SOUND DESIGN FOR VOCALIZATIONS: QUALITY IN THE WOODS, CONSISTENCY IN THE FIELDS[1]

TIMOTHY J. BROWN AND PAUL HANDFORD

Department of Zoology, B and G Building, University of Western Ontario, London, Ontario, Canada, N6A 5B7, 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 degrades less than alternative patterns during transmission through native habitat. The specific predictions are that open habitat signals should be structured as rapid AM trills, whereas closed habitat signals should be structured as low-rate AM tonal whistles. To investigate the benefit of trill- and whistle-structured signals in open and closed habitats, respectively, a high and low carrier frequency set of four synthetic signals which ranged from rapid AM trills to low rate AM whistles were transmitted 3 hours after sunrise through five different habitat types ranging from closed mature forest to open grassland. Results indicate that, on average, whistles degrade less than trills in both habitats. Trills benefit in open habitats through their tendency to be received with a more consistent quality than whistles. Such differences in transmission consistency among AM patterns are not found in closed habitats. While not degrading less on average, lower frequency signals are received with a more consistent quality than are higher frequency signals of the same AM structure, in both open and closed habitats.

Key words: acoustic adaptation hypothesis, amplitude modulation, degradation, ranging, reverberation, transmission consistency.

INTRODUCTION

Acoustic signals degrade during transmission. Degradation is "the sum of all the changes in the signal at distance X relative to the signal's structure at its origin" (Morton 1986) and does not encompass overall attenuation resulting from spherical spread. That degradation is a relevant factor in passerine communication has been demonstrated in several oscine species (Richards 1981, Wiley and Godard 1996) and a suboscine (Morton and Derrickson 1996). Behavioral responses indicate that listeners are both sensitive and responsive to degradation effects, suggesting that they assess a signaler's proximity by the level of degradation in the received signal.

The acoustic adaptation hypothesis (AAH, sensu Rothstein and Fleischer 1987) developed largely from the work of Morton (1975) and Hansen (1979). It proposes that acoustic signals are structured so as to maximize their performance under the stresses of the environmental acoustics that characterize their native habitat. The major components of degradation are frequency dependent attenuation (FDA), reverberation, and irregular amplitude fluctuations (IAFs). For transmission heights above those af- fected by ground-level effects, the patterns of FDA lead to the general prediction that signals should utilize low frequencies in all habitats if they are to minimize the FDA component of degradation. In contrast, the relative influence of reverberation and IAFs differ markedly among habitat types. Reverberations result from sound being scattered by reflective surfaces such as foliage, tree limbs and trunks and, thus, are strongly associated with closed habitats and are essentially absent in open habitats (Wiley and Richards 1982). An acoustic signal element may be viewed as a continuous trace on the signal's spectrogram (Fig. 1). Reverberation blurs the distinction between closely-placed elements as inter-element spaces fill with echoes, thus obscuring rapid amplitude modulation (AM) patterns. IAFs result from refraction as sound passes through pockets or layers of air of differing temperature or velocity, and are strongly associated with open habitats, which tend to manifest such atmospheric irregularities, and are correspondingly less prevalent in sheltered, closed habitats. IAFs impose low-rate AM changes on signals which listeners perceive as intensity fluctuations. To combat these stressors to acoustic communication, the AAH predicts that rapid AM (trills) and low rate AM (whistles) should be incorporated into the songs of open and closed habitat species, respectively.
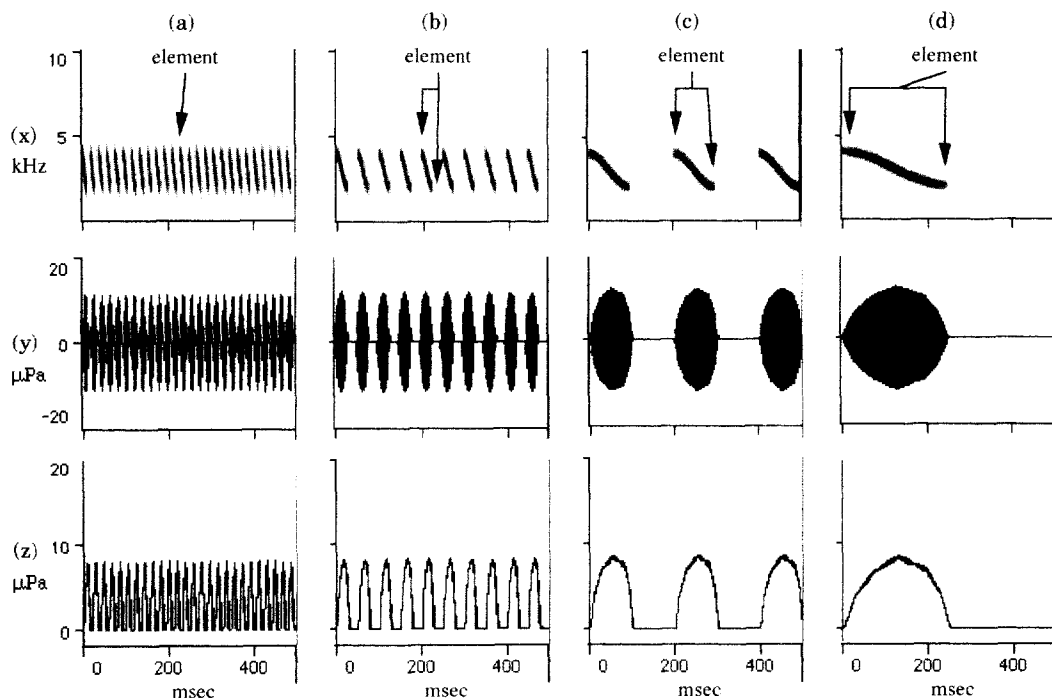
FIGURE 1.   The MiniDisc versions of the 3-kHz signal set. In the four columns are the (a) 10-msec signal, (b) 25-msec signal, (c) 100-msec signal, and (d) 250-msec signal. Across the rows, each signal is represented as (x) a spectrogram, (y) a waveform, (z) an amplitude envelope. The 5-kHz signal set was similar except the frequency sweeps were shifted up 2 kHz.

