

# ACOUSTIC SIGNAL AMPLITUDE PATTERNS: A COMPUTER SIMULATION INVESTIGATION OF THE ACOUSTIC ADAPTATION HYPOTHESIS<sup>1</sup>

TIMOTHY J. BROWN AND PAUL HANDFORD

University of Western Ontario, Department of Zoology, B and G Building,  
London, Ontario N6A 5B7, Canada, e-mail: tjbrown@julian.uwo.ca

*Abstract.* The acoustic adaptation hypothesis (AAH) predicts that vocalizations intended for unambiguous long range communication should possess amplitude modulation (AM) characteristics such that the temporal patterning of amplitude is minimally degraded (due to atmospheric turbulence and reverberation) during transmission through native habitat. Specifically, signals should possess rapid AM (trills) in open habitats and low rate AM (whistles) in closed habitats.

To determine which of these amplitude patterns incurs less degradation from its two main components, reverberation and irregular amplitude fluctuations (IAFs), we constructed two synthetic 'source' signals, a rapid AM 'trill' and a low rate AM 'whistle', from pure tone frequency sweeps. We applied the degradation components independently, thus avoiding their complex interactions typical of field recordings. Signals were degraded by various echo treatments (modeling closed habitat reverberation) or by various amplitude decrease treatments (modeling open habitat IAFs).

Results revealed that the difference in performance between signal types lies not so much in their average transmission quality, as in the variability of that quality. In closed habitats, whistled signals transmit with more consistent quality than trilled signals over biologically realistic echo delays. In open habitats, trilled signals transmit with far lower variability of quality than do whistled signals. The inherent redundancy of trills transmits information more effectively than whistles in open habitats. Our results show strong support for the AAH predictions regarding what type of signal structure is best suited for open or closed habitats. However, this support is based on variability in performance of signal types in different habitats rather than average transmission quality.

*Key words:* acoustic adaptation hypothesis; computer simulation; amplitude modulation; reverberation; irregular amplitude fluctuations; open habitats; closed habitats.

## INTRODUCTION

Acoustic signals attenuate and degrade during passage through habitat from a singer to the listener. Several studies (Morton 1975, Linskens et al. 1976, Marten and Marler 1977, Marten et al. 1977) have focused on attenuation characteristics of habitats. Though similar habitats have measurably different acoustic climates (Linskens et al. 1976), it is generally true that as long as the height of transmission is above that complicated by ground effects, attenuation of acoustic signals is frequency dependent such that the lower the frequency of vocalization, the slower it attenuates in either open or closed habitats. Marten and Marler (1977) note that frequency and delivery height are more important than habitat

type in determining the distance a signal will travel. It appears that the different types of heterogeneities that exist in open and closed habitats result in similar attenuation of signals.

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). Thus, degradation refers to changes in the temporal patterning of the signal structure, and not overall losses due to attenuation. Two major components of degradation are reverberation and irregular amplitude fluctuations (hereafter referred to as IAFs, following Wiley and Richards 1978). Reverberation results from the reflective scattering of sound by surfaces, like tree trunks and limbs, and is characteristic of signal transmission in closed habitats. While the air mass in such closed sound-reflecting habitats is commonly still or nearly so, that in open environments commonly possesses pockets or layers of air of differing temperature or velocity. Such ir-

<sup>1</sup> Received 22 September 1995. Accepted 22 March 1996.

regularities impose IAFs, mainly through refraction. A listener perceives such IAFs as fluctuations in the intensity of the signal (Wiley and Richards 1978). Any such degradation, be it reverberation or IAFs, incurred during transmission can be considered deleterious to information encoded in the temporal patterning of a signal (Richards and Wiley 1980).

The acoustic adaptation hypothesis (hereafter referred to as the AAH) is largely based on the work of Morton (1975) and Hansen (1979), though the term itself was first coined by Rothstein and Fleischer (1987), being a model which they dismissed as a possible explanation for the existence of dialects in Brown-headed Cowbirds. However, the AAH need not only apply to dialects or even whole bird songs. The AAH need only predict that signal portions intended to transmit information accurately over a distance on the order of territory diameters, should be of a form or structure that is minimally degraded on passage through native habitat. This definition removes the unnecessary expectation that entire songs be structured for maximum transmission quality, and rather it allows for the possibility that some segments of a signal could be adapted in response to other selective forces such as communication over lesser distances, or ranging (Morton 1986).

Degradation is a relevant factor in avian communication. Playback experiments have shown that *Luscinia luscinia* (Sorjonen 1983), *Parus major* (McGregor et al. 1983, McGregor and Krebs 1984), and *Sturnella neglecta* (McGregor and Falls 1984) are sensitive to the degradation of familiar signals, as individuals responded more to nondegraded than to degraded versions of a signal. More recently, Naguib (1995) showed that *Thryothorus ludovicianus* can use the reverberation or the high frequency attenuation component of degradation, independently, to estimate a singer's distance.

The AAH predicts that closed habitat species should stress tonal or whistled elements in their long range communication signals and avoid the use of trills. The rapidly repeating elements (rapid amplitude modulation or AM) of a trill become blurred and indistinguishable to a listener as the inter-element spaces fill with echoes. On the other hand, signals of species typical of open habitats should stress redundancy of signal structure through rapid repetition of elements, as is found in trills, and avoid tonal or whistled ele-

ments because substantial portions of such signals may be inaudible at the location of the listener due to the imposition of IAFs. Redundancy permits a listener to reform a signal from an incompletely received one (Romer and Lewald 1992, Wiley 1994). For a review of habitat effects and signal adaptations see Wiley and Richards (1982).

Some observational studies show agreement with AAH predictions. One persuasive case is the habitat associated dialects of the Rufous-collared Sparrow, *Zonotrichia capensis* (Handford 1988). The song consists of an opening theme and the dialect defining terminal trill. The "fastest trilled songs (trill interval < 50 msec) are typical of high grasslands and puna. Closed (mesic) habitat populations show slow to very slow trills . . ." (Handford and Loughheed 1991). Loughheed and Handford (1992) argue that the AAH is the most likely explanation for these observations. Other intraspecific observational studies have focused more on frequency characteristics of signals in relation to habitat, as opposed to amplitude patterns. Nevertheless, some support for the AAH has been found in studies on the White-throated Sparrow (Wasserman 1979, Waas 1988), Scarlet and Summer Tanagers (Shy 1983), and Northern Cardinal (Anderson and Conner 1985).

Morton's (1975) analysis of 177 neotropical species found that open habitat species tend to deliver rapid AM signals, while closed habitat species signals were mainly "pure tonelike." Wiley's (1991) study of the signals of 120 eastern North American oscine species found the three temporal properties considered (presence of sidebands or buzzes, both indicating rapid AM, and the minimal period of repeated elements) to be "strongly associated with habitat," such that most open habitat species included rapid AM in their signals, and most closed habitat species did not.

Recent work by Dabelsteen et al. (1993) used three measures to quantify degradation incurred by Blackbird (*Turdus merula*) song upon transmission through closed habitat. Only a limited amount of experimental work has looked at degradation incurred during signal transmission through native and non-native habitat. Carolina Wren signals incurred less degradation on passage through native as opposed to non-native habitat (Gish and Morton 1981). Results of transmission experiments by Brown et al. (1995), using calls of four Old World monkey species,

supported the authors' ideas that adapted signal structure is more predominant in closed habitats than in open savanna, due to visual communication constraints. Transmission experiments using cricket frog signals (Ryan et al. 1990) support the argument that habitat influences the signal structure of the subspecies *Acris crepitans crepitans*.

