequency at peak

amplitude for three recorded songs haphazardly selected from the 10 replicates of each of the 24 songs at each distance at each site. We used sonagrams and power spectra with a 300-Hz filter to measure durations, and with a 59-Hz filter to measure maximum frequency and frequency at peak amplitude of songs. While measuring song durations, power spectra were used in tandem with sonagrams to reliably assess the end of each signal (i.e. the point at which the amplitude of reverberated tails of songs falls below that of background noise). Song duration measures estimate the effects of reverberation on song structure, and measures of maximum frequency and frequency at peak amplitude were used to estimate the effects of frequency-dependent attenuation.

A three-factor ANOVA (factor 1 is species' song, factor 2 is species' habitat, factor 3 is distance) was used to determine whether the effects of reverberation and frequency-dependent attenuation varied between the four species' songs and habitats, over distances 0–100 m. For this analysis, the ratio of change in song duration, maximum frequency and frequency at peak amplitude was calculated by dividing song measures at each distance by those at source, allowing for comparisons among species (e.g. ratio of change in song duration, maximum frequency or frequency at peak amplitude at 0 m equals 1.0 for all species' songs in all habitats). The ratio of change in song duration increases over distance as a result of reverberations, but the ratio of change in maximum frequency and frequency at peak amplitude decreases over distance as a result of frequency-dependent attenuation. Since sound degradation, as opposed to attenuation, should be used by male songbirds to estimate distance, songs that were completely attenuated at 100 m were not included in the analysis.

Transmission curves were plotted to compare how songs of different species degrade over distance within a given habitat, and to determine whether songs broadcast in native habitat degrade more or less than foreign songs. If paruline songs are structured to degrade minimally in native habitat, we predicted a significant three-way interaction (three-factor ANOVA) between species' song, species' habitat and distance, indicating that songs of different species degrade differently over distance in different habitats. Then, we predicted that transmission curves would show that songs

native to the habitat in which they were broadcast degrade less than foreign songs.

RESULTS

Playback Experiments

Territorial males of each of the four species responded aggressively to both playback trials by approaching the playback speaker. Three song versions were presented to playback subjects of each species; since there was no effect of song version on subject response for any of the five behavioural categories (one-factor ANOVA; $P>0.05$), behavioural data for all song versions were pooled for each species.

Yellow warbler, common yellowthroat, ovenbird and American redstart males responded differently to playback of near versus far conspecific songs (Fig. 3). These results are consistent with the notion that males of each species may be able to estimate distance by means of sound degradation cues. Yellow warbler males made more flights towards the playback speaker, responded more quickly to playback stimuli, approached the speaker more closely and perched lower to the ground in response to near songs (relative to far songs). Common yellowthroat males made more flights towards the speaker, took less time to respond, sang less and perched lower to the ground in response to near songs than far songs. In response to near songs relative to far songs, territorial male ovenbirds made more flights towards the speaker, took less time to respond, approached the speaker more closely, and perched lower to the ground. American redstart males made more flights towards the speaker, sang less, and came closer to the speaker when responding to near songs, relative to far songs.