Strong circumstantial support for the AAH and its predictions comes from Morton's (1975) study of song structure in 177 Neotropical species. He found that songs of open habitat species tended to possess rapid AM, whereas those of closed habitat species were mainly "pure tone-like." Similar associations have been demonstrated in several similar studies (Sorjonen 1986, Wiley 1991, Badyaev and Leaf 1997). Other circumstantial support comes from studies on the Rufous-collared Sparrow (*Zonotrichia capensis*), a species characterized by dialects which are defined by the element repetition rate in the songs' terminal trill (Handford 1988). The dialects exhibit a strong habitat-specific association where "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 Lougheed 1991). The AAH is argued to be the most likely explanation for these associations (Lougheed and Handford 1992).

However, since the early development of the AAH, the rationale for its predictions, specifi-

cally to trill in open and whistle in closed habitats, have often lacked clarity. Some researchers have implied that the predicted signals maximize transmission distance (Brenowitz 1982, Crawford et al. 1997), or simply maximize transmission in some general undefined way (Blumstein and Daniel 1997). Others have stated that such signals minimize "distortion" (Bowman 1979, Anderson and Conner 1985, Brown et al. 1995). Research that has suggested direct benefits of specific signal structures in relation to habitat types has been based on the rationale that the signal type effectively combats the structure of the degradation itself, avoiding the signal masking caused by low rate AM changes imposed by IAFs or the blurring of signal elements caused by reverberation.

Brown and Handford's (1996) computer simulation lent strong support to the AAH predictions that signalers should stress rapid AM and avoid tonal whistles in open habitats, and stress tonal whistles and avoid rapid AM in closed habitats. However, this support was not entirely consonant with conventional explanations.

Brown and Handford (1996) argued that minimizing degradation is likely the benefit of structuring closed habitat signals as whistles, but similar reasoning does not provide the rationale for structuring open habitat signals as trills. Under IAF-type degradation, the trill performed no better, on average, than the whistle. Rather, a benefit of the trill was its extremely consistent transmission quality relative to the highly variable transmission quality of the whistle.

This proposed benefit of trilled and whistled signal structures in open and closed habitats, respectively, is clearer when one considers both the form and the character of the predominant component of degradation typical of each habitat. In closed habitats, the magnitude of degradation incurred is expected to be relatively consistent across time as the heterogeneities that cause reverberation do not vary substantially in size or location from moment to moment. The magnitude of degradation will vary spatially as each site will have a unique array of reflective surfaces. Thus, closed-habitat signals should be structured to cope with temporally consistent reverberation. In contrast, the magnitude of degradation incurred in open habitats is expected to vary substantially across time as thermals, wind, and other heterogeneities that cause IAFs vary from moment to moment. Thus, open-habitat signals need to be structured to combat the form of IAFs and the variability associated with the factors that cause them. This short term variability is expected to dwarf spatial variation within the habitat.

Due to these among-habitat differences in heterogeneity variability, analyses assessing among-signal performance differences in relation to habitat must not be based solely on measures of average degradation incurred, they must also consider how variable a signal's transmission quality is, particularly in open habitats. Degradation is deleterious to the information encoded in the temporal patterning of an acoustic signal (Richards and Wiley 1980). Thus, for analyses of degradation differences between signal types, it is important to focus on alterations in their temporal structuring.

Most support for the AAH comes from observational studies showing that patterns of species' vocalizations in relation to habitat types agree with predictions, again, trill in open habitats, whistle in closed. One experimental study (Gish and Morton 1981) showed that native Car-

olina Wren (*Thryothorus ludovicianus*) signals incurred less degradation than non-native signals. No studies have incorporated signal transmissions through a full range of habitat types. Here we report on a field experiment which permits direct performance comparisons, in terms of mean transmission quality and the variability about that quality, between signal forms within different habitats. The transmission of computer generated signals in this study extends, to natural conditions, the investigation of ideas developed from our earlier computer simulation (Brown and Handford 1996).

METHODS

THE SOURCE SIGNALS AND THEIR TRANSMISSION

We constructed two sets of four sine wave-shaped synthetic frequency sweeps on a Macintosh IIci computer using SoundEdit Pro 1.0 (MacroMind-Paracomp, Inc. 1992). The durations of the four sweeps were 10, 25, 100, and 250 msec, and each was followed by a silent period equal to the sweep length. In the 3 kHz signal set, the sweeps were from 4 to 2 kHz, whereas in the 5 kHz set they were from 6 to 4 kHz. Using Sound Designer II (Digidesign, Inc. 1992), each sweep, with its associated silent period, was set to loop continuously during an approximate 10-sec recording to a Sony MZ-1 Portable MiniDisc Recorder. The resultant 10 and 25 msec signals were rapid AM trill-like signals (Fig. 1a and 1b), whereas the 100 and 250 msec signals were lower rate AM whistle-like signals (Fig. 1c and 1d).

In southwestern Ontario, we selected four sites within each of five habitat types: mature broadleaf forest, broadleaf sapling woodland, scrubland, marsh, and grassland. At each site, a transmission point was selected from which a straight line was drawn over level ground through homogeneous habitat, with a receiving location being flagged at 50 m (point A), a realistic distance over which songbirds could be expected to communicate. A second receiving location (point B) was similarly flagged 90 degrees clockwise from point A.