Support for the AAH thus comes mainly from observational studies showing agreement between predicted and observed signal structure, in relation to habitat. The paucity of experimental support is, at least partially, due to the fact that the causes of degradation, including atmospheric turbulence and reflective surfaces, do not act in isolation. Results from field transmissions contain complex combinations of the various components of degradation, including IAFs and reverberations, plus complications from various sources of environmental noise like wind, rustling leaves, and insects, thus making a general measure of degradation difficult to obtain. The inability to isolate the components of degradation makes it difficult to illustrate, experimentally, which amplitude pattern in a signal results in the least amount of degradation from either reverberation or IAFs. The purpose of this study is to show, through computer simulation, which signal amplitude pattern, either a rapid AM trill or a low rate AM whistle, incurs less degradation from either reverberation or IAFs alone. The advantage of this simulation study is that we are able to completely separate the two major components of degradation and isolate their effects from other influences. This study uses two synthetic signals, a rapid AM trilled signal, and a low rate AM whistled signal. Both signals are treated with identical degradation regimes, using a single source of degradation at a time. This simulation investigation offers strong and complete support for the basis of the AAH, and reveals a hitherto unrecognized source of selection on acoustic temporal structure which raises important points of consideration for field experiments.

## METHODS

### THE SOURCE SIGNALS

Two sine wave-shaped synthetic frequency sweeps from 4 to 2 kHz were constructed using SoundEdit Pro, version 1.0 (MacroMind-Paracomp, Inc. 1992). One sweep was 10 ms long

followed by 25 ms of silence. The second sweep was 250 ms long followed by 625 ms of silence. Each sweep, with its associated silent period, was set up, via Sound Designer II (Digidesign, Inc. 1992), to loop continuously during a 10 second direct line recording from the computer to a Sony MZ-1 Portable MiniDisc Recorder. The looped 10 + 25 ms signal produced a rapid AM 'trill-like' signal (hereafter referred to as the trilled signal), while the looped 250 + 625 ms signal produced a low rate AM 'whistle-like' signal (hereafter referred to as the whistled signal). From the two resultant MiniDisc recordings, several seconds were then re-entered from the Sony MZ-1, through a MacRecorder, to the computer via Canary 1.1, the Cornell Bioacoustics Workstation (Cornell Laboratory of Ornithology 1993). From each of these re-entered signals, 3.5 seconds was used as the source signal file for this study. A portion of the source trilled signal and the source whistled signal is variously illustrated in Figure 1 and Figure 2 respectively. Both signals have an identical signal-to-silence ratio of 1:2.5, with the total 1 second of sound contained in the complete 3.5 second signal, simply being partitioned differently in the two signals.

### DEGRADATION OF SIGNALS

*Reverberation.* To model the reverberation component of signal degradation, the trilled and whistled source signals were subjected to identical treatments of synthetic reverberation using SoundEdit Pro, version 1.0 (MacroMind-Paracomp, Inc. 1992). These treatments consisted of the imposition of echoes of various strengths, occurring at various delays from the source signal. This simulated reverberation, though certainly not as complex as that resulting from transmission through a natural closed habitat, is informative in illustrating how these two different types of signals will be affected by reverberation type degradation. Degradation treatments from all the pairwise combinations between echo strengths of 4, 10, 15, 20, 25, 30, 40, and 50%, and echo delays of 1, 2, 4, 6, 8, 10, 12.5, 15, 17.5, 20, 25, 30, 40, 50, 75, and 100 ms, were imposed on both the trilled and whistled source signal (a total of 8 [strengths] × 16 [delays] = 128 different reverberation degradation treatments per signal type). For each combination between an echo strength and an echo delay, the degradation was uniform across the length of the signal, and thus, for every combination of echo

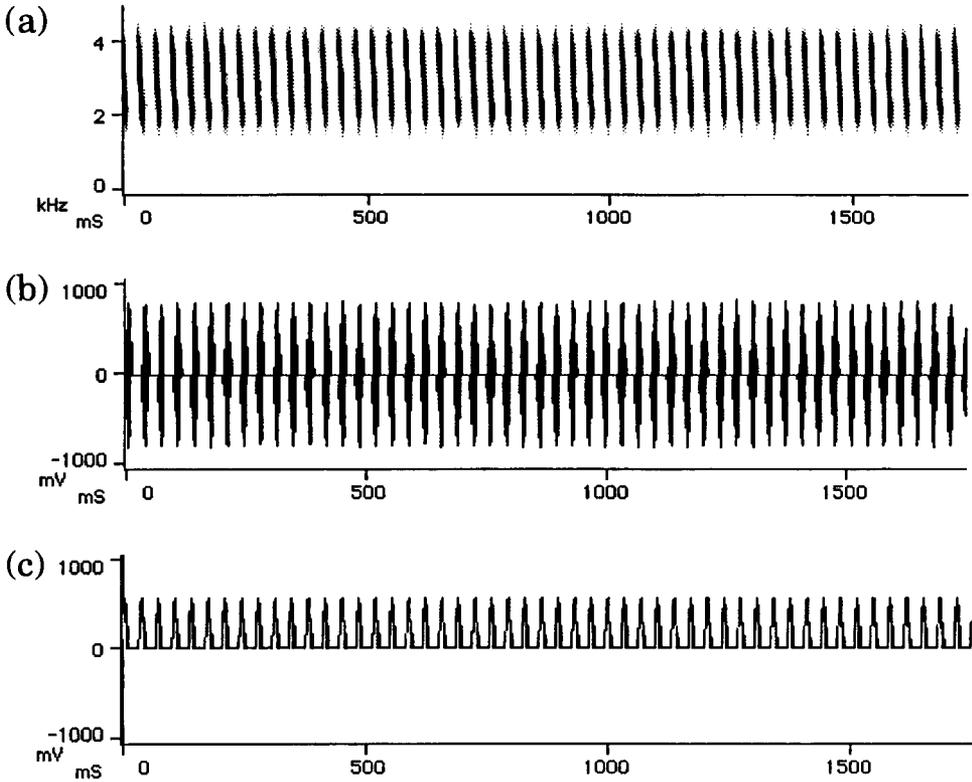


FIGURE 1. The rapid a.m. trilled source signal illustrated as (a) a spectrogram, (b) a waveform, (c) an amplitude envelope. For clarity of the signal detail only one half of the total signal length is illustrated.

strength and delay, a single degraded signal resulted from each source signal. As will be seen later in the results, the level of degradation induced by these reverberations showed a periodicity clearly related to the period of the signal itself. Therefore, to help define each source signal's individual pattern (periodicity) of degradation, additional echo delays of 35, 52.5, 70, 87.5 and 105 ms were imposed on the trilled signal across all echo strengths. Therefore, for the trilled signal, the total number of degradation treatments is  $128 + (5 \text{ [added delays]} \times 8 \text{ [strengths]}) = 168$ . Additional delays of 219, 438, 656 and 875 ms were imposed on the whistled signal across all echo strengths. Therefore, for the whistled signal, the total number of degradation treatments is  $128 + (4 \text{ [added delays]} \times 8 \text{ [strengths]}) = 160$ . An example of both the trilled and the whistled signal degraded by reverberation is illustrated in Figure 3 (a), parts i) and ii) respectively.

*Imposed Amplitude Decreases. Full Signal Anal-*

ysis. To model the IAF component of signal degradation, both source signals were subjected to identical treatments of imposed amplitude decreases (hereafter referred to as IADs). These treatments consisted of the imposition of triangular amplitude decreases onto the source signal, commencing at time zero, and being of various strengths and durations, using SoundEdit Pro, version 1.0 (MacroMind-Paracomp, Inc. 1992). Being triangular amplitude decreases, the point of maximal amplitude decrease occurred at the midpoint of its duration. An illustration of an IAD on the trilled and whistled waveforms can be seen in Figure 3 (b), parts i) and ii) respectively. Degradation from all pairwise combinations between IAD strengths of 50 and 100%, and durations of 1.0, 1.5, 2.0, 2.5, 3.0, and 3.5 seconds, were imposed on the trilled and the whistled source signal (a total of  $2 \text{ [strengths]} \times 6 \text{ [durations]} = 12$  IAD degradation treatments for each source signal). To investigate the affect of very weak IADs on signal degradation, a set