Transmission Experiments

Six versions of each of the four species' songs were broadcast in three habitats native to each species. We found a significant effect of song version on measures of reverberation and frequency-dependent attenuation for ovenbird and common yellowthroat songs (one-factor ANOVAs; $F_{1,5}>3.2$, $P<0.008$). There was also a significant effect of habitat replicate on measures of reverberation and frequency-dependent attenuation for all four species (one-factor ANOVAs; $F_{1,2}>3.7$, $P<0.03$).
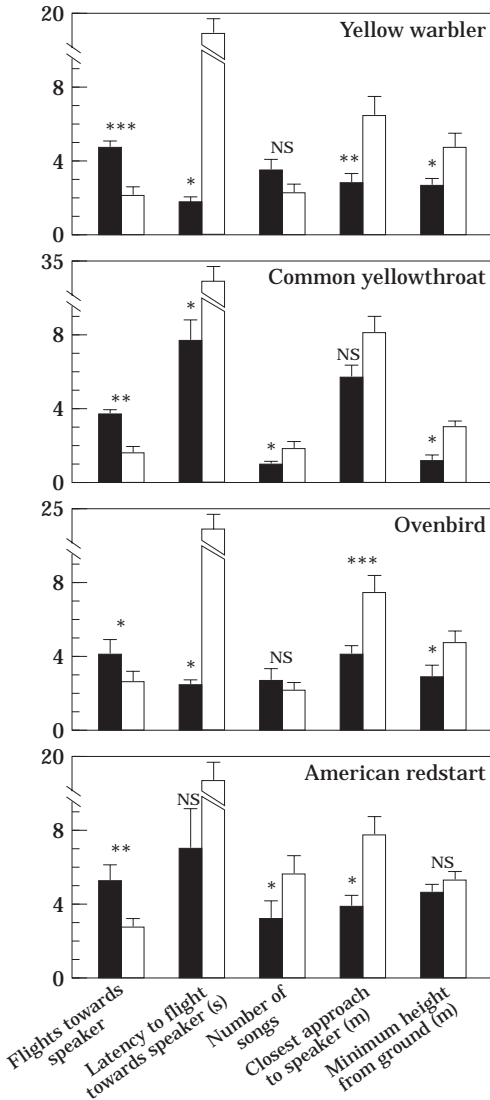
Figure 3. Response of territorial male yellow warblers, common yellowthroats, ovenbirds and American redstarts to playback stimuli of near (■) and far (□) conspecific songs (two-tailed Wilcoxon signed ranks test; $N=12$ birds). Sequential Bonferroni corrected for figure-wide significance (Rice 1989). $*P<0.05$; $**P<0.01$; $***P<0.005$.

Despite this variation within species' songs and breeding habitats, a three-factor ANOVA showed that the ratio of change in song duration, maximum frequency and frequency at peak amplitude varied significantly between yellow warbler,

common yellowthroat, ovenbird and American redstart songs in breeding habitats representative of each of the species, transmitted over distances of 0–100 m. This result was found even after we pooled data for song versions and habitat replicates for each species (Table I). Thus, the songs of different paruline species degrade differently over distance in different habitats.

Transmission curves illustrate the effects of reverberation and frequency-dependent attenuation on songs, allowing for qualitative comparisons between songs of the four species within each species' native habitat. The effects of reverberation (measured as the ratio of change in song duration) increased over distance to about 60 m, past which it decreased (Fig. 4). Although reverberation increased past 60 m, we believe that the effects of reverberation, measured as song duration, decreased due to attenuation of low amplitude ends of the songs, which resulted from decreasing signal-to-noise ratio over distance (Fotheringham & Ratcliffe 1995). This pattern was evident for all species' songs in all habitats, although reverberation in general was more pronounced in forest (ovenbird and American redstart) habitats than open (yellow warbler and common yellowthroat) habitats. Songs native to the habitat in which they were broadcast did not reverberate less than foreign songs.

The effects of frequency-dependent attenuation (measured as the ratio of change in song maximum frequency) decreased over distance for all species' songs in all but one of the habitats (Fig. 5). In common yellowthroat habitat, the maximum frequency of songs of all four species did not change over distances of 0–100 m. The ratio of change in maximum frequency of yellow warbler, common yellowthroat and American redstart songs, broadcast in native habitat, did not decrease over distance less than foreign songs. Frequency-dependent attenuation of ovenbird songs broadcast in ovenbird breeding habitat was less, however, than for songs of the other three species.

The effects of frequency-dependent attenuation (measured as the ratio of change in song frequency at peak amplitude) decreased over distance for all species' songs in all habitats (Fig. 6). High-frequency components of songs native to the habitat in which they were broadcast did not attenuate over distance less than foreign songs, with one exception; ovenbird songs broadcast in

Table I. Results of three-factor ANOVA (factor 1 is species' song, factor 2 is species' habitat, factor 3 is distance), showing that the songs of yellow warblers, common yellowthroats, ovenbirds and American redstarts degrade differently in different habitats