Transmission experiments were carried out between May 30 to October 4, 1994, and September 9 to October 3, 1995, and started 3 hours after sunrise. At each site the transmission was directed toward point B on day 1, and point A on day 2. In an effort to control for seasonal

environmental factors, such as humidity and temperature, habitats were advanced through in a nonrandom fashion, completing work at sites 1 in all habitats before commencing work on sites 2, and similarly for sites 3 and 4. The eight signals were transmitted using a Sony MZ-1 Portable MiniDisc Recorder, an Alpine 3548 amplifier set to 3/4 full gain, and a pair of Bose 101 speakers mounted side by side on a tripod stand at a height of 2.1 m. Transmissions were recorded on Sony UX-Pro 90 cassette tapes using a Marantz PMD 430 or 222 tape recorder, a Sennheiser MZA 14 TU (roll off filter set to 140 Hz)/MKH 816 T shotgun microphone held 2.1 m above ground on a MZS 816 pistol grip mounted on a tripod stand. Speakers and microphone were aligned by eye.

QUANTIFICATION OF SIGNAL DEGRADATION

From each experimental transmission, the eight signals were recorded from the Marantz PMD 430 tape 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 because low level background noise may prohibit accurate assessment of incurred degradation, nonsignal frequencies were filtered out using Canary's "Filter Around" edit command (5-kHz signals set at 6.51 to 3.30 kHz, 3-kHz signals set at 4.51 to 1.31 kHz). The first 9 sec of each signal (5 habitats $\times$ 4 sites $\times$ 2 days $\times$ 8 signals = 320 transmissions) was then divided into 9 consecutive 1-sec segments, from which five background noise-free segments were randomly selected. In some cases less than five segments were usable due to noise, and on one occasion an entire experimental run was unusable. Because we were specifically interested in degradation of the temporal patterning of amplitude, waveforms of all the processed segments were transformed into root mean-square amplitude envelopes (1 msec window width, raw values) using Signalyze 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 pre-dawn transmissions across 10 m of open field on two very calm days at a height of 2.8 m. These base transmissions were processed as were the experimental transmissions. Thus, for each signal we had 18 essentially nondegraded 1-sec segments. To determine which of these segments was least degraded, we randomly selected a 1-sec segment of each signal from the original MiniDisc, recorded it onto the computer and similarly processed it. Using Canary, for each signal type we cross-correlated both the amplitude envelope and spectrogram of the MiniDisc version with the corresponding form of the 18 1-sec segments from the base transmissions. The cross-correlation routine calculates a correlation coefficient between two signals that ranges from 0 (signals having no similarity) to 1 (identical signals). When the signals are directly overlaid, the correlation coefficient is a measure of similarity between them (Clark et al. 1987). For each signal, the 1-sec base-transmission segment having the highest average resulting from the amplitude envelope and spectrogram cross-correlations was considered the least degraded version of the signal which yet possessed alterations resulting from the equipment. It was selected as the benchmark from which to measure the degradation incurred in the experimental transmissions.

To quantify the degradation of the amplitude patterns, for each of the eight signal types we cross-correlated the amplitude envelopes of the five randomly selected 1-sec segments from each experimental transmission with the amplitude envelope 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 received and benchmark signal. This assessment corresponds directly with Morton's (1986) definition of degradation. The maximum correlation coefficient calculated between a transmitted and benchmark signal was taken to represent the maximum measure of similarity between the two signals and served as a measure of transmission quality.

STATISTICAL ANALYSES

The results present analyses of signal performance in terms of mean signal transmission quality and the variability about that quality. For each of the eight signals, the measures of transmission quality from the five randomly selected 1-sec segments were used to calculate the mean and standard deviation in transmission quality of

that signal in each experimental transmission. Signals within a frequency set are equivalent in all aspects except for AM rate, and signals of a given AM rate among frequency sets are equivalent in all aspects except for frequency. Therefore, only comparisons among signals of a given frequency set or AM rate are appropriate, with resultant differences being ascribed to the single attribute that differed.

It is necessary to clarify what comparisons are relevant in assessing signal performance. Relevant comparisons are those assessing the performance of different signal structures within given habitats, and not the performance of a given signal among habitat types. From the general AAH expectation of trilled structures in open habitats and whistled structures in closed, it does not follow that the best transmission of a trill or whistle need occur in an open or closed habitat, respectively. It is conceivable that one of these habitats is better suited for acoustic communication in general and that both signal-types may perform best, in absolute terms, in that habitat. What is required by the AAH is that within an open habitat, a trill's performance is better than that of a whistle, and vice versa in a closed habitat. Therefore, the precise question in this context is: Does a trill perform relatively better than a whistle in open habitats, and a whistle relatively better than a trill in closed habitats?

Besides being irrelevant, comparisons of a signal's performance, in terms of mean transmission quality, across open vs. closed habitats are uninterpretable. The level of incurred degradation is assessed by comparing the degraded signal with a corresponding benchmark. It is possible for a signal to be largely degraded by reverberation in one instance, and IAFs in another, with the two final assessments of incurred degradation being identical in absolute value despite the vast qualitative differences. The degradation assessment makes no distinction between the proportional influence of reverberation and IAFs. Such comparisons are uninterpretable and thus of no utility, and although other studies have made them (Blumstein and Daniel 1997), we have avoided doing so. However, we have compared mean transmission quality among habitats within general habitat classes (i.e., closed habitats—among forest and sapling; open habitats—among scrub, grasslands, and marsh). These comparisons are jus-

tified because the major component of degradation within a class is similar.

Among-habitat performance comparisons based on variability in transmission quality also are irrelevant to the AAH, but unlike such comparisons based on mean transmission quality, those based on variability are informative. A signal's mean transmission quality is a quantitative assessment of the degradation incurred, whereas its variability assesses a qualitative character of the degradation, specifically, is the degradation, regardless of its source, consistent or variable? Comparing differences in variability among habitats illustrates those qualitative differences and can illustrate the ability of a signal to combat those differences.