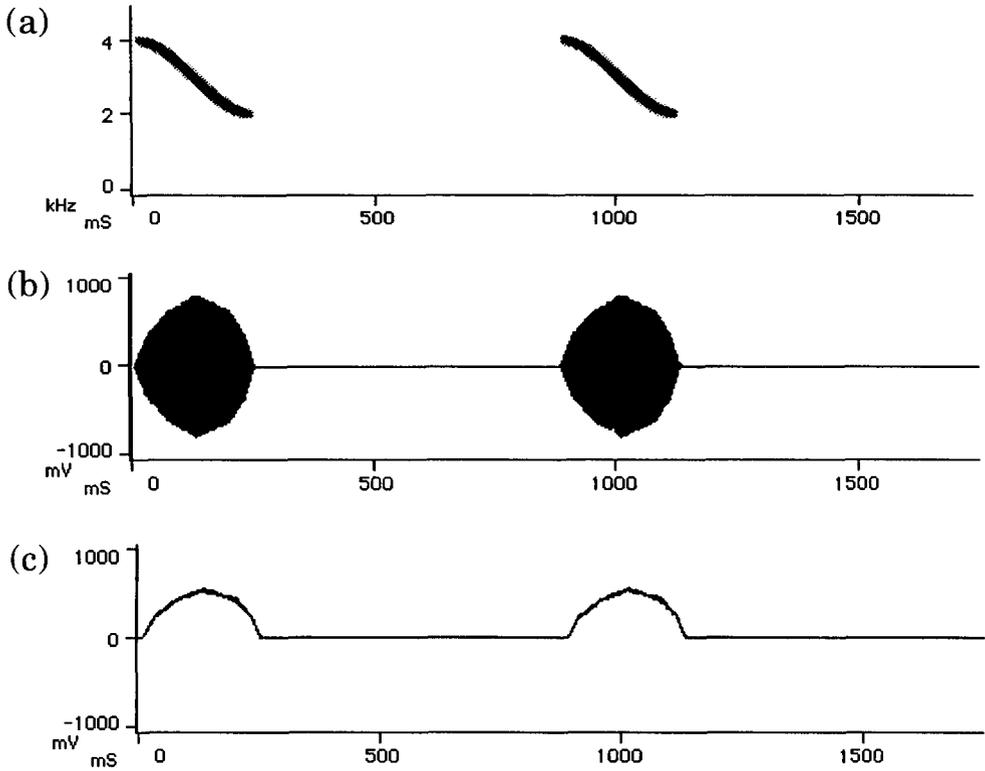


FIGURE 2. The low rate a.m. whistled source signal illustrated as (a) a spectrogram, (b) a waveform, (c) an amplitude envelope. As in Figure 1, only one half of the total signal length is illustrated.

of 10% IADs with durations of 1.0, 2.0 and 3.0 seconds were also imposed onto the source signals, thus increasing the combination of degradation treatments for each source signal, from 12 to 15.

Looking at the degraded whistled signal in Figure 3 (b), part ii), it is easy to see that, depending on where the point of maximal amplitude decrease occurs, relative to the position of the signal elements, a very differently degraded signal will emerge. For instance, if the point of maximal decrease occurred at an element, as it does in Figure 3 (b), part ii), that signal element is severely affected, being all but eliminated in a 100% decrease. However, if the point of maximal decrease occurred between signal elements, then the elements neighboring that decrease would be affected to a much lesser degree than is the second element in Figure 3 (b), part ii). To include this source of variability in this portion of the study, we constructed six additional source signals from both the original trilled and the original whistled

signal. These additional source signals were constructed by cutting the leading 0.5 seconds off the original source signal and pasting it onto the end of that same signal, thereby producing the second source signal, identical in all ways to the original, except in having its signal elements shifted in position by 0.5 seconds. This second source signal was then similarly treated, to produce the third source signal, and so on for a total of six shifts which is the total number of 0.5 second shifts that can be performed on a 3.5 second signal and still produce signals with elements in differing positions. This procedure yielded a total of seven source signals for both the trilled and whistled signal. This exercise, in effect, slid the source signal, by 0.5 second increments, along behind the given regime of IAD treatments. Thus, each of the 15 combinations of strength and duration of IADs described above, were applied to seven source trill signals, and seven source whistle signals, each of the source signals having its elements in a different position

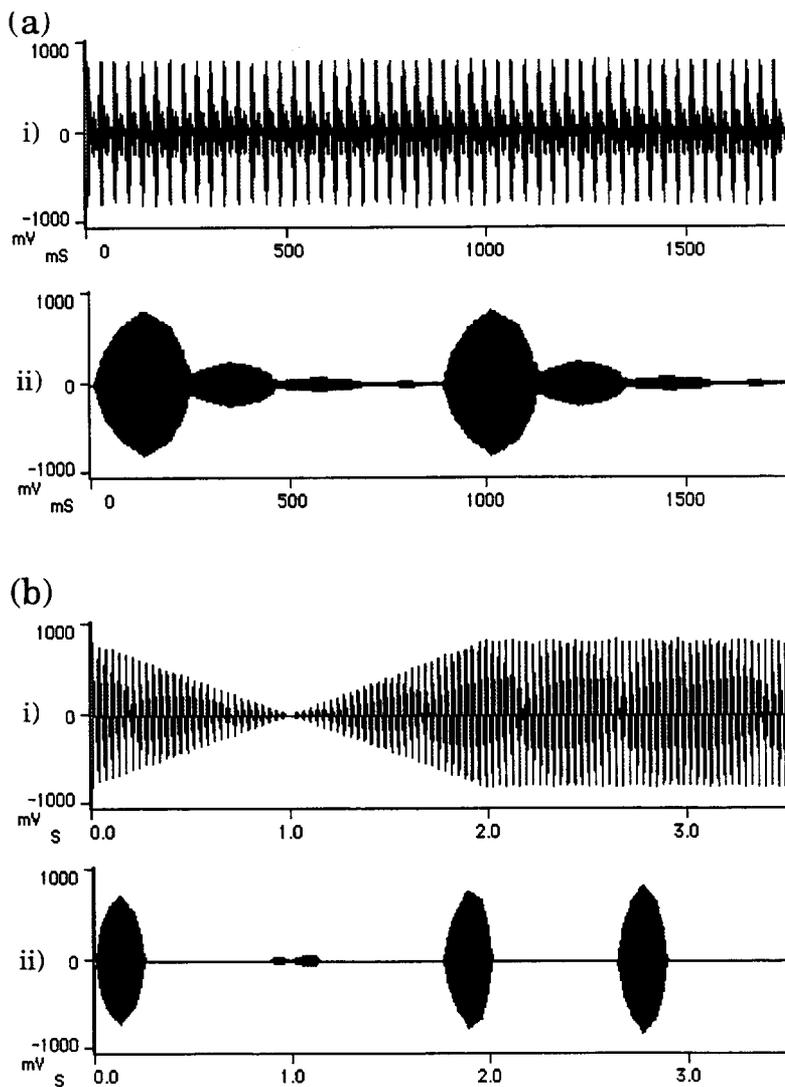


FIGURE 3. An illustration of the simulated degradation of the trilled and whistled signals. In (a), for clarity of signal detail, only one half of the signal length is illustrated, being degraded by 30% strength echoes, at delays of 15 ms in the trill (i), and 219 ms in the whistle (ii). In (b) the entire length of both the trill (i) and the whistle (ii) signal is seen degraded by a 2 second, 100% IAD.

relative to the imposed decrease, thus giving a total of  $(15 \text{ [degradation treatments]} \times 7 \text{ [source signals]})$  105 degraded trilled signals, and 105 degraded whistled signals.

**Partial Signal (Element-Level) Analysis.** Information in an acoustic signal may be encoded in the structure of the elements, and in their spacing in time. Considering the two types of signals used in this study, it can be reasonably argued that once a listener has heard two complete cycles

of either signal (element-space-element-space), the structure and spacing of the signal elements is known, and so too is all of the information that it encodes. We can think of this pair of complete cycles as the smallest 'information packet' from which the signal information can be deciphered, the rest of the signal being redundant. Thus, based on this 'information packet' reasoning, effective communication may occur even when a listener does not receive an entire signal.

