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Why birds sing at dawn: the role of consistent song transmission

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The dawn chorus is a widely observed phenomenon. One of the common, but inadequately studied, explanations for the occurrence of the dawn chorus is based on the rationale that atmospheric turbulence, which impairs acoustic communication, is least at dawn, and thus singing at dawn in some way maximizes signal performance. To investigate what possible acoustic benefit is gained through singing at dawn, we transmitted Swamp Sparrow *Melospiza georgiana* and White-throated Sparrow *Zonotrichia albicollis* song through open grassland and closed forest both at dawn and at midday. The transmitted songs were re-recorded at four distances from 25 to 100 m. Our results show that the mean overall absolute transmission quality of the signals was not significantly better at dawn than at midday. However, the signal transmission quality was significantly more consistent at dawn than at midday. Also, in general, signal transmission quality decreased with increasing distance. Variability in the transmission quality increased with distance for the White-throated Sparrow song, but not for the Swamp Sparrow song. Consistency in signal transmission quality is a factor that, arguably, is crucial for the identity function of song. This study strongly supports the acoustic transmission hypothesis as an explanation for the existence of the dawn chorus while the demonstration of variability as a key factor in singing at dawn is novel.

The dawn chorus is a widely observed and well-known phenomenon. Most studies of the dawn chorus have been observational, describing things such as the participant individuals and taxa, and the timing of peak singing activity (Keast 1994, Horn 1996, Woodall 1997). Few studies have reported experimental investigations of factors that might explain why the chorus itself occurs at dawn.

One common explanation for the timing of the chorus is based on the rationale that the impediments to acoustic communication are least at dawn. Several authors (Keast 1994, Catchpole & Slater 1995, Staicer *et al.* 1996) cite Henwood and Fabrick (1979) as the sole support for this argument. Henwood and Fabrick's paper provides a persuasive environmental acoustics argument for the existence of the dawn chorus. However, it is a theoretical paper based on a mathematical model that considers effective distance to be the signal transmission characteristic that is optimized by singing at dawn. Based on their model, Henwood and Fabrick conclude that 'the penalties in calling into a highly competitive … sound environment are apparently offset by the order of magnitude increases in broadcast area that are achievable over similar efforts at midday.'

Brenowitz (1982) has been the only work on songbirds (Red-winged Blackbirds) to investigate dawn's favourable acoustic conditions experimentally. He showed that, due to relatively low turbulence and background noise, signal broadcast area is greater at dawn than at other times of day. Comparable experimental studies on the dawn chorus in primates (Waser & Waser 1977) and the night chorus in bladder grasshoppers (Römer & van Staaden 1997) have similarly illustrated a significant increase in the effective signal transmission distance at the time of the chorus relative to that obtained at other times of day. Thus, in these three experimental investigations, as in the work of Henwood and Fabrick (1979), the maximization of signal transmission distance is the only acoustic benefit of the chorus that has been considered. A typical conclusion of these studies is that: '… dawn is the best time for sound transmission in a wide variety of environments because of microclimatic conditions. In particular, local air turbulence, which causes attenuation of sound and creates background noise thus reducing the effective transmission distance

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of acoustic signals, is minimal at that time of day' (Waser & Waser 1977).

However, signals not only attenuate during transmission, they also degrade. Degradation is 'the sum of all the changes in the signal at distance X relative to the signal's structure at its origin or source' (Morton 1986) and thus is independent of attenuation resulting from spherical spread. Two major components of degradation are reverberation (i.e. echoes) and irregular amplitude fluctuations (IAFs). Reverberations result from sound being scattered by reflective surfaces, are primarily associated with closed habitat types, and cause the distinction between closely placed elements to become blurred as interelement spaces fill with echoes. IAFs result from sound being refracted as it travels through pockets or layers of air of differing temperature or velocity (i.e. atmospheric heterogeneities), are primarily associated with open habitats, and result in low-rate AM changes being imposed on the signal, which listeners perceive as fluctuations in signal intensity. Wiley and Richards (1982) provide a complete review of the habitat associations of degradation components.

Previous studies into the benefits of the dawn chorus have not considered acoustic degradation. Therefore, how degradation levels vary with the time of signal delivery, and how such differences may ultimately have influenced the timing of the chorus have not been investigated. The purpose of the present study is to add to the experimental investigation of the acoustic benefits of singing at dawn. Further, in assessing signal performance in terms of transmission quality and the variability about that quality, we believe this to be the first experimental investigation to consider an acoustic benefit of the dawn chorus in terms of performance characteristics other than transmission distance.