Statistical analysis was performed using Minitab, release 8.21 (Minitab Inc. 1991). Data were tested and found not to depart significantly from normality. With a significance level set at $P \leq 0.05$, testing for significant differences among the means or the standard deviations of the variables (AM rate, frequency, habitat, and site) and their interactions was accomplished using analysis of variance (ANOVA). Although each site was visited twice, the factor of day was dropped to the error term in all the analyses because the original intent of including two visits was to comprehend the magnitude of the variability within a site.

RESULTS

MEAN TRANSMISSION QUALITY

Within habitats. Figure 2 shows the measures of mean transmission quality for the 3 and 5 kHz signals. Analysis of the mean transmission quality of each signal type for each experimental run within habitats revealed no significant differences among the frequency sets in any habitat (Table 1), although, for at least the rapid AM signals, the 5-kHz signals appear to have degraded more than the corresponding 3-kHz signals. Low-rate AM signals performed significantly better than rapid AM signals in every habitat (Table 1). Site was a significant factor in all habitats, as was the site × AM-rate interaction, whereas the site × frequency interaction was significant in all habitats except marsh (Table 1).

Among habitats, within general classes. Mean transmission quality did not differ significantly among forest and sapling habitats, nor among frequencies in closed habitats (Table 2). AM pat-
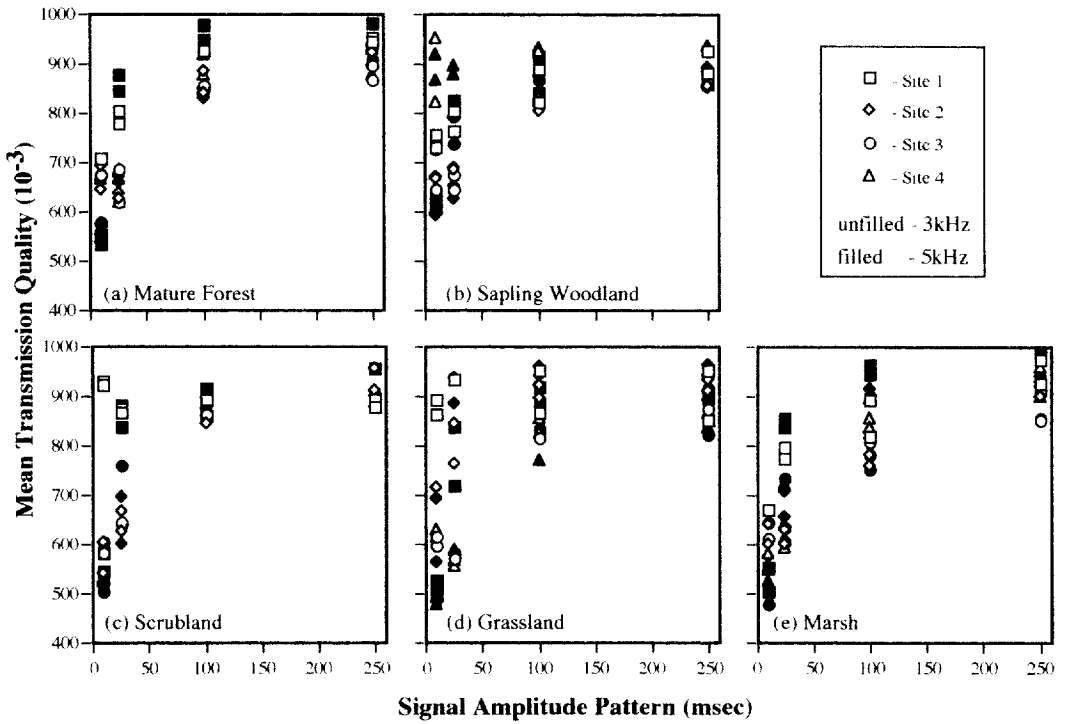
FIGURE 2.   The mean measures of transmission quality for each 3 and 5-kHz signal through (a) mature forest. (b) sapling woodland, (c) scrubland, (d) grassland, (e) marsh.

tern (within frequency) was a significant factor, as was site (within habitat). The significant habitat × AM-pattern interaction is evident in the tendency for the best transmission of trills (10 and 25 msec) to occur in the sapling woods, whereas that of the whistles (100 and 250 msec) occurs in the forest (Fig. 2a and 2b).

Due to unbalanced nesting in the open habitat data, site 4 was dropped from this part of the analysis. Transmission quality did not differ significantly among open habitats, nor among frequencies (Table 2). Again, AM pattern (within

frequency) and site (within habitat) were significant factors. The interaction between habitat and AM pattern was not significant.

STANDARD DEVIATION IN MEAN TRANSMISSION QUALITY

Within habitats. Analysis of the standard deviation (SD) in transmission quality from each experimental run for the 3-kHz signals (Fig. 3) reveals a significant difference among AM patterns in sapling woodlands ($F_{3,9} = 7.5$, $P < 0.01$), a near significant difference in forest hab-

TABLE 1.   Degrees of freedom and F-values from ANOVAs on signal mean transmission quality from all experimental runs within each habitat type.

Factor	Forest df	Forest F	Sapling df	Sapling F	Scrub df	Scrub F	Grass df	Grass F	Marsh df	Marsh F
Frequency	1, 3	0.2	1, 3	0.5	1, 2	1.5	1, 3	2.3	1, 3	2.5
AM pattern	6, 18	53.9**	6, 18	10.0**	6, 12	9.9**	6, 18	17.3**	6, 18	51.1**
Site	3, 28	34.2**	3, 28	44.7**	2, 23	52.1**	3, 26	49.7**	3, 27	13.8**
Site × AM	18, 28	5.0**	18, 28	5.1**	12, 23	11.2**	18, 26	5.1**	18, 27	2.3*
Site × Freq.	3, 28	4.5**	3, 28	3.3*	2, 23	8.2**	3, 26	8.0**	3, 27	0.5

* $P \leq 0.05$. ** $P \leq 0.01$.

