

**Amanda Jobbins**  
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## **Effect of Habitat on Bird Song**

Some of the major functions of bird song include mate attraction, species recognition, and the establishment and defense of territory. Bird song is also closely linked to individual fitness; therefore, songs that maximize effective communication of signals should increase the fitness of that individual. Bird song can be absorbed and or reflected by physical objects, even by such tenuous physical objects as wind. Different wavelengths of sound are absorbed and reflected to a lesser or greater degree by different objects. In deciduous or tropical forest, the best 'sound window' occurs between 1.5 kHz and 2.5 kHz where sound in between these wavelengths survives and travels better than sound with higher or lower frequencies than this range. In coniferous forest, transmission of sounds between 1 and 3 kHz is enhanced by the vegetation. The range of frequencies at which birds call in an environment varies with the habitat and the ambient noise.

Many studies report both interspecific and intraspecific bird song divergence correlated with acoustic properties of the habitat. Song divergence can also be related to morphology, physiology, and life history. Research into bird song has found that lower frequencies travel the farthest regardless of habitat (Wiley and Richards 1982) and higher frequencies have a greater tendency to be scattered by foliage in comparison to lower frequencies (Wiley 1991). These characteristics imply that high frequencies may be constrained by habitat (Wiley 1991). Furthermore, higher frequencies are affected by different levels of background (ambient) noise (Ryan and Brenowitz 1985). In terms of habitat, closed habitats may cause greater attenuation (reduction) in songs, and reverberation is thought to influence the length of notes and the amount of time between notes (Tubaro and Segura 1995). Therefore, birds that live in habitats with numerous scattering surfaces (e.g. leaves, branches) may adopt the following strategies: avoid using rapidly modulated (vary amplitude or frequency) signals; use shorter notes; and put more space between notes to mitigate reverberations.

Related areas of research to the effect of habitat on bird song includes: the Acoustic Adaptation Hypothesis (AAH); the acoustic niche; and the effect of noisy environments on song. AAH states that animal calls should adapt to their environment. Specifically for bird song, AAH predicts that calls should possess rapid calls (trills) in open habitats and low rate calls (whistles) in closed habitats. Papers addressing AAH are included in the annotated bibliography below. Additional research papers specifically on this topic, but not discussed, include:

Boncoraglio, G. and Saino, N. 2007. Habitat Structure and the Evolution of Bird Song: A Meta-Analysis of Evidence for the Acoustic Adaptation Hypothesis. *Functional Ecology*, 21, 134-142

Nicholls, K.A. and Goldizen, A.W. 2006. Habitat type and density influence vocal signal design in satin bowerbirds. *Journal of Animal Ecology*, 75, 549-558

Colbeck, G. 2006. A test of the acoustic adaptation hypothesis using the black-throated blue warbler. *Dendroica caerulescens*. *The Ecological Society of America 2006 Annual Meeting*, Poster Session

Blumstein, D.T. and Turner, A.C. 2005. Can the Acoustic Adaptation Hypothesis Predict the Structure of Australian Birdsong? *Acta Ethologica*, 8, 35-44

Brown, T.J. and Handford, P. 2000. Sound Design for Vocalizations: Quality in the Woods, Consistency in the Fields. *The Condor*, Vol. 102, No. 1, 81-92

Khanna, H. 1999. Testing the acoustic adaptation hypothesis for eastern and spotted towhee song. *The Journal of the Acoustical Society of America*, Volume 106, Issue 4, 2131

Tubaro, P.L. and Segura, E.T. 1994. Dialect Differences in the Song of *Zonotrichia capensis* in the Southern Pampas: A Test of the Acoustic Adaptation Hypothesis. *The Condor*, Vol. 96, No. 4, 1084-1088

The acoustic niche describes the hypothesis that the available frequency range is partitioned, and birds call so that overlap between different species in frequency and time is reduced. This work is presented in the following paper:

Krause, B.L. 1993. The Niche Hypothesis. *The Soundscape Newsletter 06*

Finally, the effect of noisy environments on birds has been noted where in urban areas, with a lot of low-frequency noise, birds sing louder and at a higher pitch. Research in this area includes:

Brumm, H. 2004. The impact of environmental noise on song amplitude in a territorial bird. *Journal of Animal Ecology*, 73 (3), 434-440.

Slabbekoorn, H. and Peet, M. 2003. Birds sing at a higher pitch in urban noise. *Nature*, 424, 267

The following is a comprehensive list of references of research work into the effect of habitat on bird song. Following from this list is an annotated bibliography of these references.