MATERIALS AND METHODS

The signals and their transmission

Using Peterson's Field Guide to Bird Song on CD (Cornell Laboratory of Ornithology & Interactive Audio 1990), Swamp Sparrow *Melospiza georgiana* and White-throated Sparrow *Zonotrichia albicollis* songs (Figs 1 and 2, respectively) were digitized via a MacRecorder onto a Macintosh IIci computer using SoundEdit Pro 1.0 (MacroMind-Paracomp, Inc. 1992). These signals exemplify the extreme contrast in general acoustic structure that can exist among different species' songs. Swamp Sparrow song is a rapid amplitude modulated (AM) redundant signal, whereas the White-throated Sparrow song is a low-rate AM whistle. The songs are, in this study, not to be interpreted as being representative of the song of the species to which they belong. Rather, these signals will help provide replicate illustrations of the basic signal performance benefits that are gained through singing at dawn, while, at the same time, illustrating that these benefits are similar even among very different signal structures. However, the signals are ecologically relevant as both species are active participants in the dawn chorus (for Swamp Sparrow, see Mowbray *et al.* 1997; for White-throated Sparrow, see Falls & Kopachena 1994). The Swamp Sparrow 'song' is actually a combination of two signals as labelled in Fig. 1. Each species' signal was concatenated to produce a digital file of five identical repeats. Using Sound Designer II (Digidesign, Inc. 1992), these files were joined in succession and set to loop continuously while being recorded onto a cassette tape (Type II, CrO_2) driven by a Marantz tape deck. Nine complete loops, thus 45 repeats of

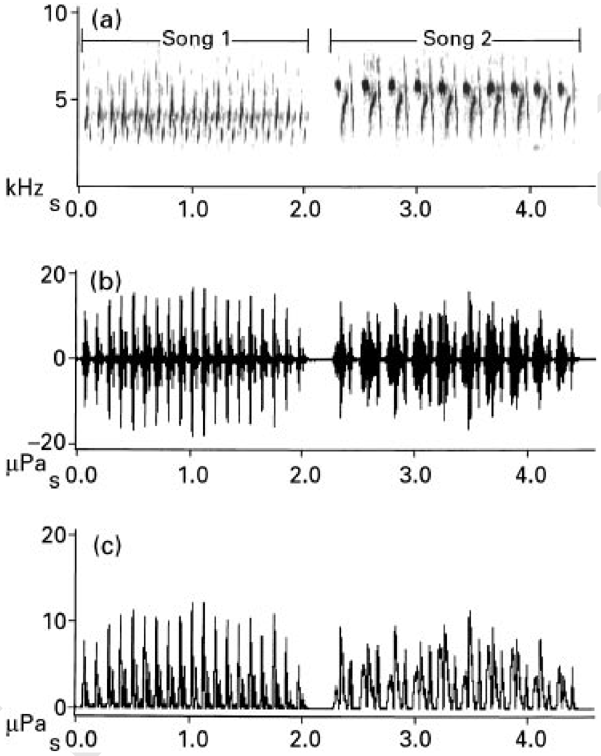

Figure 1. The base non-degraded Swamp Sparrow signal (actually composed of two individual songs as labelled) represented as: (a) a spectrogram, (b) a waveform, (c) an amplitude envelope.

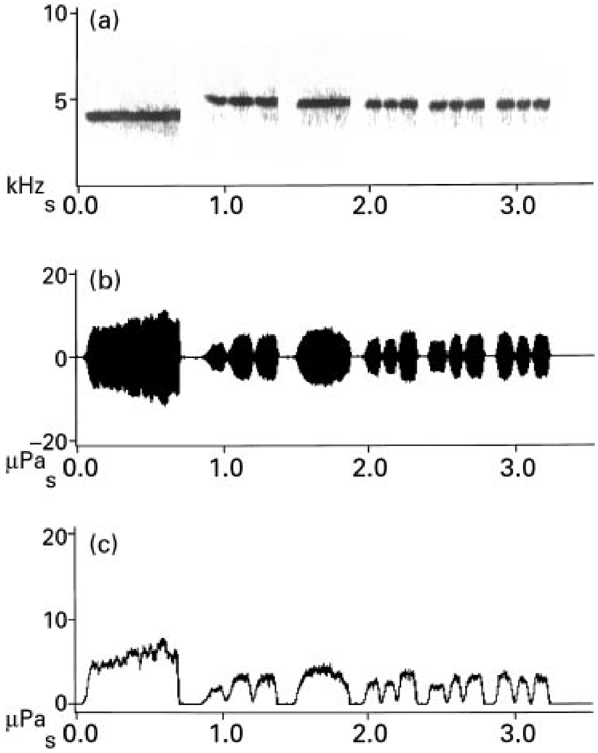

Figure 2. The base non-degraded White-throated Sparrow song represented as: (a) a spectrogram, (b) a waveform, (c) an amplitude envelope.

each species' signal, were recorded onto the master tape. This tape was then copied onto five double-sided source tapes for use in the field experiments.