Investigating the transmission quality of these information packets is the purpose of the partial signal, or element-level, analysis. In this analysis, the information packet becomes the unit of concern, rather than fixed time frames as was the case in the full signal analysis.

Two pairs of complete cycles, or 'information packets', were drawn from the waveform of each of the 14 (7 trilled + 7 whistled) source signals (7 [source trill signals]  $\times$  2 [information packets drawn from each] = 14 source trill information packets; same for whistle source signals), and each of the degraded signals (recall, 105 [degraded trill signals]  $\times$  2 [information packets drawn from each] = 210 degraded trill information packets; same for degraded whistle signals) from the full signal IAD analysis described above. For all of the trilled signals, both source and degraded, one pair of complete cycles was drawn from the portion of the signal between 1.18667 s and 1.25532 s, and a second pair of complete cycles was drawn from between 2.37333 s and 2.44198 s. These points of selection were chosen simply because they represent the 1/3 and 2/3 point in the total duration of the trilled signal. For all of the whistled signals, both source and degraded, the complete 3.5 second signal length was simply divided in half, each half containing two complete cycles.

#### PREPARATION OF SIGNALS FOR DEGRADATION ANALYSIS

Since, in this investigation, we are interested in the degradation of the temporal patterning of amplitude in a signal, we transformed all source and degraded signal waveforms, from all three portions of this study (Reverberation, IADs-full signal analysis, IADs-partial signal analysis), into root mean square amplitude envelopes (using 1 ms window width, raw values) using the signal analysis program *Signalize*, version 3.12 (Keller 1994). This transformation has the effect of removing all frequency information from the signal, while leaving information about the signal's amplitude pattern in tact. The use of amplitude envelopes renders the quantification of degradation between two signals (source signal vs. degraded version), less sensitive to the minute changes that may occur within the very large number of data points (22,254.5 in 1 second) contained in signal waveforms that have a sampling frequency of 22,254.5 Hz. A portion of the amplitude envelope of the original trilled and

whistled source signals are illustrated in parts (c) of Figure 1 and Figure 2, respectively.

#### QUANTIFICATION OF DEGRADATION

The amount of degradation incurred by a signal, as a result of one of the various degradation treatments described above, was quantified by cross-correlating the amplitude envelope of the degraded version of the signal with the amplitude envelope of the corresponding source signal. The same cross-correlation procedure was carried out on the information packets (source vs. degraded) from the partial signal analysis. The cross-correlations of the amplitude envelopes were performed using the waveform cross-correlation routine in *Canary 1.1*, the Cornell Bioacoustics Workstation (Cornell Laboratory of Ornithology 1993). This routine incrementally slides the two signals past each other, and at successive discrete time offsets, calculates a correlation coefficient between them, that ranges from 0 (having no similarity) to 1 (being completely similar). In this study, the value of the correlation coefficient at a time offset of 0 seconds, which corresponds to the two signals being perfectly aligned, was taken as the measure of similarity between the source signal and the degraded version. The lesser the measure of similarity, the greater degraded the signal. In the performance of these calculations, the amplitude envelopes of the two signals are normalized, each being given equal weighting. Thus, this calculation considers relative changes within the signal itself, and not overall amplitude differences between the source signal and the degraded version. This corresponds directly to the definition of degradation offered by Morton (1986) as stated in the introduction of this paper.

In the reverberation portion of this study, each pairwise combination between echo strength and echo delay resulted in a single degraded version of both the trilled and whistled signal (except for the signal specific delays used to define the patterns [periodicity] of degradation, resulting in a degraded version of the specific signal to which it was applied), the amplitude envelope of which was cross-correlated with that of the corresponding source signal. Thus, for each signal type, a single data point exists for every pairwise combination of echo strength and echo delay, of which there are, as described earlier, 168 for the trilled signal, and 160 for the whistled signal.

In the IAD-full signal analysis portion of this study, each pairwise combination between IAD

strength and IAD duration resulted in a degraded version of each of the seven source trill signals and the seven source whistle signals, the amplitude envelopes of which were cross-correlated with the corresponding version of the source signal. Therefore, in the results, for every pairwise combination of strength and duration of IAD, there are correspondingly seven measures of similarity for the degraded trilled signals, and seven measures of similarity for the degraded whistled signals.

In the IAD-partial signal analysis portion of this study, two pairs of complete cycles, or information packets, were drawn from each of the IAD degraded signals resultant from the IAD-full signal analysis portion of this study. Each packet was transformed into an amplitude envelope and cross-correlated with the amplitude envelope of the corresponding information packet from the corresponding source signal. Since there were seven trilled and seven whistled degraded signals for each pairwise combination of

IAD strength and duration, with two pairs of complete cycles drawn from each, then 14 measures of similarity of trilled information packets, and 14 measures of similarity of whistled information packets exist for every pairwise combination of IAD strength and duration.

Because the design of this investigation is deterministic and repeatable, we use the term 'variability' rather than 'variance' when referring to our results. Because of a lack of random treatments, statistical analysis (e.g., *t*-tests, *F*-statistics) of our results may be held to be technically inappropriate. However, we believe that such tests are appropriate in so far as they can be used as illustrative aids to clarify the magnitude of the differences that obviously exist in the results.

RESULTS

REVERBERATION

*Trilled Signal.* As can be seen in Figure 4 (a) and (b), the cross-correlations between the am-

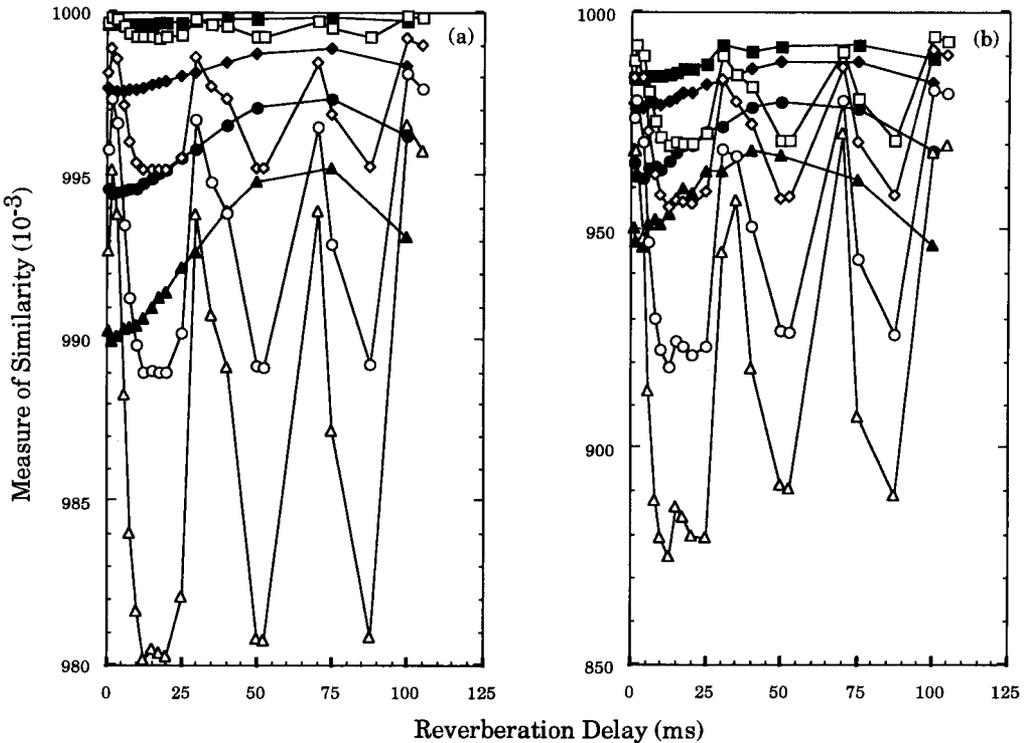


FIGURE 4. Measures of similarity between the amplitude envelope of the trilled or whistled source signal, and versions degraded by imposed reverberations of various delays and strengths. Open symbols are trill results, filled symbols are whistle results. In (a), the symbols (open or filled) correspond to echo strengths of: □ = 4%, ◇ = 10%, ○ = 15%, and △ = 20%. In (b), the symbols correspond to echo strengths of: □ = 25%, ◇ = 30%, ○ = 40%, and △ = 50%.