TABLE 2. Degrees of freedom and F-values from ANOVAs on signal mean transmission quality from all experimental runs within general habitat classes.

Factor	df	F
Closed Habitats		
Habitat	1, 6	0.3
Frequency	1, 6	0.1
AM pattern	6, 36	46.8**
Site (habitat)	6, 56	41.1**
Habitat × AM	6, 36	3.3**
Open Habitats		
Habitat	2, 6	0.2
Frequency	1, 6	1.3
AM pattern	6, 36	43.2**
Site (habitat)	6, 36	34.6**
Habitat × AM	12, 36	0.3

* $P \leq 0.05$, ** $P \leq 0.01$.

itat ($F_{3,9} = 3.6$, $P = 0.06$), and no difference in the three open habitats. In closed habitats, the highest variability in transmission quality tends to be associated with the rapid AM signals. Site was significant in the grasslands ($F_{3,11} = 3.9$, P

$= 0.04$), whereas its interaction with AM pattern was not significant in any habitat.

For the 5-kHz signals (Fig. 3), the SD in transmission quality did not differ significantly among AM patterns in any habitat. Site was only significant in the forest ($F_{3,15} = 7.6$, $P < 0.01$), whereas its interaction with AM pattern was not significant in any habitat.

Analysis of the SD in transmission quality from each experimental run for the combined 3 and 5 kHz data, within each habitat, reveals that the high frequency signals were significantly more variable than the low ones in the sapling ($F_{1,3} = 23.0$, $P < 0.05$) and grassland habitat ($F_{1,3} = 14.2$, $P < 0.05$). Although not significant, similar trends are evident for the forest and scrubland data. The SD in transmission quality did not differ significantly among signal AM rates (within frequencies).

Among habitats, within general classes. In closed habitats, transmissions of the 3-kHz signals in the sapling woodland were significantly more variable than those in mature forest (Table 3), and although a similar difference was not
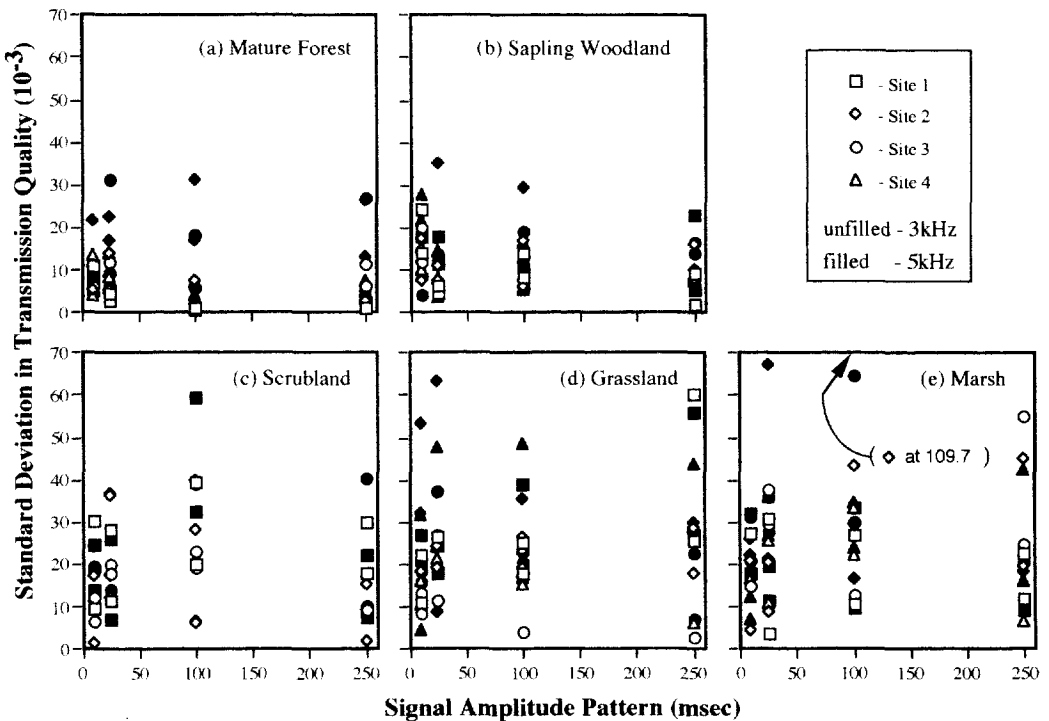

FIGURE 3. Measures of standard deviation in transmission quality for each 3 and 5-kHz signal resulting from transmission through (a) mature forest, (b) sapling woodland, (c) scrubland, (d) grassland, (e) marsh.

TABLE 3. Degrees of freedom and F-values from ANOVAs on the standard deviation in transmission quality for the 3 and 5-kHz signals from all experimental runs within general closed habitat.

| | Frequency | | | |
| | 3-kHz | | 5-kHz | |
Factor	df	F	df	F
Habitat	1, 6	32.4**	1, 6	0.0
AM Pattern	3, 18	6.9**	3, 18	0.6
Site (Habitat)	6, 25	0.5	6, 31	3.9**
Habitat × AM	3, 18	3.6*	3, 18	0.2

* $P \le 0.05$. ** $P \le 0.01$.

found for the 5-kHz signals, the least variable transmissions did tend to occur in the mature forest (Fig. 3). Within the 3-kHz signal set, low-rate AM signals transmitted more consistently than rapid AM signals, but a similar difference was not found for the 5-kHz signals (Table 3). Site (within habitat) was not significant for the 3-kHz transmissions but it was in the 5-kHz signals. The habitat × AM-pattern interaction was significant for the 3-kHz transmissions (likely due to the tendency for habitat differences to be less evident in the 25-msec signal than they are in the other three signals) but not for the 5-kHz transmissions (Table 3).