Four open-field sites were located near London, Ontario, Canada. Four forest sites were selected within the Catfish Creek Conservation Authority's 106-ha old-growth Carolinian forest at Springwater Forest (42°45′N, 81°3′W) in Elgin County, Ontario (Edwards 1969). From a transmission point at each site, a 100-m straight line was drawn through homogeneous habitat, over level ground, with receiving locations being flagged at 25, 50, 75 and 100 m.

Transmission experiments were carried out from 28 June to 26 October 1993. Transmissions alternated day-to-day between habitat types, with a single broadcast distance at a given site being used on a given day. In an effort to control for seasonal environmental factors, such as humidity and temperature, sites were worked in sequence, completing work at sites 1 in both habitats before commencing work at sites 2, etc. An early transmission was performed either 1 h 15 min before sunrise, or 15 min after sunrise. The difference in starting times was due to the running of a concurrent experiment, the results of which are not reported here. A late transmission commenced 6 h after the start of the early run, by which time substantial air turbulence had usually developed.

To avoid source tape wear, a new source tape was shared between habitats for each site number. The signals were broadcast using a Marantz PMD 222 tape recorder, an Alpine 3548 power amplifier set to full gain and a pair of Bose 101 speakers mounted side-by-side on a tripod at a height of 4 m. The transmissions were recorded, at a given distance, using a Marantz PMD 430 tape deck (Type II, CrO_2 cassette), a Sennheiser MZA 14 TU (roll off filter set to 140 Hz)/MKH 816 T shotgun microphone held 4 m above ground on an MZS 816 pistol grip mounted on a tripod. Speakers and microphone were aligned by eye.

Quantification of signal degradation

For both signals, we randomly selected one of the five repeats from each of the nine loops from each experimental transmission run. To avoid compromising the assessment of incurred degradation, each of the randomly selected signals was assessed by the same individual (T.J.B.) and only signals found to be free of excessive background noise were used. If a selected signal was unusable, one of the remaining usable repeats from the same loop was randomly selected as an alternative. Owing to excessive background noise, sometimes all five repeats within a loop were unusable and on two occasions an entire experimental run was unusable.

The selected recordings were input from the Marantz PMD 430 recorder into a Power Macintosh 7100/80 computer (44.1 kHz sampling frequency; 16 bit sample size) via Canary 1.2 (Cornell Laboratory of Ornithology 1995). We were specifically interested in the performance of the signals themselves and since low-level background noise may prohibit accurate assessment of incurred degradation, non-song frequencies were filtered out using Canary's 'Filter Around' edit command (Swamp Sparrow song set at 2.01–9.00 kHz, White-throated Sparrow song set at 2.49–6.30 kHz). This investigation is solely concerned with assessing the degradation of a signal's temporal patterning of amplitude, and to this end all of the filtered waveforms were transformed into root mean square amplitude envelopes (1 ms window width, raw values) using Signalyse 3.12 (Keller 1994).

To obtain versions of the signals that were not degraded by the environment yet possessed alterations imposed by the transmission and reception equipment, we performed predawn transmissions of all recordings across 10 m of open field on two calm days at a height of 2.8 m (height selected for the concurrent experiment mentioned above). Thus, for each species' signal we had 90 essentially non-degraded base transmissions. These were processed in the same way as the experimental transmissions. To determine which base transmission was least degraded, we randomly selected a single signal repeat of each species' song from the original master tape, processed it as we had done the others, and then cross-correlated both its amplitude envelope and spectrogram with the corresponding form of the 90 base transmissions. The cross-correlation routine calculates a correlation coefficient, between the two signals, that ranges from 0 (signals having no similarity) to 1 (identical signals). When the signals are directly overlain, the correlation coefficient is a measure of similarity between them (Clark *et al.* 1987). For each species, the base transmission found to have the highest average (i.e. average correlation) resulting from the amplitude envelope and spectrogram cross-correlations was considered the least degraded version of the signal. It served as the benchmark from which to measure the degradation incurred in the experimental transmissions.

The degradation of the amplitude pattern of each randomly selected experimental transmission was quantified by cross-correlating its amplitude envelope with that of the corresponding benchmark signal. In this routine, the amplitude envelopes of the two signals being compared are normalized, each being given equal weighting. Thus, what is assessed is the amount of relative change within the signal itself, not any overall amplitude differences between the signals. This assessment corresponds directly with Morton's (1986) definition of degradation. The maximum correlation coefficient calculated between a transmitted and benchmark signal, representing their maximum similarity, was taken as a measure of transmission quality (see also Brown & Handford 1996).