Seddon, N. 2005. Ecological Adaptation and Species Recognition Drives Vocal Evolution in Neotropical Suboscine Birds. *Evolution*, 59 (1) , 200-215

Patten, M.A., Rotenberry, T. and Zuk, M. 2004. Habitat Selection, Acoustic Adaptation, and the Evolution of Reproductive Isolation. *Evolution*, Vol 58, 10, 2144-2155

Slabbekoorn, H. and Smith, T.B. 2002. Habitat-Dependent Song Divergence in the Little Greenbul: An Analysis of Environmental Selection Pressures on Acoustic Signals. *Evolution*, Vol. 56, No. 9, 1849-1858

Slabbekoorn, H. and Smith, T.B. 2002. Bird Song, Ecology and Speciation. *Philosophical Transactions: Biological Sciences*, Vol. 357, No. 1420, Reviews and a Special Collection of Papers on Human Migration, 493-503

Slabbekoorn, H., Eilers, J. and Smith, T.B. 2002. Birdsong and Sound Transmission: The Benefits of Reverberations. *The Condor*, Vol. 104, No. 3, 564-573

Hylton, R. and Godard. R.D. 2001. Song properties of Indigo Buntings in open and forested habitats. *Wilson Bull*, 113(2), 243-245

Badyaev, A.V. and Leaf, E.S. 1997. Habitat Associations of Song Characteristics in Phylloscopus and Hippolais Warblers. *The Auk*, Vol. 114, No. 1, 40-46

van Buskirk, J. 1997. Independent Evolution of Song Structure and Note Structure in American Wood Warblers. *Proceedings: Biological Sciences*, Vol. 264, No. 1382, 755-761

Tubaro, P.L. and Segura, E.T. 1995. Geographic, Ecological and Subspecific Variation in the Song of the Rufous-Browed Peppershrike (*Cyclarhis gujanensis*). *The Condor*, Vol. 97, No. 3, 792-803

Wiley, R.H. 1991. Associations of Song Properties with Habitats for Territorial Oscine Birds of Eastern North America. *The American Naturalist*, 138, 973-993

Ryan, M.J. and Brenowitz, E.A. 1985. The Role of Body Size, Phylogeny, and Ambient Noise in the Evolution of Bird Song. *The American Naturalist*, Vol. 126, No. 1, 87-100

Wiens, J.A. 1982. Song Pattern Variation in the Sage Sparrow (*Amphispiza belli*): Dialects or Epiphenomena? *The Auk*, Vol. 99, No. 2, 208-229

Wiley, R. H. and Richards, D.G. 1982. Adaptations for acoustic communication in birds: sound propagation and signal detection. Kroodsma, D.E. and Miller, E.H (eds.), *Acoustic Communication in Birds*, Vol. 1, Academic Press, New York, 131-181

Richards, D.G. and Wiley, R. H. 1980. Reverberations and Amplitude Fluctuations in the Propagation of Sound in a Forest: Implications for Animal Communication. *The American Naturalist*, 115, 381-399

Hunter, M. L. and Krebs, J.R. 1979. Geographic Variation in the Song of the Great Tit *Parus major* in Relation to Ecological Factors. *Journal of Animal Ecology*, 48, 759-785

Morton, E.S. 1975. Ecological Sources of Selection on Avian Sounds. *The American Naturalist*, 109, 17-34

The following papers are also relevant to the area of the effect of habitat on bird song; however, they were not thoroughly reviewed for this annotated bibliography because the abstracts revealed they covered areas that were already addressed in other reviewed papers.

Handford, P. and Loughheed, S.C. 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. *The Condor*, Vol. 93, No. 3, 644-658

Anderson, M.E. and Conner, R.N. 1985. Northern Cardinal Song in Three Forest Habitats in Eastern Texas. *Wilson Bull*, 97, 436-449

Gish, S.L. and Morton, E.S. 1981. Structural Adaptations to Local Habitat Acoustics in Carolina Wren Songs. *Z. Tierpsychol*, 52, 74-84

Handford, P. 1981. Vegetational Correlates of Variation in the Song of *Zonotrichia capensis*. *Behavioral Ecology Sociobiology*, 8, 203-206

## **Annotated Bibliography**

### **Seddon, N. 2005. Ecological Adaptation and Species Recognition Drives Vocal Evolution in Neotropical Suboscine Birds. *Evolution*, 59 (1) , 200–215**