Effect	Measure	df	F	P
Song	Reverberation*	3	103.8	0.002
	Frequency-dependent attenuation I†	3	25.6	0.002
	Frequency-dependent attenuation II‡	3	2.3	0.07
Habitat	Reverberation	3	26.9	0.002
	Frequency-dependent attenuation I	3	47.2	0.002
	Frequency-dependent attenuation II	3	53.8	0.002
Distance	Reverberation	5	122.0	0.002
	Frequency-dependent attenuation I	5	141.2	0.002
	Frequency-dependent attenuation II	5	155.2	0.001
Song+habitat	Reverberation	9	2.4	0.04
	Frequency-dependent attenuation I	9	2.4	0.03
	Frequency-dependent attenuation II	9	2.3	0.02
Song+distance	Reverberation	15	6.6	0.001
	Frequency-dependent attenuation I	15	4.3	0.001
	Frequency-dependent attenuation II	15	2.9	0.001
Habitat+distance	Reverberation	15	21.2	0.001
	Frequency-dependent attenuation I	15	26.3	0.001
	Frequency-dependent attenuation II	15	13.4	0.001
Song+habitat+distance	Reverberation	45	1.8	0.004
	Frequency-dependent attenuation I	45	2.5	0.001
	Frequency-dependent attenuation II	45	2.4	0.001

Sequential Bonferroni corrected for table-wide significance (Rice 1989).
*Measured as proportional change in song duration.
†Measured as proportional change in maximum frequency of song.
‡Measured as proportional change in frequency at peak amplitude of song.

ovenbird breeding habitat degraded less than songs of the other three species. In sum, only ovenbird songs appeared to retain their structure better than the others over distance in native habitat, and this is true for measures of frequency-dependent attenuation but not reverberation.

DISCUSSION

Playback Experiments

Territorial male yellow warblers, common yellowthroats, ovenbirds and American redstarts responded to near songs as they would to a conspecific territorial intruder, and with less intensity to far songs. These results suggest that male paruline warblers may be able to perceive song degradation and estimate distance, because playback subjects responded less aggressively, took longer to respond and sang more from higher perches in response to far songs relative to near songs. Such differences have commonly been interpreted as evidence for distance estimation (McGregor 1994).