Statistical analysis

The results present analyses of signal performance in terms of mean transmission quality, and the variability of that quality (in terms of the coefficient of variation), for each experimental transmission run. For both species' signals, these values are calculated from the (usually) nine transmissions that were randomly selected from each experimental run. It is important to realize that due to the numerous inequalities between the two songs, such as their differing frequency range and signal length, direct comparisons of absolute results among signals are inappropriate. Therefore, the axes in Figs 3 and 4 have different scales. Rather, the evidence of the acoustic benefit of singing at dawn is illustrated by the among-species similarity in general signal performance patterns, in terms of mean transmission quality, and the variability of that quality, and how these patterns differ between the early and late deliveries.

Statistical analysis was performed using Minitab, 8.21 (Minitab Inc. 1991). With a significance level set at $P = 0.05$, tests of significant effects of the variables (distance, time), and their two-way interactions, among the means or coefficients of variation in transmission quality were accomplished using analysis of variance (ANOVA). The inclusion of four sites within each habitat was intended to help quantify the variability within habitats. Due to this, and the fact that each transmission distance for a given site was performed on separate days, with associated differences in specific transmission conditions, site effects determined from these multifactor ANOVAS are not discussed in the results. With the data that were used to calculate the mean transmission quality for each experimental run, we performed one-way ANOVAS to analyse the effect of site for each transmission distance. The influence of site will be discussed in relation to habitat type.

RESULTS

Mean transmission quality

Open habitats

Swamp Sparrow. Although, in aggregate, the early Swamp Sparrow song transmissions did not differ significantly from the late ones (Fig. 3a), the best and worst (or nearly the worst, see 50 m) mean transmission quality results for each distance were from an early and late run, respectively. Mean transmission quality decreased significantly with increasing distance (ANOVA: $F_{3,3} = 42.6$, $P = 0.01$). From the one-way ANOVAS on site that used the data from each distance (approximately nine transmissions per experimental run) for both times of day (4 distances × 2 times = 8