Analysis of the combined 3 and 5 kHz data reveals that the SD in transmission quality of the 5-kHz signals was greater than that for the 3-kHz signals ($F_{1,6} = 10.0$, $P < 0.05$).

Analysis of the combined 3 and 5 kHz data from open habitats reveals that the SD in transmission quality did not differ significantly among habitats nor among AM patterns. However, the 5-kHz signals were significantly more variable than the 3-kHz signals ($F_{1,6} = 6.9$, $P < 0.05$). Site (within habitat) was not a significant factor, nor was the habitat × AM-pattern interaction.

Although AM pattern was not a significant factor, 17 (38.6%) of the open habitat runs clearly showed the predicted trend for increased variability in transmission quality with decreasing AM rate, whereas only 8 (18.2%) showed the opposite trend. The remaining 19 runs showed no clear trend (4 = possible weak expected trend, 6 = possible weak opposite trend, 9 = no apparent trend at all). Considering the 25 transmissions that showed a clear trend, the proportion of runs showing the expected trend versus those showing the reverse, is significantly dif-
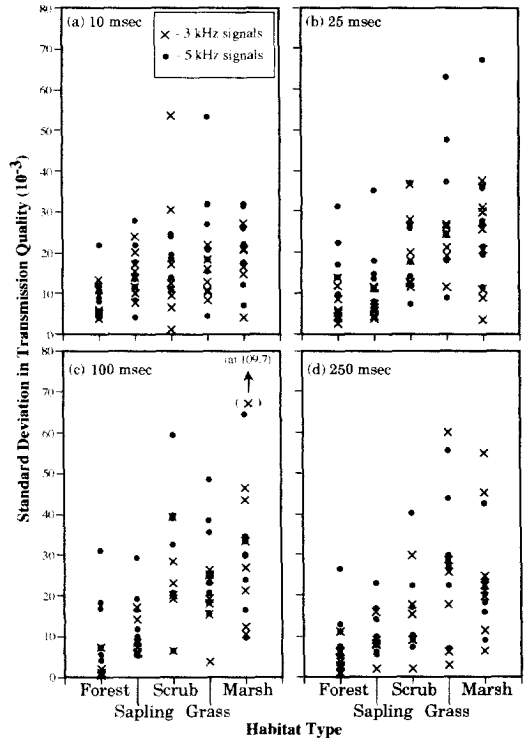

FIGURE 4. An across-habitat summary, for the 3 and 5-kHz signal sets, of the standard deviation in transmission quality resulting from each experimental transmission run for the (a) 10-msec signal, (b) 25-msec signal, (c) 100-msec signal, and (d) 250-msec signal. Although scrubland is displayed in the figure, due to unbalanced nesting it is not part of the analysis discussed in the Results.

ferent (test of proportions: $Z_{24} = 3.6$, $P < 0.01$). Therefore, in open habitats, the transmission quality of trills did tend to be more consistent than that of whistles.

Among all habitats. Analysis of the data from both signal sets in four of the habitats, with scrubland being dropped due to unbalanced nesting, reveals that the SD in transmission quality differed significantly among habitats ($F_{3,12} = 13.8$, $P < 0.01$). Figure 4 summarizes each signal's performance across the habitats. It is clear that the transmissions in closed habitats were less variable than those in open habitats. The SD in transmission quality also differed among frequencies ($F_{1,12} = 17.5$, $P < 0.01$), evidenced by the greater dispersal of 5-kHz signal data relative to that of the 3-kHz signals. The SD in transmission quality did not differ significantly among signal AM patterns (within frequency)

$(F_{6,72} = 0.7, P = 0.64)$, although the visual trend evident in Figure 4 [compare parts (a) through (d)] indicates that in open habitats, rapid AM signals tend to be less variable than low-rate AM signals.

DISCUSSION

TRILLS AND WHISTLES: HABITAT-ASSOCIATED PERFORMANCE

In this experimental investigation of the acoustic adaptation hypothesis (AAH), two sets of computer-generated signals were transmitted through various habitat types. The transmitted signals were recorded at 50 m and, through a method of degradation assessment previously used by Brown and Handford (1996), a measure of the transmission quality was obtained. Signals within frequency sets were identical in all aspects except for AM pattern, thus permitting direct among-signal performance comparisons within sets, with resultant differences being largely attributable to the differences in AM rate. Similarly, differences found among signal-sets can be attributed to the differences in frequency. The 5-kHz signals did not degrade more, on average, than the 3-kHz signals, however, they were more variable in their transmission quality. On average, low-rate AM signals transmitted with a higher quality than rapid-rate AM signals, but in open habitat they also tended to be more variable. These results strongly support our argument (Brown and Handford 1996) that variability in a signal's transmission quality is equally as, or more, important and informative a character to consider when assessing a signal's performance in relation to habitat, as is consideration of average transmission quality.

In terms of mean transmission quality, the results substantiate the AAH predictions for closed habitat signals to possess whistled elements; on average, the amplitude temporal pattern of a low-rate AM whistle is less degraded by reverberation than is that of an equivalent rapid AM trill. In considering the consistency of habitat heterogeneities, we have argued (Brown and Handford 1996) that in a closed habitat, the signal that performs best on average is the most appropriate. For the 3-kHz signals in both of the closed habitats, the variability in the transmission quality tended to be less for the whistles than for the trills, thus reinforcing the prediction that a whistled signal structure is best for communication in closed habitats. The lack of a sim-

ilar result for the 5-kHz signals is not a concern because the level of degradation a signal incurs is expected to be relatively consistent in closed habitats. Thus, we would not consider it necessary for a whistled signal's transmission quality to be significantly more consistent than that of a trill.