Our methods do not rule out the possibility that degraded songs elicited a different (weaker) response because they lack some species-specific information. We suggest that future experiments testing auditory distance perception in songbirds use a third playback stimulus, in addition to near and far songs. Interpreting differences in response to near and far songs may be facilitated by measuring the response of playback subjects to songs re-recorded at a distance approximating the radius of an average territory. If males respond to 'half territory' degraded songs as they do to near songs and still respond with less intensity to far songs, then one could argue that distance is being assessed, because the perceived distance of 'half territory' degraded songs is still within the territory boundary. If, however, response to 'half territory' degraded songs is diminished or different from that observed when near songs are broadcast near the territory boundary, then
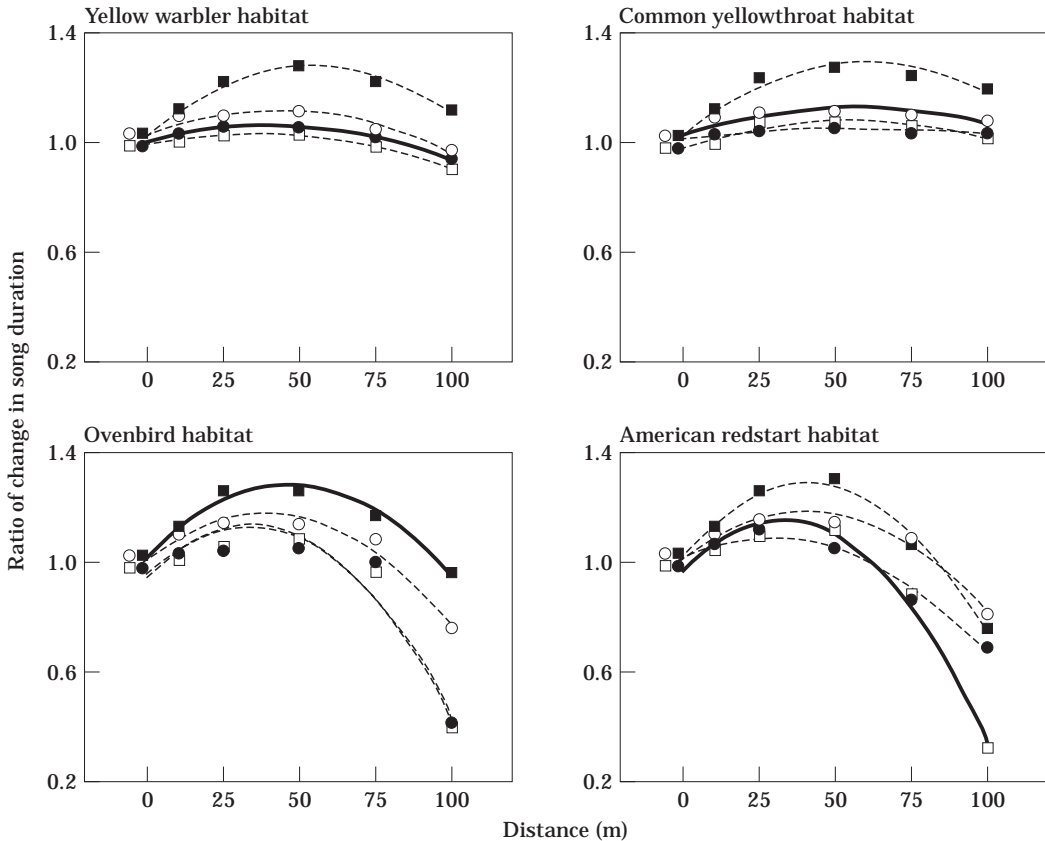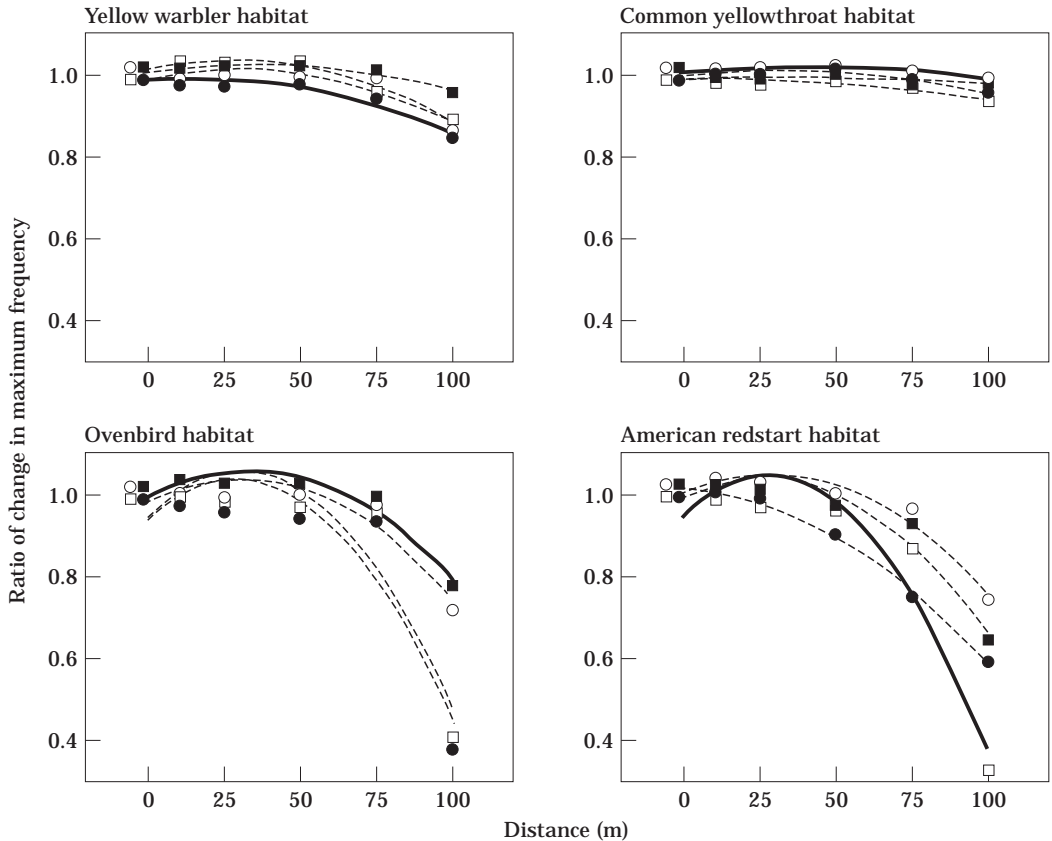
Figure 4. Transmission curves showing the effects of reverberation on yellow warbler (●), common yellowthroat (○), ovenbird (■) and American redstart (□) songs over distance in habitats both native and foreign to each species. Each symbol represents the mean ratio of change in song duration measured from three sonagrams (haphazardly selected from 10 replicates) of each of the six song versions from each species (second-order polynomial regressions: $r > 0.58$, $P < 0.03$). Solid lines represent proportional measures for songs native to the habitat in which they were broadcast; dashed lines represent foreign songs.

differences in response to near and far songs would appear to result from factors other than estimation of acoustic distance (e.g. degraded songs may lack some species-specific information).