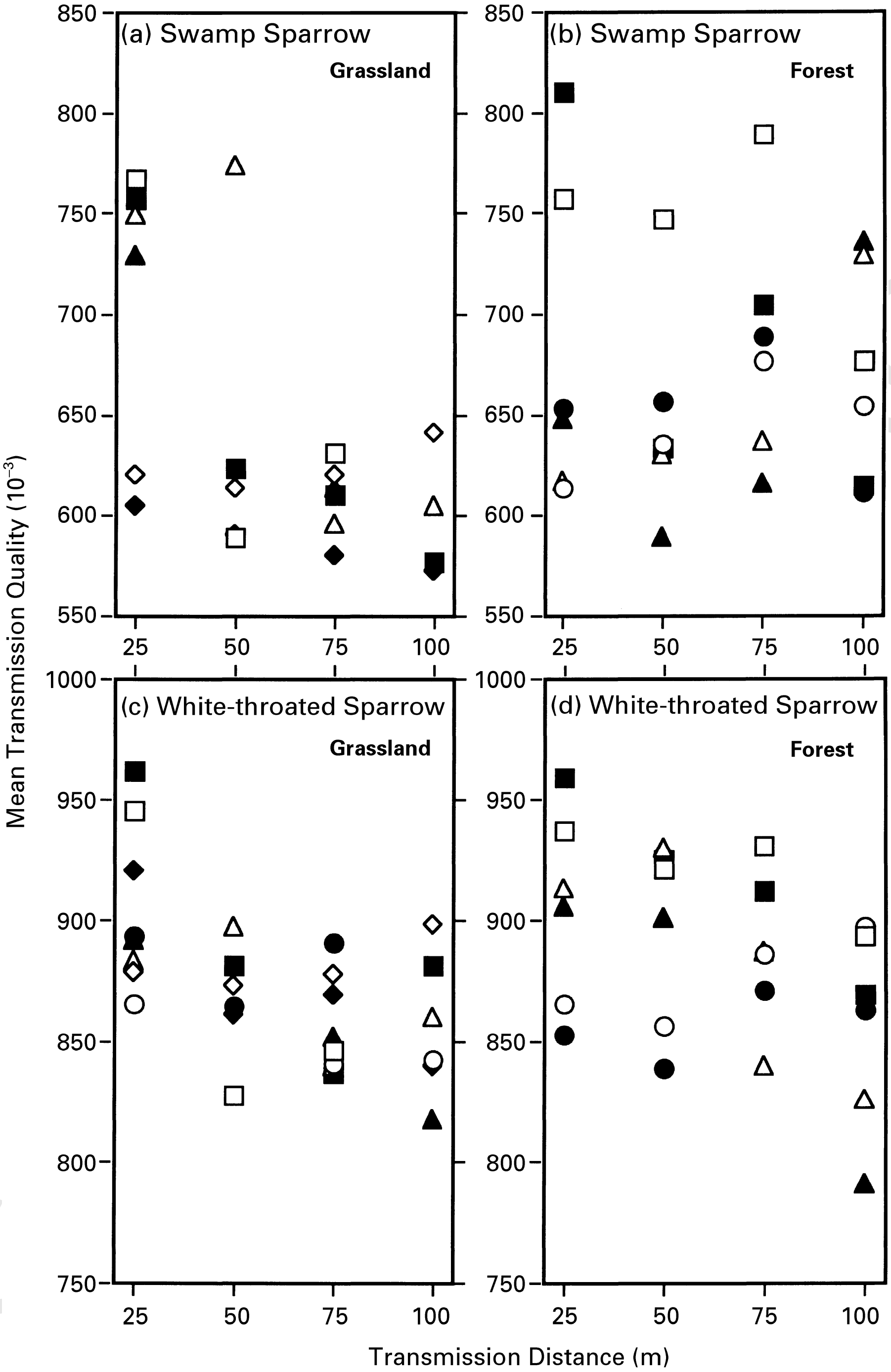

Figure 3. Mean transmission quality of both the Swamp Sparrow and White-throated Sparrow song resultant after transmission through 25–100 m of open grasslands [(a) and (c), respectively] and closed forest [(b) and (d), respectively] at dawn and 6 h later (□ – site 1; ◇ – site 2; ○ – site 3; △ – site 4; unfilled symbols – early; filled symbols – late).

one-way ANOVAS), site was found to be a significant factor in transmission quality for each distance in the early runs, but only for the 25-m transmissions in the late runs (Table 1).

White-throated Sparrow. White-throated Sparrow song mean transmission quality (Fig. 3c) did not differ significantly among delivery times, but it did decrease significantly with increasing transmission