This paper presents an investigation into three hypotheses about why mating signals are thought to diverge: (1) due to a by-product of morphological adaptation (e.g. longer bills produce lower frequencies); (2) direct adaptation to the environment (effects of habitat); and (3) to facilitate species recognition. The author studied a bird species whose song is not considered dependent on learning – 163 species of antbird (Thamnophilidae). This was a good, unprecedented approach because it avoided the variable of learned behavior rather than a specific adaptation to the habitat. Furthermore, this paper presents a comprehensive study where a combination of factors influencing bird song is considered (i.e. morphology, habitat, and speciation). The results show a correlation between song structure, morphology, and habitat, which concurs with a study by Buskirk (1997). In addition, the paper states that the results support AAH – birds that habitually sing in the understory and canopy produce high-pitched songs than those that sing in the midstory.

### **Patten, M.A., Rotenberry, T. and Zuk, M. 2004. Habitat Selection, Acoustic Adaptation, and the Evolution of Reproductive Isolation. *Evolution*, Vol 58, 10, 2144-2155**

This paper reports on an investigation into the barriers to gene flow in a hybrid zone of the song sparrow. It is found that plumage and song are associated with the environment, which leads to assortative mating. Furthermore, song elements vary by environment as predicted by AAH. However, this paper is more of an examination of gene flow rather than the effects of habitat on bird song.

### **Slabbekoorn, H. and Smith, T.B. 2002. Habitat-Dependent Song Divergence in the Little Greenbul: An Analysis of Environmental Selection Pressures on Acoustic Signals. *Evolution*, Vol. 56, No. 9, 1849-1858**

A study into bird song variation across a rainforest gradient in central Africa is presented in this paper. A rainforest with a densely foliated forest and continuous canopy about 30m high is compared to a rainforest-savanna boundary (ecotone forest) with open forest and a canopy about 20-25m high. Two possible selection pressures on acoustic signals are considered: sound transmission and ambient noise, and three bird song features are measured – minimum and maximum frequency, and peak frequency (the highest amplitude). However, this feature set is limited in comparison to other similar studies. For example, Badyaev and Leaf (1997) looked at nine features in their research on warblers, and Buskirk (1997) considered twelve features. The conclusion is that ambient noise is possibly a selective pressure on bird song – bird song in the rainforest habitat is lower frequency. However, this result simply concurs with previous research. In 1985, Ryan and Brenowitz showed that ambient noise affects bird song. In this work, it is reported that there was no dialectal variation – songtypes are not dependent on habitat but song characteristics are.

**Slabbekoorn, H. and Smith, T.B. 2002. Bird Song, Ecology and Speciation,”**  
*Philosophical Transactions: Biological Sciences*, Vol. 357, No. 1420, Reviews and a Special Collection of Papers on Human Migration, 493-503

This paper reviews work on how geographical variation in song may affect gene flow through its influence on the ability of males to attract females or to establish territory. It reports that habitat-dependent selection on both song and fitness characteristics can lead to parallel divergence in these traits. Bird song may, therefore, provide females with acoustic cues to find males that are most fit for a particular habitat. In the paper, studies are described that demonstrate bird song is important for mate choice and reproductive divergence, and that across environmental gradients, research suggests that fitness-related traits may dominate despite a lot of gene flow. This paper provides a useful outline of the research in the area of bird song and speciation.

**Slabbekoorn, H., Ellers, J. and Smith, T.B. 2002. Birdsong and Sound Transmission: The Benefits of Reverberations.** *The Condor*, Vol. 104, No. 3, 564-573

This paper presents research into reverberations and amplitude fluctuations in the propagation of sound in a forest. It is reported that reverberations lead to longer and louder songs. However, this result was originally shown by Richards and Wiley in their 1980 paper on reverberations and amplitude fluctuations – reverberations can attenuate bird song. New work in this paper is a finding that territorial males of a passerine bird have a stronger behavioral response to longer bird notes. Also, this paper provides a good review of how bird song is shaped by the environment including how different habitats create different reverberations and attenuate bird song.

**Hylton, R. and Godard, R.D. 2001. Song properties of Indigo Buntings in open and forested habitats.** *Wilson Bull*, 113(2), 243-245

This paper investigates the breeding calls of Indigo Buntings across two habitats: open and forest. The study examines four features of bird song: minimum and maximum frequency; dominant frequency; and note-internote duration between songs (the time interval between songs). However, no significant variations are reported except for a “marginally significant difference” in one note of male songs across habitats. This study monitored birds that sang from song posts with a similar neighboring habitat; therefore, given the habitats are similar, the conclusion that no differences are found based on habitat may not be robust.