In our playback experiments, territorial males of all four warbler species approached the playback speaker to less than 6 m in response to far songs (Fig. 3); perhaps, during the 1-min period of playback of far songs, males moved to several locations around the playback speaker and used triangulation or repeated distance cues during approach to the speaker to assess distance. We recommend that future experiments testing auditory distance perception in songbirds use playback trials shorter than 1 min, to preclude

subjects' close-range experience with the playback speaker (Naguib 1995, 1996b).

Similar studies testing auditory distance perception in other species have shown that near and far songs can be discriminated only when playback subjects are familiar with the song types used as stimuli (McGregor et al. 1983; McGregor & Falls 1984; McGregor & Krebs 1984; but see Wiley & Goddard 1996). These results suggest that male songbirds estimate distance by comparing degraded songs that they hear from afar with a predefined, undegraded 'internal standard' (Morton 1982). Test birds in our study were presumably familiar with the song types used as playback stimuli; although common yellowthroats
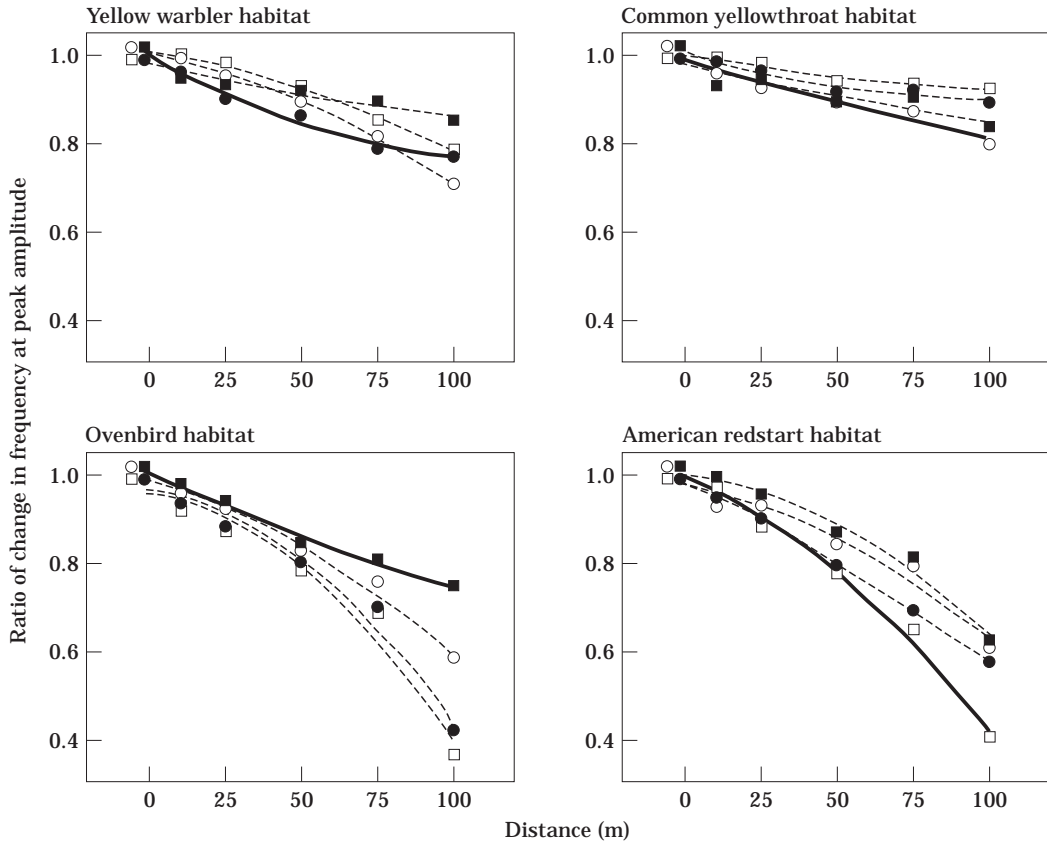
Figure 5. Transmission curves showing the effects of frequency-dependent attenuation on yellow warbler (●), common yellowthroat (○), ovenbird (■) and American redstart (□) songs over distance in habitats both native and foreign to each species (second-order polynomial regressions: $r>0.54$, $P<0.05$). Solid lines represent proportional measures for songs native to the habitat in which they were broadcast; dashed lines represent foreign songs.

and ovenbirds sing only one primary song type, yellow warbler and American redstart males have relatively small song repertoires (1–5 songs per individual; Lemon et al. 1987). Also, all songs used as playback stimuli were originally recorded at QUBS in 1993, where playback studies were carried out on the same populations 1 year later.