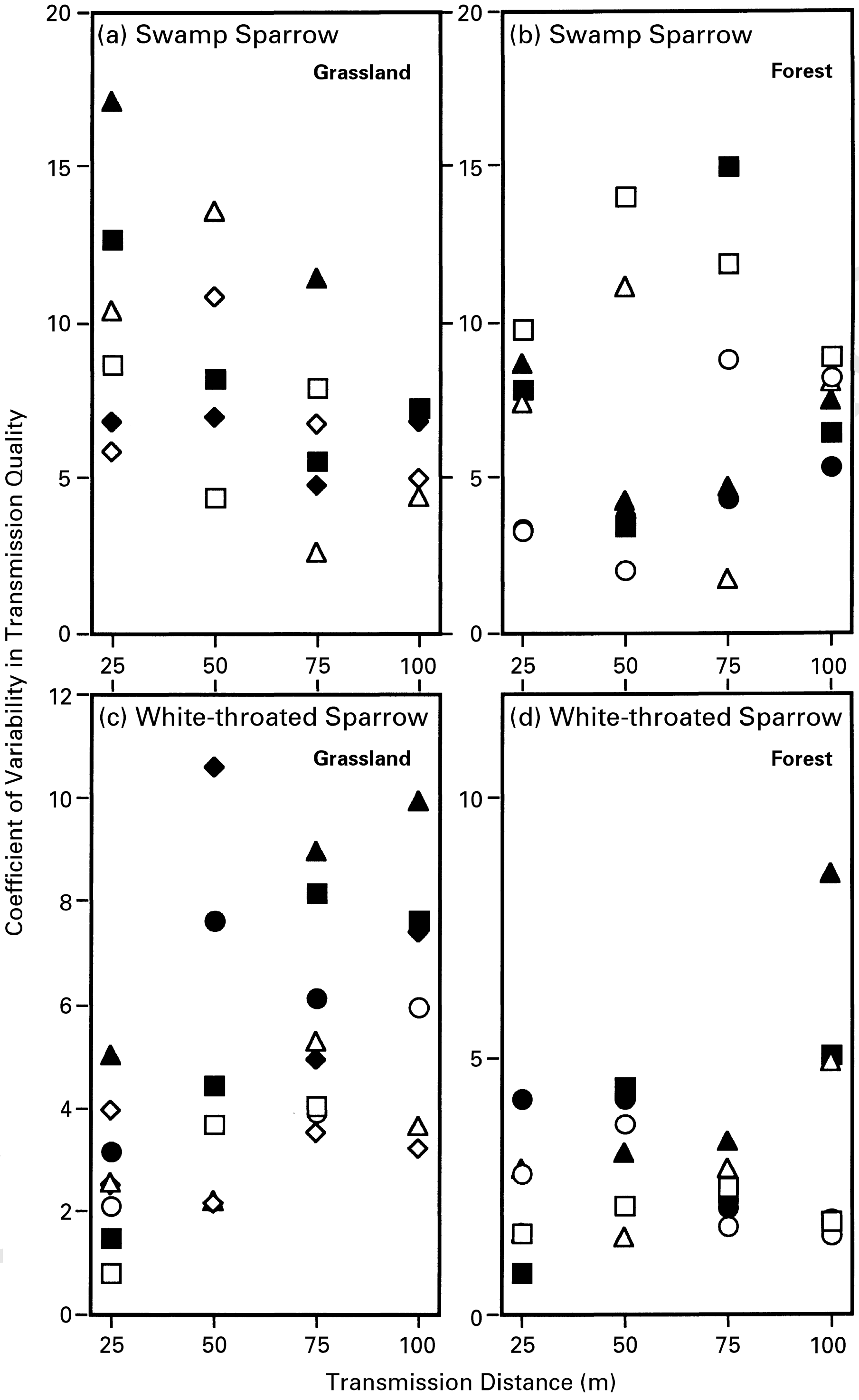

Figure 4. Standard deviation in transmission quality of both the Swamp Sparrow and the White-throated Sparrow song resultant after transmission through 25–100 m of open grasslands [(a) and (c), respectively] and closed forest [(b) and (d), respectively] at dawn and 6 h later (□ – site 1; ◇ – site 2; ○ – site 3; Δ – site 4; unfilled symbols – early; filled symbols – late).

Table 1. Results from the one-way ANOVAs on site for the data from each distance at each time of day for both the Swamp and the White-throated Sparrow signal transmissions in open and closed habitats.

Distance (m)	Early				Late			
	Swamp		White-throated		Swamp		White-throated	
	df	*F*	*df*	*F*	*df*	*F*	*df*	*F*
Open								
25	3,32	17.4***	3,31	19.3***	3,30	12.0***	3,30	11.4***
50	2,22	14.9***	2,24	20.2***	1,16	2.4	2,22	0.2
75	3,29	4.7**	3,30	2.1	2,24	1.4	3,30	1.1
100	2,22	4.4*	3,24	4.7**	1,15	0.0	2,21	1.7
Closed								
25	3,30	11.7***	3,32	26.0***	3,29	11.3***	3,27	50.5***
50	2,19	6.2**	2,22	25.2***	2,20	18.4***	2,17	10.2***
75	3,26	5.6**	3,31	24.6***	3,28	3.5*	3,27	6.5***
100	3,25	3.7*	3,25	15.8***	3,27	14.3***	3,22	3.8*

*$P = 0.05$, **$P = 0.01$, ***$P = 0.001$.

distance (ANOVA: $F_{3,5} = 10.6$, $P = 0.01$). One-way ANOVAs on site for the data from each distance for both times of day showed that while site was a significant factor in transmission quality for three of the four early run distances, it was only significant for the 25-m distance in the late runs (Table 1).

Closed habitats

Swamp Sparrow. The lack of any clear pattern in the degradation of Swamp Sparrow song with respect to either time or distance in closed habitat (Fig. 3b) is reflected in the lack of significance of either of these factors. One-way ANOVAs on site for the data from each distance for both times of day showed site significance in all eight cases (Table 1).

White-throated Sparrow. White-throated Sparrow song mean transmission quality (Fig. 3d) did not differ significantly among delivery times, but did decrease significantly with increasing transmission distance (ANOVA: $F_{3,6} = 9.5$, $P = 0.01$). One-way ANOVAs on site for the data from each distance for both times of day showed site significance in all eight cases (Table 1).

Variability in transmission quality

Open habitats

Swamp Sparrow. There is a trend (Fig. 4a) for the late transmissions of the Swamp Sparrow song to be more variable than the early ones (ANOVA: $F_{1,3} = 6.9$, $P = 0.08$). Although not significant, the variability in the received quality appears to decrease with increased transmission distance.

White-throated Sparrow. Late transmissions of White-throated Sparrow song (Fig. 4c) were significantly more variable than early transmissions (ANOVA: $F_{1,5} = 14.5$, $P = 0.01$). Variability also increased significantly with increasing distance of transmission (ANOVA: $F_{3,5} = 5.2$, $P = 0.05$).

Closed habitats

Swamp Sparrow. The variability in transmission quality of the Swamp Sparrow song in closed habitats (Fig. 4b) differed in no regular way with either time or distance.

White-throated Sparrow. Late transmissions of White-throated Sparrow song (Fig. 4d) were significantly more variable than early ones (ANOVA: $F_{1,6} = 11.4$, $P = 0.05$) and the variability in transmission quality increased significantly with distance (ANOVA: $F_{3,6} = 4.6$, $P = 0.05$).