That trills perform worse, on average, than equivalent whistles in open habitats seems to conflict with the standard understanding of AAH predictions. However, in open habitats, average transmission quality of a signal may not be the most important factor by which to judge signal performance (Brown and Handford 1996). Rather, one might expect to illustrate the adaptive benefit of an open habitat signal in its ability to combat the inherent variability of the factors that cause irregular amplitude fluctuations (IAFs).

The proportion of experimental runs showing the expected trend of increased variability in transmission quality with decreasing AM rate (17/25) differs significantly from the proportion showing the reverse trend (8/25). It is relevant to note that two of the reverse-trend days had unusual weather conditions. At 7°C, grassland site 4, day 2, was unusually cool relative to a mean temperature of 19.7°C (± 1.82°C) for the other days. Grassland site 3, day 2, was the only day noted to have no discernible breeze. Under such conditions, atmospheric heterogeneities would be relatively minor and the adaptive benefit of rapid AM signals would be less evident. Our results demonstrate that the benefit of a trilled over a whistled signal structure in open habitats is a reduced variability in transmission quality.

The lack of a difference between forest and sapling woodland, in terms of signal mean-transmission quality, does not indicate that the degradation incurred in these habitats was similar. For the 3-kHz signals, the transmission quality was more variable in the sapling woodlands than it was in the mature forest, indicating that the source of degradation in the sapling woodlands was more variable than that in the forest, which suggests a greater influence of IAFs. The lack of a similar finding in the 5-kHz results may be due to the fact that higher frequency signals are more susceptible to IAFs. This increased sensitivity would increase the variability of the signal transmissions as they encounter even the minimal variable heterogeneities that are present in forest habitats. In turn, this may obscure the dif-

fering proportional influence of IAF-type degradation that exists between forest and sapling woodland. Signal performance, in terms of either mean transmission quality or its variability, did not differ significantly among the three open habitats, suggesting that the level and proportional influence of degradation sources in these habitats were similar.

In our consideration of all the habitats, transmissions were least variable in mature forests, more variable in sapling woods, and most variable in open habitats. This indicates that qualitative differences in the proportional influence of degradation components exist among habitat types. This advances a point we made earlier, namely, making among-habitat comparisons of absolute signal degradation levels is inappropriate because, although absolute levels of degradation may be similar, they may differ qualitatively, even when those habitats appear similar in their gross structure, as in the case of mature forests and sapling woodlands.

Finally, it may seem surprising that high and low frequency signals of a given AM rate did not differ significantly in their mean transmission quality. However, the transmission quality of high frequency signals in general closed or open habitats is significantly more variable than the transmission quality of similarly patterned low frequency signals. Therefore, structuring signals with low frequencies would gain benefit not only from decreased attenuation, but also from increased consistency in transmission quality.

AN ADAPTIVE FIT FOR PREDICTABILITY

Song functions in conveying, to the listeners, accurate information about the distance of the singer. Numerous studies have demonstrated that birds are sensitive to acoustic degradation contained in transmitted signals. The results from these studies imply that individuals are in fact able to use degradation to range (assess) the distance of singing conspecifics. Signals need to degrade predictably if it is to be possible for listeners to range them.

Due to the sheltered nature and fixed heterogeneities of closed habitats, the degradation incurred by signals during transmission can be expected to be predictable, and thus ranging seems feasible. The unsheltered nature and variable heterogeneities typical of open habitats, which induce IAFs, can be expected to result in much less predictable levels of degradation, thereby making ranging a more difficult problem. Perhaps partially due to such expectations, the preponderance of ranging studies, including the initiatory work of Richards (1981), have been carried out under closed-habitat degradation conditions. These studies have produced their degraded signals by transmitting them through natural reverberative habitats (Fotheringham and Ratcliffe 1995, Morton and Derrickson 1996) or acoustically active rooms (Naguib 1995, Wiley and Godard 1996), with the latter method being described as one that specifically avoids the incorporation of IAFs (Naguib 1996, 1997). Apparently, the only work on ranging carried out under expressly open conditions is that of McGregor and Falls (1984). Two other studies likely involved complex interactions of open and closed type degradation that would result from mixed habitats (McGregor et al. 1983, McGregor and Krebs 1984). Thus, questions regarding the feasibility of ranging in open habitats have gone largely unanswered, leaving any mechanism for such a possibility unresolved. The results from this study and Brown and Handford (1996) show that although trills incur greater degradation than whistles, their benefit in open habitats is that they have a more predictable transmission quality than the alternative whistle structure. Structuring signals with rapid AM trills would seem to be an adaptive mechanism to combat the unpredictable nature of signal degradation in open habitats. A trill's increased predictability in transmission quality also could be enhanced through the use of lower frequencies.

Another hypothesized function of song is to convey signaler identity information to the listener (Lind et al. 1996). A signaler would augment its identifiability by producing a signal which maximized the consistency of its transmission quality at the point of the listener because greater similarity among received transmissions lowers the ambiguity of the message. Therefore, a signaler would gain advantage by structuring its song to maximize predictability. Under open habitat conditions, the goals of maximizing the quality of transmission and the consistency of that quality are apparently mutually exclusive, because whereas trills incur more degradation than whistles, they are more consistent and therefore less ambiguous and better suited to the function of identity. Under closed

habitat conditions, the goals of maximizing both the quality and the consistency of transmission apparently are not mutually exclusive. In closed habitats, whistles incur less degradation than trills and apparently transmit with a consistency at least comparable to that of trills, and are therefore best suited to the function of identity.