Transmission Experiments

Results from transmission experiments indicate that songs of three of the four paruline species are not structured to minimize degradation in the native habitats we examined. Only ovenbird songs appeared to degrade less in native breeding habitat relative to the other songs, and this was true only for measures of frequency-dependent attenuation.

Perhaps ovenbird songs retain their frequency characteristics over distance more than the other three species because ovenbird territories are, on average, three times larger than territories of the other species. In southeastern Ontario and the northeastern United States, yellow warbler, common yellowthroat and American redstart territories average less than 0.6 ha, but ovenbird territories average over 1.8 ha (Sherry & Holmes 1985; Villard et al. 1993; S. Yezerinac, personal communication). Since neighbouring ovenbird males are presumably spaced further apart than males of the other species, the frequency characteristics of ovenbird songs may need to be retained over a distance of greater than 100 m to allow for effective communication, whereas the frequency characteristics of songs of the other warbler species may not.

Figure 6. Transmission curves showing the effects of frequency-dependent attenuation on yellow warbler (●), common yellowthroat (○), ovenbird (■) and American redstart (□) songs over distance in habitats both native and foreign to each species (second-order polynomial regressions: $r>0.76$, $P<0.002$). Solid lines represent proportional measures for songs native to the habitat in which they were broadcast; dashed lines represent foreign songs.

In our transmission experiments with yellow warbler, common yellowthroat and American redstart songs, we did not find evidence to support the acoustic adaptation hypothesis. Perhaps there is no advantage to males of these three species that structure their songs to maximize transmission distance; for example, the potential cost of attracting predators from a large area (Wiley & Richards 1982) may outweigh the benefits of attracting conspecific females from afar. Also, acoustic adaptation to the local environment may be constrained by temporal and spatial variation in habitat structure within each species (Jacobson et al. 1987).

When territorial paruline males gather distance information from sound degradation, it is not known which aspect(s) of degradation they attend to. Naguib (1995) showed that male Carolina wrens, *Thryothorus ludovicianus*, can use either reverberation or frequency-dependent attenuation as a cue for assessing the distance to vocal conspecifics. He also suggested that the accuracy of auditory distance assessment may be enhanced by pooling information from reverberations and frequency-dependent attenuation of songs. Wiley & Goddard (1996) showed that, for Kentucky warblers, *Oporornis formosus*, assessment of reverberation is sufficient for distance estimation. Results of our transmission experiments suggest that male yellow warblers, common yellowthroats, ovenbirds and American redstarts may use frequency characteristics of song degradation for distance perception. Paruline males could compare relative intensities in different frequency

bands of a degraded song with a song at source to most accurately estimate distance. Frequency-dependent attenuation would give the most accurate information about distance, because the ratio of change in frequency at peak amplitude of paruline songs decreased monotonically over distance (Fig. 6), but the ratio of change in song duration, a measure of the effects of reverberation, did not. As shown in Fig. 4, the effects of reverberation increased over distance to about 60 m. At distances greater than 60 m, although true reverberation actually increased, the measurable effects of reverberation decreased due to attenuation of low amplitude ends of the songs. It remains to be seen whether males could assess distance reliably using song duration at distances over 60 m. For example, in cases where receivers detected songs with low signal-to-noise ratios, they might compensate for decreasing song duration by using different criteria for associating reverberation with distance.

General Implications

The ranging hypothesis (Morton 1982, 1986) proposes that auditory distance perception has evolved from an 'arms race' between signallers and receivers. Although selection should favour signallers that structure songs to minimize their degradation, so that songs function to disrupt or intimidate other conspecific males by providing unreliable distance cues, selection should also favour receivers that develop improved abilities to assess limited degradation cues, to accurately estimate distance to signallers.