DISCUSSION

This study investigated possible acoustic benefits of singing at dawn. Swamp and White-throated Sparrow songs were transmitted through 25–100 m of open and closed habitat at dawn and again 6 h later. Signal performance was assessed on the basis of the mean overall absolute transmission quality (average quality) of the signals, and the variability of that quality. The among-species parallels in patterns of signal performance, as assessed by these two metrics, and despite the great difference in acoustic structure, illustrate the benefit of singing at dawn to be as follows. The average quality of dawn transmissions was not significantly greater than those of midday, in either habitat. Rather, the clear advantage gained by transmitting signals at dawn was a reduction in the variability in transmission quality.

Discussion of our results requires a clear understanding of how open and closed habitats differ with respect to their primary sources of acoustic degradation. In closed habitats, reverberation results from sound reflection off solid objects, specifically tree trunks and limbs, that do not vary in magnitude or location across relevant time frames. That is, the level of degradation incurred is not expected to vary significantly from moment to moment, while it is likely to vary among sites, since each will possess unique structural characteristics. This picture contrasts with degradation in open habitats, where the atmospheric heterogeneities that generate IAFs vary in magnitude and location from moment to moment: resultant degradation will therefore vary from moment to moment. This temporal variability could dwarf spatial variation within the habitat. As a day progresses, wind activity and the sun's heating typically increase, and so, it may be expected, does the influence of IAFs in open habitats. Any such increased IAF influence with time in closed habitats, on the other hand, is likely to be minimal because such sites are largely sheltered from both sun and wind. Therefore, while degradation in open habitats is expected to vary from moment to moment (and increasingly as a day progresses), degradation in closed habitats is expected to vary among sites while varying relatively little with time of day.

The one-way ANOVAs that consider the effect of site on transmission quality support the idea of this among-habitat difference in heterogeneity variability. For both species' song in closed habitats, site was significant for each distance in both the early and the late transmissions, showing that the stable site-specific factors are important influences on the degradation incurred throughout the day. In contrast, the open habitat results show that although site was a significant factor in all but one early transmission, it was only so for the 25-m transmission distance of both signals late in the day. This indicates that in the early morning, when atmospheric heterogeneities are minimal, the stable site-specific factors are significant influences on the degradation incurred, but that later in the day, when atmospheric heterogeneities are more severe and variable, the relative influence of site-specific factors is reduced. Therefore, although we found no difference in mean transmission quality among transmission times in either habitat, a change in the causative factors leading to those similar levels of degradation is indicated for the open habitat, while no such change is indicated for closed habitats. It may seem surprising that the average quality of the dawn transmission was not significantly better than those performed at midday. However, we should recall that this kind of benefit of the dawn chorus has yet to be demonstrated. Our results clearly demonstrate that an acoustic benefit of signalling at dawn is an increased consistency in transmission quality.

Of what significance is increased signal transmission consistency? Bird song transmits identity information about the singer (Dabelsteen & Pedersen 1988, Lind *et al.* 1996). McGregor (1993) stated that it is 'crucial' for individuals to be able to identify each other by song. Variability in signal transmission quality would necessarily increase ambiguity in the message. Thus, if communication of identity information were crucial, individuals would enhance the transference of this information by adopting behaviours that increased the consistency of signal transmission quality. Thus, by singing at dawn, a signal's effectiveness is increased through the 'principle of reduction of ambiguity' (Krebs & Davies 1981).

That the consistency of signal transmission quality is highest at dawn is in agreement with the common observation that, in those species with multiple song types, dawn song is more complex than the daytime song (Davis 1958, Kroodsma 1977, Staicer 1989). The stable atmospheric conditions present at dawn permit a complex song to be transmitted with a greater consistency in quality – a clearer message sent – than would be possible under the variable conditions typical of later in the day. In order for late-day transmissions to maintain message clarity, the level of complexity in a signal would need to be reduced.

Although the results for the Swamp and White-throated Sparrow songs were similar in many respects, there were three differences, of which only the first is directly relevant to the dawn chorus. This was that while the late transmissions of White-throated Sparrow song were significantly more variable than the early ones in both habitats, those of the

Swamp Sparrow, while tending to be more variable than the early transmissions in open habitats, revealed no such relationship in closed habitats. We have previously demonstrated (Brown & Handford 1996) that rapid-trilled signals are resistant to the variability inherent in IAF type degradation, while low-rate AM whistled signals are sensitive to it. Thus, the increased variability that can be expected to accompany IAF degradation later in the day, particularly in open habitats, may be effectively combated by the rapid trill structure of the Swamp Sparrow song. That a time effect is seen in the White-throated Sparrow song, even in the closed habitat where the increase in IAF type degradation is expected to be minimal, suggests that, as we have predicted (Brown & Handford 1996), a low-rate AM signal structure is very sensitive to variable, as opposed to static, forms of degradation. This performance difference, among these contrasting signal structures, is consistent with Morton's (1975) observation that open habitat songsters possessing rapid AM signals tend to vocalize throughout the day while those with low-rate AM signals tend to vocalize only during a restricted early morning period. We regard this observation as an important corroboration of the significance of signal consistency in avian vocalizations.