**Badyaev, A.V. and Leaf, E.S. 1997. Habitat Associations of Song Characteristics in Phylloscopus and Hippolais Warblers.** *The Auk*, Vol. 114, No. 1, 40-46

This paper reports on research into 30 taxa of warblers (Phylloscopus and Hippolais). Warblers are widely distributed and occupy a variety of habitats. Most warblers are poorly differentiated by morphology (except for body mass); however they show an extensive variation in vocalization, even in a subspecies. Two hypotheses are tested for: (1) frequency characteristics of song should correlate with body mass, and (2) temporal characteristics of song should be affected by habitat structure. The research controls for phylogenetic properties of birds, and nine features of bird song are measured including the number of syllables and song length. However, the selection of the bird song feature set appears to be fairly ad hoc. Other work has looked at less features such as three (Slabbekoorn and

Smith 2002) and more features – up to twelve (Buskirk 1997). Different nesting habitats are selected, which are ranked 1-4, including open fields, bushes, intermediate habitat between bushes and forest, and deciduous forest. Details about how these habitat distinctions are determined is not given. The habitat results show that: higher frequencies varies with habitat openness; temporal parameters are strongly affected by habitat structure; and species in closed habitats use fewer but longer notes, and have longer intervals between notes. These findings are consistent with other studies (e.g. Wiley 1991; Tubaro and Segura 1995). They also report that only high frequencies were affected by habitat structure, which is different to the findings of Slabberkoorn and Smith (2002) where both high and low frequencies in bird song were affected by habitat.

**van Buskirk, J. 1997. Independent Evolution of Song Structure and Note Structure in American Wood Warblers. *Proceedings: Biological Sciences*, Vol. 264, No. 1382, 755-761**

An investigation into the songs of 51 North American wood warblers is presented in this paper. Twelve features are examined, which is the most extensive feature set in this research area. The feature set includes the usual characteristics of bird song considered in other work, such as maximum frequency, but also includes features such as the number of inflection points in the slope of frequency modulation and the proportion of notes adjacent to an identical note. Furthermore, more features were initially considered but subsequently rejected based on principle component analysis then multivariate correlation analysis. This paper stands out as the most robust approach to its selection of song features. The work estimates how variance in song similarity is associated with phylogeny, habitat similarity, and other factors. It is found that the structure of warbler songs is correlated with habitat but the structure of the notes that comprise the songs is relatively unaffected by habitat and is more closely related to phylogenetic history. This provides an interesting differentiation because much of the work in this area focuses on either correlating bird song in its entirety to habitat, morphology, or phylogenetics. With regard to morphology, this work also found that associations between song and habitat cannot be explained by variation among species in body size.

**Pablo L. Tubaro and Enrique T. Segura. 1995. Geographic, Ecological and Subspecific Variation in the Song of the Rufous-Browed Peppershrike (*Cyclarhis gujanensis*). *The Condor*, Vol. 97, No. 3, 792-803**

This paper reports on a study into the song of a single species of bird – Rufous-Browed Peppershrike. This paper is interesting because it considered the effects of latitude on bird song, which may be attributable to different habitats. It was found that the characteristics of songs in equatorial regions differed from those in temperate regions. In addition, consistent with other research in this area, songs are also found to differ based on specific habitat differences – open, mixed, and closed.

**Wiley, R.H. 1991. Associations of song properties with habitats for territorial oscine birds of eastern North America. *The American Naturalist*, 138, 973-993**

Wiley did a lot of work on animal acoustics in the 1980s including the effect of habitat on bird song. In this paper, he reports on the acoustic properties of territorial bird calls across habitats and species – eastern North American oscines. He reports that lower frequencies travel the furthest regardless of habitat, which was initially reported in his previous work (Wiley and Richards 1982). He also reports that high frequencies have a greater tendency to be scattered by foliage than by lower frequencies. This

result also leads on from other earlier work where it was reported that environments with many scattering surfaces, such as foliage, produce more reverberations (Richards and Wiley 1980).

**Ryan, M.J. and Brenowitz, E.A. 1985. The Role of Body Size, Phylogeny, and Ambient Noise in the Evolution of Bird Song. *The American Naturalist*, Vol. 126, No. 1, 87-100**

This paper looks at how bird song is selected for with regard to body size and evolutionary history together with the spectral distribution of ambient noise. They report that a combination of morphological features and habitat contributes to bird song. Therefore, across habitat variations in song may be attributable to different-size birds. In this work it was found that higher frequencies are affected by different levels of background (ambient) noise. More significantly, it is reported that the main selection pressure on bird song that may vary by habitat is the sound transmission properties associated with signal interference from local, ambient noise patterns. This work is the first report of the effect of ambient noise on bird song. In a later study on the Little Greenbul bird, ambient noise was again found to be a selective pressure (Slabbekoorn and Smith 2002).