If the conveyance of the signaler's identity is a function of song, ranging may not be so much a function of song as it is an adaptive exploitation of information that is necessarily contained in the transmission of a signal that is adapted to unambiguously convey identity. Thus, structuring signals to degrade predictably may be an adaptation for maximizing identifiability, while at the same time necessarily providing information which can secondarily be utilized by listeners to range the signaler.

Our results, and their interpretation, necessitate a revision of the acoustic adaptation hypothesis. The general AAH predictions that signals in open and closed habitats should be structured as trills and whistles, respectively, have been well supported, but the underlying rationale requires clarification. Minimizing the degradation incurred is not the only, nor perhaps even the main, concern in structuring signals adaptively in relation to habitat. To incorporate these ideas, the AAH could be restated as: signal portions intended to transmit information accurately over a relevant distance, as on the order of territory diameters, should be structured so as to minimize the degradation and/or the variability of that degradation incurred during transmission through native-type habitat. This definition still amounts to trills and whistles being favored in open and closed habitats, respectively, while recognizing that the favored signal is one that achieves the best balance between degradation level and variability. The proportional influence of these factors in determining the appropriate signal structure differs greatly among habitat types.

It is not uncommon for the songs of open or closed habitat birds to be composed of a mixture of trilled and whistled structures, while in some cases, such as a fully trilled song in a forest, entire signals may seem nonadaptive. Some specific expectations pertaining to either song function or use follow from such apparent mismatching between song and habitat type. It is possible that the mismatched song or song portion functions in short rather than long distance communi-

nication. Alternatively, details regarding signal delivery may explain the apparent mismatching. A bird which typically dwells beneath the canopy of a forest but flies to the tree tops to deliver its song is essentially singing in an open habitat where trills would be the expected structure. Such apparent mismatches between song and habitat type could be easily investigated, with questions of song function being studied through playback experiments, and those of song delivery being investigated through detailed observational studies.

ACKNOWLEDGMENTS

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.

BADYAEV, A. V., AND E. S. LEAF. 1997. Habitat associations of song characteristics in *Phylloscopus* and *Hippolais* warblers. Auk 114:40–46.

BLUMSTEIN, D. T., AND J. C. DANIEL. 1997. Inter- and intraspecific variation in the acoustic habitats of three marmot species. Ethology 103:325–338.

BOWMAN, R. J. 1979. Adaptive morphology of song dialects in Darwin's finches. J. Ornithol. 120:353–389.

BRENOWITZ, E. A. 1982. Long-range communication of species identity by song in the Red-winged Blackbird. Behav. Ecol. Sociobiol. 10:29–38.

BROWN, C. H., R. GOMEZ, AND P. M. WASER. 1995. Old World monkey vocalizations: adaptation to the local habitat? Anim. Behav. 50:945–961.

BROWN, T. J., AND P. HANDFORD. 1996. Acoustic signal amplitude patterns: a computer simulation investigation of the acoustic adaptation hypothesis. Condor 98:608–623.

CLARK, C. W., P. MARLER, AND K. BEEMAN. 1987. Quantitative analysis of animal vocal phonology: an application to Swamp Sparrow song. Ethology 76:101–115.

CORNELL LABORATORY OF ORNITHOLOGY. 1995. Canary: the Cornell Bioacoustics Workstation. Ver-

sion 1.2. Bioacoustics Research Program, Cornell Univ., Ithaca, NY.

CRAWFORD, J. D., P. JACOB, AND V. BENECH. 1997. Sound production and reproductive ecology of strongly acoustic fish in Africa: *Pollimyrus isidori*, Mormyridae. Behaviour 134:677–725.

DIGIDESIGN, INC. 1992. Sound Designer II, Version 2.5. Digidesign, Inc., Menlo Park, CA.

FOTHERINGHAM, J. R., AND L. RATCLIFFE. 1995. Song degradation and estimation of acoustic distance in Black-capped Chickadees (*Parus atricapillus*). Can. J. Zool. 73:858–868.

GISH, S. L., AND E. S. MORTON. 1981. Structural adaptations to local habitat acoustics in Carolina Wren song. Z. Tierpsychol. 56:74–84.

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 Inc., Lausanne, Switzerland.

LIND, H., T. DABELSTEEN, AND P. K. MCGREGOR. 1996. Female Great Tits can identify mates by song. Anim. Behav. 52:667–671.

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, Inc., San Francisco.

MCGREGOR, P. K., AND J. B. FALLS. 1984. The response of Western Meadowlarks (*Sturnella neglecta*) to the playback of undegraded 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.

MINITAB INC. 1993. Minitab, release 8.21. Minitab Inc., State College, PA.

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.

MORTON, E. S., AND K. C. DERRICKSON. 1996. Song ranging by the Dusky Antbird, *Cercomacra tyrannina*: ranging without song learning. Behav. Ecol. Sociobiol. 39:195–201.

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.

NAGUIB, M. 1996. Ranging by song in Carolina Wrens *Thryothorus ludovicianus*: effects of environmental acoustics and strength of song degradation. Behaviour 133:541–559.

NAGUIB, M. 1997. Ranging of songs with the song type on use of different cues in Carolina Wrens: effects of familiarity. Behav. Ecol. Sociobiol. 40:385–393.

RICHARDS, D. G. 1981. Estimation of distance of singing conspecifics by the Carolina Wren. Auk 98:127–133.

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.

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.

SORJONEN, J. 1986. Factors affecting the structure of song and the singing behaviour of some northern European passerine birds. Behaviour 98:286–304.

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., AND R. GODARD. 1996. Ranging of conspecific songs by Kentucky Warblers and its implications for interactions of territorial males. Behaviour 133:81–102.

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.