The ability of trills to combat the variability inherent in IAF type degradation probably explains the second among-signal difference in performance patterns. Whereas the variability in transmission quality of the White-throated Sparrow song increased with distance in both habitats, it did not do so for the Swamp Sparrow song in either habitat. Apparently, the low-rate AM structure of the White-throated Sparrow song makes it so sensitive to variable IAF type degradation that variability in transmission quality increased with distance even in closed habitats where the influence of IAFs is much reduced. In contrast, the trilled Swamp Sparrow song combats the variability inherent in IAF-type degradation through high levels of signal redundancy. The performance of the Swamp Sparrow signal is remarkable in that its consistency in transmission quality actually seems to increase with distance in open habitats.

Finally, although degradation increased with transmission distance for both signals in the open habitat, in the closed habitat a similar increase was only evident for the White-throated Sparrow song. Signals transmitted in open habitats refract as they encounter atmospheric heterogeneities, causing portions of the signal to be directed away, and thus lost, from the line of transmission. Since complete removal is the only limit to the amount of signal that can be lost during transmission, a significant increase in degradation with distance is the expected result for any signal. In contrast, reverberation, the predominant source of degradation in closed habitats, may be characterized as additive (with strict respect to its effect on the signal's temporal patterning, and not considering differential frequency losses due to reflection). Echoes are added over the signal length, being most noticeable in the interelement spaces. Once echoes have filled those spaces, the addition of more echoes would have little further impact and a degradation threshold may be reached. Brown *et al.* (1995) found that in the transmission of Old World monkey vocalizations, significant reverberation was evident at 12.5 m, with only a small increase from those levels being evident at 100 m. If echo-degradation thresholds exist, it is reasonable to suggest that White-throated Sparrow song would have a higher threshold than Swamp Sparrow song because White-throated Sparrow song elements are widely spaced, and thus require extended-delay echoes to fill them. Long-delay echoes are weak, having travelled greater distances, and they have correspondingly less impact on signal degradation. The short-delay echoes required to fill the small interelement spaces of the Swamp Sparrow song would be correspondingly more intense, and thus have a greater impact on degradation. For the White-throated Sparrow song, the strong, short-delay echoes would be largely 'absorbed' within the long-duration notes. Having a higher threshold, White-throated Sparrow song would therefore be expected to show a continued increase in degradation over extended distances, while Swamp Sparrow song, having a low threshold, would become maximally degraded within a short distance and not show continued increasing degradation with distance.

Since the early work of Marler (1955), it has been suggested that song is adaptively structured to maximize performance. In addition to signal structure, the behaviour associated with song emission may itself be adapted to augment signal performance. The dawn chorus has commonly been described as such an adaptive behaviour, taking advantage of the typically calm weather conditions so as to, in some way, maximize signal performance. The benefits gained by singing during these periods must outweigh any negative influences caused by acoustic interference that results from the large numbers of species participating in the dawn chorus (Dabelsteen & Methevon 1999). However, little has changed since Kacelnik and Krebs (1983) noted that there is in fact 'little evidence to show that sound transmission is better at dawn', even though the theoretical arguments (Henwood & Fabrick 1979) are convincing. In a recent review of the dawn chorus, Staicer *et al.*'s (1996) acoustic transmission hypothesis argues that the chorus occurs at dawn because that is when 'such sounds should travel farther'. However, distance is only one of several transmission characteristics that can be used to assess signal performance. Others that have been used are the level of degradation incurred, or transmission quality (Gish & Morton 1981) and, more recently, the variability in transmission quality (Brown & Handford 1996, 2000).

Overall, our results show that, contrary to what previously may have been assumed, the mean overall absolute transmission quality of songs transmitted at dawn is not significantly better than that of songs transmitted later in the day. However, our results clearly indicate that signal transmission quality at dawn is significantly more consistent than it is later in the day. Since variability in signal transmission quality increases ambiguity in the message, consistency is essential if individuals are to be able to recognize each other by song. Thus, combining this benefit with that previously demonstrated by Brenowitz (1982), singing at dawn, as opposed to later in the day, permits a singer to send an unambiguous message further.

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