**Wiley, R. H. and Richards, D.G. 1982. Adaptations for acoustic communication in birds: sound propagation and signal detection. Kroodsma, D.E. and Miller, E.H. (eds.), *Acoustic Communication in Birds*, Vol. 1, Academic Press, New York, 131-181.**

Following another set of experiments by these researchers into the effects of habitat on bird calls, this paper reports on the propagation of song at different frequencies. It is reported that lower frequencies travel the furthest regardless of habitat. This work represents some of the earlier research into vegetation structure and its influence on bird song, and it summarizes habitat properties that limit signal transmission. Also, this paper shows that signals can be degraded while traveling through a habitat.

**Wiens, J.A. 1982. Song Pattern Variation in the Sage Sparrow (*Amphispiza belli*): Dialects or Epiphenomena?" *The Auk*, Vol. 99, No. 2, 208-229**

This work investigates the songs of different populations of Sage Sparrows. The sparrows sing a single song type that does not alter according to the time of the day, through the breeding season, or between years. Song features, such as duration and notes, vary across individuals and populations. However, no pattern in variation is found. Furthermore, the variations that do occur are not correlated to the habitat. This study is interesting because it represents a case where bird song appears to actually be unaffected by different habitats.

**Richards, D.G. and Wiley, R.H. 1980. Reverberations and Amplitude Fluctuations in the Propagation of Sound in a Forest: Implications for Animal Communication. *The American Naturalist*, 115, 381-399**

Richards and Wiley were prominent researchers in the field of habitat affecting bird song. This paper reports on a variety of experiments they conducted in this area. Findings include that for closed habitats (e.g. woodland, forest) frequencies in the range 2 to 8 kHz are optimal for long-range calls, and signals, such as bird song, will degrade. For open habitat, they report that temperature and air humidity can contribute to acoustic degradation, and also that wind may significantly influence bird calls. The paper

also addresses reverberations. This paper is a comprehensive study of the effect of habitat on bird calls, and the research findings are still pertinent in the present day.

**Hunter, M.L. and Krebs, J.R. 1979. Geographic Variation in the Song of the Great Tit *Parus major* in Relation to Ecological Factors. *Journal of Animal Ecology*, 48, 759-785**

This paper investigates the song of the Great Tit (*Parus major*), which is known to have variation across populations. Territorial songs of Great Tits at sites that are either in dense forest or open ground, such as parkland and hedgerows, are recorded. This paper concurs with Morton's earlier work, that bird song in forest habitats have lower frequencies and fewer notes than birds in open habitat. However, this paper is interesting because it investigates an intraspecific example, whereas Morton's work looked at 177 species rather than one. Therefore, this paper shows that bird song within a species differs based on habitat variations, as well as across species, which was shown by Morton (1970). However, they discount the significance of morphological features as accounting for differences in song, whereas later work has shown that morphology does play a role (e.g. Ryan and Brenowitz 1985).

**Morton, E.S. 1975. Ecological Sources of Selection on Avian Sounds. *The American Naturalist*, 109, 17-34**

In this paper, seminal work on the topic of how habitat influences bird calls is presented, which is based on Morton's PhD thesis of the same title from 1970. Passerine bird songs that communicate over long distances are investigated across three habitats: forest, edge, and grasslands. The research examines the acoustics of natural environments and looks for a correlation between the physical structure of bird sounds and differences in habitat acoustics. He analyzes 177 species of neotropical birds and reports that significant support is found for a correlation in differences in bird song frequency to habitat differences rather than taxonomic differences. This work is groundbreaking because no previous studies have reported such an association. Morton also found that the average emphasized frequency in the songs of tropical bird species in low-forest habitats is lower than that of species in grassland or edge habitats. He suggests there are selectional forces to produce songs with these frequencies in order to increase the transmission distance of the songs. This paper is the first work to suggest that structural differences in habitat may affect how bird song is transmitted. This paper is also the first to suggest that habitat acoustics produce selective forces on birds. Morton's paper provides the groundwork for many later studies including: the findings of Richards and Wiley in their 1980 paper on the affect of reverberation on bird song; work in the general area of correlating bird song to habitat; and the potential of selective pressures based on this association.