plitude envelopes of the trilled source signal and those of versions degraded by echoes show cycling between higher and lower similarity measures across the delays for a given echo strength. The cycling is an artifact resulting from combinations of the echo delays and the periodicity of the signal elements. Short delay echoes ( $\leq 4$  ms) occur very close to the elements from which they arose, and are almost indistinguishable from them, thus resulting in a high measure of similarity. When echo delays are about half the periodicity of the signal elements, or about 12.5–17.5 ms, the echoes occur about midway between signal elements. This midway point represents the greatest distance they can be from an element, and a minimum similarity measure results. As echo delays increase to about 30 ms, the echo event begins to approach the element that follows the one from which it arose, becoming nearly indistinguishable from it, and a maximum similarity measure is again the result. For the various echo strengths, the cycling pattern across the delays is very similar, the pattern is simply shifted down the measure of similarity scale, for obviously, as the echo event increases in strength, the resultant degraded signal is decreasingly similar to the source signal.

*Whistled Signal.* Figure 4 (a) and (b) show that similar cycling is not evident in the similarity measures of the whistled signals degraded in exactly the same way as the trilled signals. The longer periodicity of the whistled signal elements requires longer echo delays to illustrate such cycling in the results. In Figure 5, such cycling is evident for the whistled signal results when extended delays that correspond to the signal element periodicity are used, such as 438, 656, and 875 ms.

Figure 4 (a) and (b) and Figure 5 together show that for a given echo strength, a much longer echo delay is required to degrade the whistled signal to a minimum, than is required to similarly degrade the trilled signal. In Figure 4 (a) and (b) the degraded trilled signal reaches its first minimum similarity measure, and thus its maximum degradation, around 12.5 to 20 ms. Figure 5 shows that a minimum similarity measure for degraded whistled signals is not incurred until a delay of about 500 ms.

In comparing Figure 4 (a) and (b) with Figure 5, it is important to note that for a given echo strength, both signals ultimately incur a similar

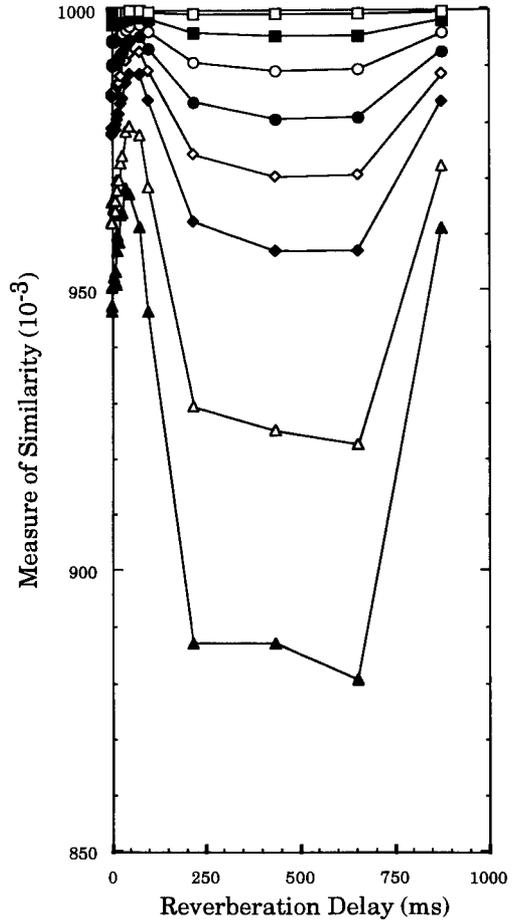


FIGURE 5. Measures of similarity between amplitude envelopes of the whistled source signal, and versions degraded by imposed reverberations of various strengths and extended delays, revealing cycling of resultant measures. Symbols and their corresponding echo strengths are:  $\square$ , open = 4%, filled = 10%;  $\circ$ , open = 15%, filled = 20%;  $\diamond$ , open = 25%, filled = 30%;  $\triangle$ , open = 40%, filled = 50%.

amount of maximum degradation, it just occurs at a different echo delay. Considering the first cycle of similarity measures for the trilled and whistled signal, which occur within about the first 30 ms and the first 875 ms respectively, both the maximum and minimum similarity measures are not significantly different between signal types for a given echo strength (minimum similarity measure or maximum degradation, two tailed paired *t*-test, mean difference = 1.632, *df* = 7, *P* = 0.062; maximum similarity measure or

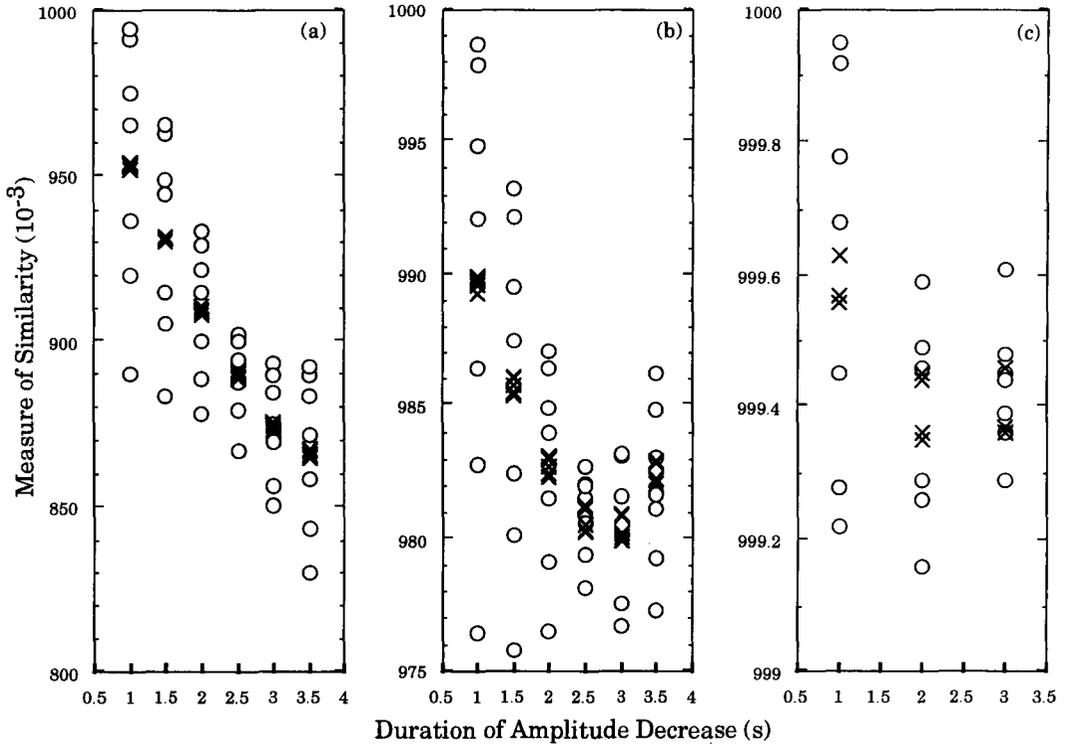


FIGURE 6. Measures of similarity between amplitude envelopes of the trilled or whistled source signals, and those signals degraded by imposed amplitude decreases of various durations, at strengths of (a) 100%, (b) 50%, and (c) 10%. The X symbols = trilled signal results, the O symbols = whistled signal results.

minimum degradation, two tailed paired *t*-test, mean difference = -0.1105, *df* = 7, *P* = 0.14).