To date, the ranging hypothesis has not been explicitly tested; however, separate studies, when considered together, provide preliminary evidence to support it. Gish & Morton (1981) recorded songs from male Carolina wrens in two habitats with different vegetation (Maryland and Florida). They found that Maryland songs degraded significantly less in Maryland than in Florida habitats, and the same trend was apparent (but not significant) for Florida songs. Hunter & Krebs (1979) found that great tit, *Parus major*, songs in certain habitats were also structured to reduce degradation. In playback experiments, territorial males of both species were able to perceive sound degradation and estimate distance to conspecific singers (e.g. Richards 1981; McGregor et al. 1983).

At first, these studies appear to support predictions from the ranging hypothesis, with song receivers winning the evolutionary arms race. Although signallers structure their songs to reduce degradation in native habitat, thereby withholding information about distance, receivers are able to estimate distance using limited degradation cues. The interpretation of results from these studies, however, is complicated by several factors. For example, Carolina wrens from Maryland and Florida are considered different subspecies (American Ornithologists' Union 1957), so differences in the song structure between the two may be for reasons other than different sound transmission characteristics of their breeding habitats (McGregor 1994). Similarly, Hunter & Krebs (1979) found that only forest-dwelling great tit males sing songs that are designed to reduce degradation in their native habitat (woodland males do not).

In general, results from our transmission experiments suggest that selection on male paruline warblers to structure their songs to minimize degradation is weak or non-existent. In addition, results from playback experiments suggest that males of all four species may have assessed distance by means of song degradation cues. Together, these results contradict predictions from the ranging hypothesis.

The feasibility of the ranging hypothesis rests not only on the assumption that songs are structured to minimize degradation in native breeding habitat, but also on the ability of male songbirds to sing songs that do not provide cues for distance assessment (Morton 1982, 1986). Transmission studies, however, have shown that song degradation is both unavoidable and predictable over distance in any relatively homogeneous environment (e.g. Wiley & Richards 1982); i.e. potential cues exist for estimating distance in any song transmitted through the natural environment. Only by singing songs that are unfamiliar to the receiver could males produce sounds that could not be used for distance estimation (Morton 1982). Playback experiments indicate that any song learned for production or discrimination is familiar and can be used to estimate distance (McGregor & Krebs 1984), so any advantage gained by a male singing unfamiliar songs would last only as long as it takes for his songs to be learned for identification. Therefore, Morton's (1982) suggestion that songs function to disrupt

or intimidate receivers by providing unreliable degradation cues for estimating distance is untenable over time for any species with the ability to learn songs for discrimination (McGregor 1994).

The acoustic adaptation hypothesis has been supported by many large-scale studies (Morton 1975; Marten & Marler 1977; Shy 1983; Sorjonen 1986; Wiley 1991). In contrast, our study may be added to a growing list of those which fail to find support for the acoustic adaptation hypothesis (Lemon et al. 1981; Rothstein & Fleischer 1987; Handford & Lougheed 1991; Date & Lemon 1993; Williams & Slater 1993; Tubaro & Segura 1994; Woodward 1995). We propose that, in some species, selection may favour males that do not structure their songs to minimize degradation in native breeding habitat, so that females may locate potential mates by means of song degradation cues. Whether female songbirds, like their male counterparts, can estimate distance by means of acoustic cues has yet to be investigated.

McGregor (1994) suggested that the ability to perceive song degradation and estimate distance may be advantageous to both signalling and receiving males. Similarly, Wiley & Richards (1982) argued that a potent and locatable song may function to discourage rival males from settling close to established singers, thereby decreasing competition for local resources and avoiding potential confrontations, to the mutual benefit of signallers and receivers. The notion of communication as a cooperative exchange of mutually beneficial information among signallers and receivers (Smith 1977) has been criticized for its lack of theoretical evolutionary integrity. For example, Morton (1982) argued that cooperative systems of communication cannot evolve among songbirds because signallers and receivers are often at odds with one another; he proposed that selection may favour the use of songs that manipulate or misinform receivers (see also Wallace 1973; Dawkins & Krebs 1978). For auditory distance perception to evolve, there need not be selection pressure on signallers to provide distance information in their songs; all songs, regardless of structure, are subject to degradation, which is predictable in any relatively homogeneous environment. Therefore, differences in the interests between signallers and receivers may not necessarily preclude the evolution of auditory distance perception in songbirds.

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