IMPOSED AMPLITUDE DECREASES

*Full Signal Analysis.* Figure 6 (a), (b), and (c) show the similarity measures from cross-correlations between the amplitude envelopes of the entire 3.5 second whistled or trilled source signals (seven of each), and those signals degraded by amplitude decreases of various strengths and durations. Figure 6 shows that, for any combination of duration and strength of amplitude decrease, the similarity measures from the degraded trilled signals are contained in a narrow range of intermediate values relative to those of similarly degraded whistled signals. Under all IAD degradation regimes, the mean similarity measure of the degraded trilled signals does not differ from that of the similarly degraded whistled signals (two sample *t*-tests). However, it is clear from Figure 6 and the results in Table 1, that for

a given strength and duration of amplitude decrease, the variability in the similarity measures for degraded whistled signals is enormously greater than that for the degraded trilled signals, except for the small 10% amplitude reductions of the longest durations, but even those differences are significant.

*Partial Signal (Element-Level) Analysis.* The resultant similarity measures from the partial signal analysis, in which two element pairs were sampled from each degraded signal and cross-correlated with the corresponding element pair from its source signal, are seen in Figure 7 (a) and (b). Across all durations of the 50% amplitude decreases, the mean measures of similarity are greatly worse for the element pairs drawn from the degraded whistled signals than those drawn from similarly degraded trilled signals (two sample *t*-tests: 1.5 s, *df* = 13, *P* = 0.028; 2.0 s, *df* = 13, *P* = 0.039; 2.5 s, *df* = 13, *P* = 0.0027; 3.0 s, *df* = 13, *P* = 0.000; 3.5 s, *df* = 13, *P* = 0.000, note that for IAD durations of 1.0 s, there

TABLE 1. Values of *F*-statistics with their associated *P*-value, resultant from the comparison of the range in the seven similarity measures of IAD degraded whistle signals with that of the seven similarly degraded trill signals, for the different strengths of amplitude decrease, across the six durations (only three durations for the 10% decreases) ( $F_{6,6,0.005} = 11.07$ ).

Duration of decrease (s)	Strength of decrease					
	100%		50%		10%	
	<i>F</i> value	<i>P</i> -value	<i>F</i> value	<i>P</i> -value	<i>F</i> value	<i>P</i> -value
1.0	3311.35	<0.005	1261.16	<0.005	140.96	<0.005
1.5	1838.41	<0.005	445.07	<0.005	—	—
2.0	544.79	<0.005	161.98	<0.005	10.37	<0.1
2.5	165.31	<0.005	14.68	<0.005	—	—
3.0	255.37	<0.005	31.64	<0.005	4.72	<0.05
3.5	743.23	<0.005	58.68	<0.005	—	—

was no variability in the similarity measures for the trilled signal packets). In fact, looking at Figure 7 (a), it can be seen that in nearly every case, the similarity measures of the sampled trilled elements were very near 1.0. It is evident from

Figure 7 (b), that across all durations of the 100% amplitude decreases, with the obvious exception of 2.5 seconds, the mean measures of similarity are greatly worse for the element pairs drawn from the degraded whistled signals than those

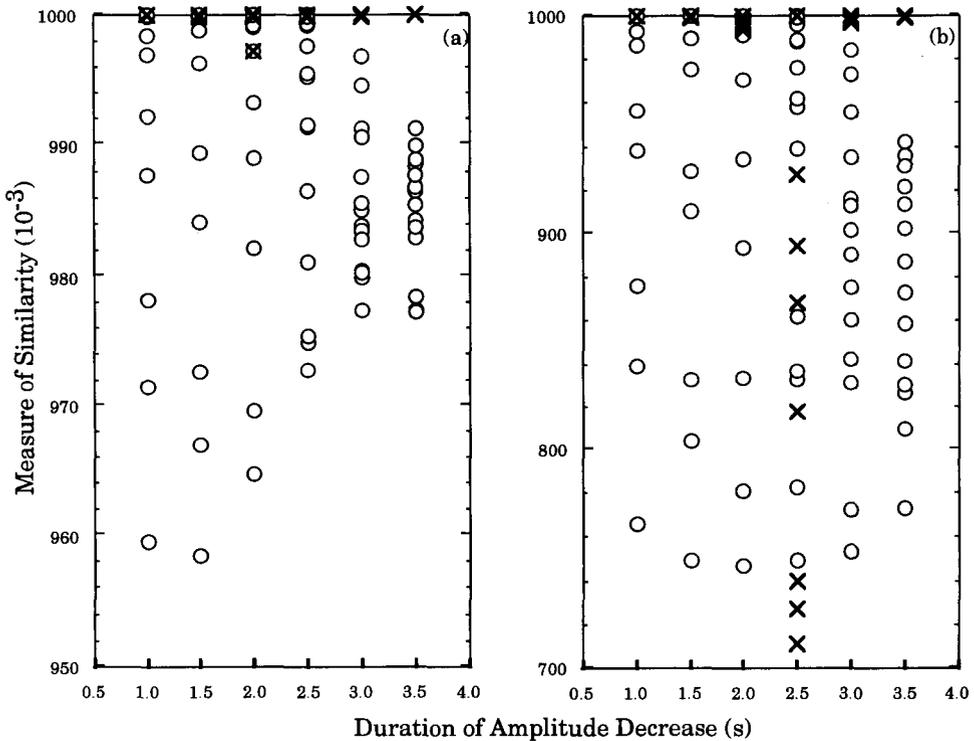


FIGURE 7. Measures of similarity between the amplitude envelopes of element pairs sampled from the trilled or whistled source signals, and the corresponding element pairs from versions degraded by the imposed amplitude decreases of various durations, at strengths of (a) 50%, (b) 100%. The X symbols = trilled signal results, the O symbols = whistled signal results.

drawn from similarly degraded trilled signals (two sample *t*-tests: 1.5 s, *df* = 13, *P* = 0.027; 2.0 s, *df* = 13, *P* = 0.028; 2.5 s, *df* = 13, *P* = 0.73; 3.0 s, *df* = 13, *P* = 0.000; 3.5 s, *df* = 13, *P* = 0.000, note that for IAD durations of 1.0 s, there was no variability in the similarity measures for the trilled signal packets).

## DISCUSSION

### REVERBERATION

The results from simulated transmissions in a reverberant environment support the acoustic adaptation hypothesis. Results agree with the prediction that a whistled (tonal) signal is better suited than a trilled signal for transmission in a closed habitat because it is less degraded by short delay echoes.

Both signals ultimately incur similar degradation levels. The significant difference between their performance lies in the echo delay required to produce maximum degradation, and the variability of degradation incurred by either signal type across relevant echo delays. The trill incurs maximum degradation with an echo delay around 12.5 to 20 ms, while a delay of 438 to 656 ms is required to similarly degrade the whistle. Relative to a straight line transmission, echo delays of 12.5 to 20 ms, and 438 to 656 ms, correspond to extra path distances of 4.3 to 6.9 m, and 150 to 225 m, respectively. A mature forest would have ample reflective surfaces at appropriate distances to provide echo delays which would result in the maximum degradation of both the trilled and whistled signals. However, given the same source output level, the decisive factor would be the echo strength at the point of the listener. The computer simulation gives equivalent echo strengths across all delays. However, in a natural setting, as the echo delay increases, echo strength decreases. Attenuation from spherical spread alone decreases signal strength by about 6 dB per doubling of distance. The extra path distance of the echo delay leading to maximal degradation of the whistled signal, represents between approximately four and five doublings of the distance of that required to similarly degrade the trill, and thus a decrease in echo strength of 24–30 dB. In a natural setting, the actual decrease would be considerably larger due to the increased amount of scattering sur-

faces associated with the larger number of trees in the extended extra path distance. Thus, echoes which could, in principle, seriously degrade whistled signals would, in practice, be too weak to have much influence. On the other hand, strong, short delay echoes, which cause serious degradation to trilled signals, would be commonplace. Thus we can now see, considering the results involving these short echo delays, the whistled signal is a much more reliable structure in transmitting information in a reverberant environment than is the largely variable, and thus correspondingly poor performing, trilled signal.

Large observational studies (Morton 1975, Wiley 1991) have shown support for the AAH in that there were significant tendencies for closed habitat species to stress tonal elements and avoid the use of rapidly repeating ones. However, observational agreement with the theory's predictions leave measurable demonstration of the theory basis unaddressed. This simulation investigation permits the manipulation of reverberation treatments, and has demonstrated that trilled signals should be avoided in forested habitats because, unlike whistled signals, their amplitude patterning is strongly degraded by short delay, and correspondingly strong, echoes.

### IMPOSED AMPLITUDE DECREASES

*Full Signal Analysis.* Results from the simulated degradation by IADs strongly support the acoustic adaptation hypothesis, though in a manner less direct than that seen in the reverberation results. Trilled signals are better suited for transmission in open habitats, not because they transmit with a better average quality than whistled signals, but because they transmit with a more consistent quality. That is, the variability in degradation imposed on trilled signals by IADs, is greatly lower than that imposed on whistled signals.

The 'hit or miss' transmission quality of the whistle results from the IADs being of a duration comparable to the periodicity of the whistle signal elements. If the IAD occurs during an inter-element gap, the transmission quality is high and the singer scores a 'hit'. In this study, a single whistle is 25% of the total signal space. If the IAD occurs during an element, then a relatively large portion of the signal is affected, the transmission quality is poor, and the singer scores a

'miss'. The signal space of a trill is divided into numerous small packets evenly distributed over the length of the signal. Thus, an IAD cannot affect as large a portion of signal space as it can in a whistled signal, and no matter where the IAD occurs the same amount of signal space is affected.

The large observational studies by Morton (1975), and Wiley (1991), showed significant tendencies for open habitat species to use rapid AM signals. Also, open habitat species that used whistled signals tended to sing only at dawn or dusk, while species with rapid AM signals were more likely to sing throughout the day (Morton 1975), when IAFs are most severe. Our simulation investigation illustrates the basis of the theory through manipulation of the signals, showing that a trill is more consistent in transmitting information than is a whistle when both are exposed to similar IADs. This greater reliability in the transmission quality of trills, due to their decreased variability, could easily provide a powerful source of selection favoring this acoustic structure to deal with the unpredictable heterogeneities typical of open habitats.

That the signals differ in their variability of transmission quality, not in their mean quality of transmission, leads to an important consideration for field tests of signal transmissions, particularly those in open habitats. Investigating differences between mean signal transmission qualities may not be as useful as analyses considering the variances in quality. Since the question is really one of variance, and not differences in mean quality, field studies must ensure adequate sampling to avoid confounding results due to chance sampling of more 'hits' than 'misses', or vice versa.

Another important point illuminated by this study is that even low strength IADs, such as 10%, result in significant differences between the ranges of the signal transmission qualities. Wiley and Richards (1978) noted that signal transmissions in closed habitats, in the presence of "even the slightest wind" resulted in noticeable IAFs. This fact highlights the advantage of this simulation in its ability to completely separate the components of degradation, allowing us to discern which signal structure best combats which component of degradation.

*Partial Signal (Element-Level) Analysis.* The results from the transmission quality of element

pairs, sampled from IAD degraded signals, give clear and strong support for the basis of the acoustic adaptation hypothesis. The results show, based on redundancy theory as outlined in the Methods, that under open habitat type IAD conditions, trilled elements transmit information better than whistled elements.

Morton (1975) discusses the redundant structure of the call of the open habitat species *Hylophilus flavipes* stating that such a redundant form could enhance the "communication efficiency" of open habitat species. Marten et al. (1977) point out that there is a large amount of 'moment-to-moment' variation in sound attenuation, particularly in open habitats. The authors argue that an increased vocalization rate would increase the chance that a transmission could coincide with optimal conditions. Gerhardt (1983), and Romer and Lewald (1992), argue that to combat communication difficulties due to IAFs, which occur predominantly in open habitats, a rapid AM structure is desirable. Though the transmissions are periodically degraded, the redundancy inherent in trilled signals (rapid AM) allows the receiver "more than one chance for correct detection of the signal" (Wiley 1994) and the possibility to reform the signal though it is incompletely received. Thus, increasing the number of information packets successfully transmitted from singer to listener increases the chance of correct signal detection by the listener, which is the supposed advantage of redundant signals.

The longer duration of a whistle packet means it is more likely to be influenced by a large proportion of an IADs entire length, while the short length of a trill packet means it is influenced by a correspondingly small portion of the same IAD, and in some cases may escape it entirely. Considering Morton's (1986) definition of degradation, which considers relative changes within the received signal structure, and not overall attenuation, the whistled packet is generally more degraded, because it is more likely to show a severe difference between the structure of its two elements. There are exceptions, as seen with the 2.5 second, 100% IAD where no significant difference in packet transmission quality was seen between the trill and whistle. This exception resulted from a coincidental occurrence in the specific sampling regime. As described earlier, the first pair of elements from each degraded trilled

signal was drawn from the area between 1.18667 to 1.25532 seconds. This time frame coincidentally includes the point of maximum amplitude decrease (1.25 s) for the 2.5 second duration IAD. Thus, within the time frame from which the first element pair from each degraded trill signal was sampled, was also the point where the 100% IAD decreased the signal amplitude to zero, resulting in unusually high amounts of degradation to be incurred by the trill elements. Rather than dismissing this case as an artifact of the sampling technique, it should be considered a worst case scenario for transmission quality of a trilled packet. Even in this worst case scenario, the trilled packet did no worse than the whistled packet. In all of the other cases, the trilled packets transmitted with significantly better quality. These results then, strongly support the basis of the AAH, showing that trills are better than whistles for transmitting information through open habitats.

## GENERAL DISCUSSION

Numerous observational field studies, and a limited number of experimental ones, have investigated the AAH by analyzing signal structure and/or signal transmission quality in relation to habitat. It is important that field studies of this kind heed the conclusions of Date and Lemon (1993), in that "acoustic environments of individuals ultimately shape the songs more toward an average rather than towards distinction." Though this point is important, it should not be surprising, since organismal traits are the result of compromises between various selective forces (Ryan and Brenowitz 1985). Previous studies have suggested that population density (Tubaro and Segura 1994), distance assessment cues (Wiley 1991), whether species are resident or migratory (Sorjonen 1986a), and whether species are early or late season migrants (Sorjonen 1986b), could all play a role in signal design. With all the possible selective forces acting on signal design, investigators looking for specific or finely detailed differences within or among species, across habitats, should not be surprised to find results that do not always agree with AAH predictions.

Smith and Yu (1992) performed a rather specific investigation of the signal structure of 12 Taiwanese passerines across a limited array of habitat types (three habitats, all of which were

various degrees of being closed) and, perhaps not surprisingly, found no agreement between the observed and AAH predicted signal amplitude patterns. Impressive support for the AAH comes from those studies considering large numbers of species (in excess of 100) across a wide range of habitat types (ranging from wide open grasslands, to closed mature forests) like those of Morton (1975) and Wiley (1991). These studies are able to demonstrate the general trends in signal structure across various habitat types, and the trends which have emerged from such large scale studies have been in agreement with the AAH predictions. Single species studies may also offer strong support for the AAH if the species under investigation shows variation in its vocalization, and inhabits a wide range of habitats ranging from open to closed types. This type of support for the AAH is evident in the numerous studies on the vocalizations of *Zonotrichia capensis* (Handford 1981, Handford 1988, Handford and Lougheed 1991, Tubaro et al. 1993). This computer simulation investigation, looking at the levels of degradation incurred by rapid AM versus low rate AM signals upon exposure to two of the major components of degradation, has shown strong and complete support for the very basis of the AAH predictions.

## ACKNOWLEDGMENTS

We are grateful for the time spent, and helpful comments made, by Stephen Rothstein on an earlier draft of this manuscript. The valuable comments made by three anonymous reviewers were of great aid in improving our original manuscript. This work was supported by a Natural Sciences and Engineering Research Council of Canada Operating Grant to P. Handford.

## LITERATURE CITED

- ANDERSON, M. E., AND R. N. CONNER. 1985. Northern Cardinal song in three forest habitats in eastern Texas. *Wilson Bull.* 97:436-449.
- BROWN, C. H., R. GOMEZ, AND P. M. WASER. 1995. Old World monkey vocalizations: adaptation to the local habitat? *Anim. Behav.* 50:945-961.
- CORNELL LABORATORY OF ORNITHOLOGY. 1993. Canary: the Cornell bioacoustics workstation, Version 1.1. Bioacoustics Research Program, Ithaca, NY.
- DABELSTEEN, T., O. N. LARSEN, AND S. B. PEDERSEN. 1993. Habitat-induced degradation of sound signals: quantifying the effects of communication sounds and bird location on blur ratio, excess at-

- tenuation, and signal-to-noise ratio in blackbird song. *J. Acoust. Soc. Am.* 93:2206-2220.
- DATE, E. M., AND R. E. LEMON. 1993. Sound transmission: a basis for dialects in birdsong? *Behaviour* 124:291-312.
- DIGIDESIGN INC. 1992. Sound designer II, Version 2.5. Digidesign Inc., Menlo Park, CA.
- GERHARDT, H. C. 1983. Communication and the environment, p. 82-113. *In* T. R. Halliday and P. J. B. Slater [eds.], *Animal behaviour*, Vol. 2; Communication. W. H. Freeman, New York.
- GISH, S. L., AND E. S. MORTON. 1981. Structural adaptations to local habitat acoustics in Carolina Wren songs. *Z. Tierpsychol.* 56:74-84.
- HANDFORD, P. 1981. Vegetational correlates of variation in the song of *Zonotrichia capensis*. *Behav. Ecol. Sociobiol.* 8:203-206.
- HANDFORD, P. 1988. Trill rate dialects in the Rufous-collared Sparrow, *Zonotrichia capensis*, in northwestern Argentina. *Can. J. Zool.* 66:2658-2670.
- HANDFORD, P., AND S. C. LOUGHEED. 1991. Variation in duration and frequency characters in the song of the Rufous-collared Sparrow, *Zonotrichia capensis*, with respect to habitat, trill dialects and body size. *Condor* 93:644-658.
- HANSEN, P. 1979. Vocal learning: its role in adapting sound structures to long-distance propagation, and a hypothesis on its evolution. *Anim. Behav.* 27:1270-1271.
- KELLER, E. 1994. Signalyze, Version 3.12. InfoSignal, Lausanne, Switzerland.
- LINSKENS, H. F., M. J. M. MARTENS, H. J. G. M. HENDRIKSEN, A. M. ROESTENBERG-SINNIGE, W. A. J. M. BROUWERS, A. L. H. C. VAN DER STAAK, AND A. M. J. STRIK-JANSEN. 1976. The acoustic climate of plant communities. *Oecologia* 23:165-177.
- LOUGHEED, S. C., AND P. HANDFORD. 1992. Vocal dialects and the structure of geographic variation in morphological and allozymic characters in the Rufous-collared Sparrow, *Zonotrichia capensis*. *Evolution* 46:1443-1456.
- MACROMIND-PARACOMP, INC. 1992. SoundEdit pro, Version 1.0. MacroMind-Paracomp, San Francisco, CA.
- MARTEN, K., AND P. MARLER. 1977. Sound transmission and its significance for animal vocalization. I. Temperate habitats. *Behav. Ecol. Sociobiol.* 2:271-290.
- MARTEN, K., D. QUINE, AND P. MARLER. 1977. Sound transmission and its significance for animal vocalization. II. Tropical forest habitats. *Behav. Ecol. Sociobiol.* 2:291-302.
- MCGREGOR, P. K., AND J. B. FALLS. 1984. The response of Western Meadowlarks (*Sturnella neglecta*) to the playback of degraded and degraded songs. *Can. J. Zool.* 62:2125-2128.
- MCGREGOR, P. K., AND J. R. KREBS. 1984. Sound degradation as a distance cue in Great Tit (*Parus major*) song. *Behav. Ecol. Sociobiol.* 16:49-56.
- MCGREGOR, P. K., J. R. KREBS, AND L. M. RATCLIFFE. 1983. The reaction of Great Tits (*Parus major*) to playback of degraded and undegraded songs: the effect of familiarity with the stimulus song type. *Auk* 100:898-906.
- MORTON, E. S. 1975. Ecological sources of selection on avian sounds. *Am. Nat.* 109:17-34.
- MORTON, E. S. 1986. Predictions from the ranging hypothesis for the evolution of long distance signals in birds. *Behaviour* 99:65-86.
- NAGUIB, M. 1995. Auditory distance assessment of singing conspecifics in Carolina Wrens: the role of reverberation and frequency-dependent attenuation. *Anim. Behav.* 50:1297-1307.
- RICHARDS, D. G., AND R. H. WILEY. 1980. Reverberations and amplitude fluctuations in the propagation of sound in a forest: implications for animal communication. *Am. Nat.* 115:381-399.
- RÖMER, H., AND J. LEWALD. 1992. High-frequency sound transmission in natural habitats: implications for the evolution of insect acoustic communication. *Behav. Ecol. Sociobiol.* 29:437-444.
- ROTHSTEIN, S. I., AND R. C. FLEISCHER. 1987. Vocal dialects and their possible relation to honest status signalling in the Brown-headed Cowbird. *Condor* 89:1-23.
- RYAN, M. J., AND E. A. BRENOWITZ. 1985. The role of body size, phylogeny, and ambient noise in the evolution of bird song. *Am. Nat.* 126:87-100.
- RYAN, M. J., R. B. COCROFT, AND W. WILCZYNSKI. 1990. The role of environmental selection in intraspecific divergence of mate recognition signals in the cricket frog, *Acris crepitans*. *Evolution* 44:1869-1872.
- SHY, E. 1983. The relation of geographical variation in song to habitat characteristics and body size in North American Tanagers (Thraupinae: *Piranga*). *Behav. Ecol. Sociobiol.* 12:71-76.
- SMITH, J. I., AND H.-T. YU. 1992. The association between vocal characteristics and habitat type in Taiwanese passerines. *Zool. Sci.* 9:659-664.
- SORJONEN, J. 1983. Transmission of the two most characteristic phrases of the song of the Thrush Nightingale *Luscinia luscinia* in different environmental conditions. *Ornis Scand.* 14:278-288.
- SORJONEN, J. 1986a. Factors affecting the structure of song and the singing behaviour of some northern European passerine birds. *Behaviour* 98:286-304.
- SORJONEN, J. 1986b. Song structure and singing strategies in the genus *Luscinia* in different habitats and geographical areas. *Behaviour* 98:274-285.
- TUBARO, P. L., AND E. T. SEGURA. 1994. Dialect differences in the song of *Zonotrichia capensis* in the southern pampas: a test of the acoustic adaptation hypothesis. *Condor* 96:1084-1088.
- TUBARO, P. L., E. T. SEGURA, AND P. HANDFORD. 1993. Geographic variation in the song of the Rufous-collared Sparrow in eastern Argentina. *Condor* 95:588-595.
- WAAS, J. R. 1988. Song pitch—habitat relationships in white-throated sparrows: cracks in acoustic windows? *Can. J. Zool.* 66:2578-2581.
- WASSERMAN, F. E. 1979. The relationship between habitat and song in the White-throated Sparrow. *Condor* 81:424-426.
- WILEY, R. H. 1991. Associations of song properties with habitats for territorial oscine birds of eastern North America. *Am. Nat.* 138:973-993.

- WILEY, R. H. 1994. Errors, exaggeration, and deception in animal communication, p. 157-189. *In* L. A. Real [ed.], Behavioral mechanisms in evolutionary ecology. Univ. of Chicago Press, Chicago.
- WILEY, R. H., AND D. G. RICHARDS. 1978. Physical constraints on acoustic communication in the atmosphere: implications for the evolution of animal vocalizations. *Behav. Ecol. Sociobiol.* 3:69-94.
- WILEY, R. H., AND D. G. RICHARDS. 1982. Adaptations for acoustic communication in birds: sound transmission and signal detection, p. 131-181. *In* D. E. Kroodsma and E. H. Miller [eds.], Acoustic communication in birds, Vol. 1. Academic Press, New York.