

Effect of Vegetation Structure on Bird Vocalizations

Ore Carmi

I. Reviews

1. R. HAVEN WILEY AND DOUGLAS G. RICHARDS. 1982. "Adaptations for Acoustic Communication in Birds: Sound Transmission and Signal Detection." In DONALD E. KROODSMA AND EDWARD H. MILLER, eds., *Acoustic Communication in Birds, Vol. 1: Production, Perception and Design Features of Sounds*. (Academic Press, New York, London) pp. 131-181.

In preparing for my presentation, I was recommended several review articles from compilations on bird vocalizations. I based much of my presentation on this particular review. It is a bizarre combination of a little bit of ethology and a good many predictions on how environmental features should influence the evolution of characteristics of bird song such as frequency, amplitude, modulatory emphasis (frequency or amplitude), song speed, and repetition rate of consecutive notes of the same frequency (referred to as "trill-rate" in some articles). Many of the predictions are based on previous experimental acoustic work that did not directly involve birds.

Up front, a couple of shortcomings of the article:

- a. During my presentation, Dr. Connor noted that some of the effects described are expected to influence bird song only above a frequency of 10 kHz, and that (certain) habitat effects on bird vocalizations might be expected to be minimal. Most birds sing below this frequency. For instance, forest passerines in temperate North America sing at frequencies from 2 to 8 kHz, and forest passerines in the tropics sing at frequencies from 1 to 8 kHz. This somewhat escaped me until Dr. Connor mentioned it, but it is perceptive. Not *all* effects described in WILEY AND RICHARDS were limited to the frequencies above the typical range of songbirds. Within coniferous forests, this is certainly so, but there are differential effects *between* habitats. In (dense) brushy habitat, Wiley and Richards even claim there are differential effects *within* the frequency range of typical of songbirds—however, the reference they cite to support this claim [AYLOR 1971, REF. 5] seems to me to suggest otherwise.
- b. I mentioned in my presentation that one characteristic of vocalizations, "timbre," is often neglected, and that this was the case in this article. Lohr and Dooling [1998. "Detection of changes in timbre and harmonicity in complex sounds by Zebra Finches (*Taeniopygia guttata*) and Budgerigars (*Melopsittacus undulatus*)."*Journal of Comparative Psychology* **112**(1): 36-47] offer a correction to my categorization of timbre as a 'characteristic of sound.' It is actually a "perceptual phenomenon." I also mentioned in my presentation that timbre is difficult to define rigorously, but that it is what enables us to tell apart the sound of two different musical instruments, for instance, playing a note of the same frequency, at the same amplitude, and I outlined various characteristics of sound adding up to timbre, including the overtone and attenuation patterns of the sound. Lohr and Dooling offer some corrections here too: They only seem to consider overtones as involved in perception of "timbre." However, it isn't the *pattern* of overtones, but the "relative amplitudes of different harmonics," that matters. Our ability to distinguish different sounds (as, for instance, musical instruments) *does* also rely on the sound's pattern of attenuation. However, as defined by Lohr and Dooling, attenuation pattern does not bear on "timbre." The main point, here, in any case, is that structural characteristics of sound other than frequency and amplitude should be considered in studying the effect of environment on bird vocalization, and they haven't been in this case.

[The importance of timbre to the study of bird vocalizations was suggested to me by Jay McEntee, currently a graduate student in U.C. Berkeley.]

Here is a brief summary of some of the findings of the review:

A. Acoustic effects:

Two classes of environmental effects on sound are discussed: attenuation and degradation. Attenuation is the reduction of intensity over distance, which may be frequency-dependent or not. Degradation is the loss over distance of detectability of the amplitude- or frequency-*pattern* of a sound.

1. Attenuation:

- a. Over a homogeneous medium, sound attenuates in proportion to the square of the distance from the source, without differential effect on different frequencies. This is known as Spherical Spread. Sound intensity decreases by 6 dB (decibels) per doubling of distance. The decibel scale is a log scale.

Non-homogeneous media effect differential attenuation at different frequencies of sound. Temperature and humidity also affect attenuation differentially by frequency. Details are as follows:

- b. “Atmospheric Absorption” refers to the dissipation of energy from sound waves as heat through absorption by the atmosphere. In general, higher frequencies are disproportionately affected. (In cold, dry air, the effect is opposite. However, this is not predicted to be of much significance.) In referring to one of the sources, HARRIS 1966 [REF. 4], it appears to me that Atmospheric Absorption really can have a significant effect on differential attenuation within the range of frequencies typical of songbirds.
- c. “Scattering” increases attenuation via interference from reflected, diffracted and refracted sound waves. Scattering may be caused by vegetation. Here, the diameter of the scattering objects (e.g. branches, leaves) relative to the wavelength, as well as the objects’ density, make a difference. Therefore, higher frequencies are effectively scattered by smaller and smaller objects, so that in an environment with different sizes of scattering objects, such as a forest, sounds of higher frequencies are expected to be scattered more than those of lower frequencies. Empirical studies in forests have apparently shown that the effect is not different within the range of frequencies of 2 kHz to 11 kHz. Hence, Dr. Connor’s point, which I mention above, to the extent that the effects of vegetative structure should not be predicted to affect songbirds in the same forest habitat differentially, is merited. However, Wiley and Richards cite empirical evidence for differences in attenuation for this frequency range *between* types of forest (e.g. broad-leaf vs. coniferous, relative to open habitats—needles, apparently, scatter very little sound below 10 kHz). As I mention above, Wiley and Richards also claim that in shrubby habitat, there is differential attenuation *within* the range of frequencies typically used by songbirds, but, in my eyes, this is not supported by the reference they cite for this claim [AYLOR 1971, REF. 4].

Scattering can also be caused by atmospheric turbulence (which here is defined to encompass sharp differences both in air velocity and in air temperature). Again, higher frequencies are differentially affected. The effect within forest is predicted to be greatest near the ground and near the canopy. Open habitat is expected to attenuate frequencies within the frequency range of the songs of songbirds less than forested habitat on calm

days, but equally on windy days. (Evidence is, however, that birds of open habitats sing at higher frequencies. This is mentioned in REF. 2 below).

- d. “Boundary Interference” comprises a complex set of attenuating effects on sound near the ground. I will not detail them here.

2. Degradation

- a. “Reverberations,” which result from the same forces that cause scattering, tend to blend sounds together and mask any modulation in amplitude. Therefore, in complex habitats, or habitats with high levels of atmospheric turbulence, birds should be more likely to evolve songs that rely on frequency-modulation, rather than amplitude modulation, and should be more likely to evolve a slower rate of repetition of notes of the same frequency, which would otherwise blend together and fail to be received as separate notes, assuming the song is intended to be “received” at long distance.
- b. “Amplitude fluctuations” are caused by turbulence, and mask amplitude patterns on a scale coarser than that masked by reverberations, thus further predicting evolution away from reliance on amplitude-pattern in the songs of birds in complex habitats.

B. Ethology:

One important consideration the article raises is that a bird may wish to effectively transmit information in its song to certain entities, but wish to effectively conceal information from other entities. This can complicate empirical studies of the evolution of vocalizations if one simplistically assumes that all vocalizations are intended to be transmitted with as little loss of information as possible. This relates to another consideration raised by Dr. Connor during my presentation: a bird may choose to sing differently (e.g. softer or louder) based on the size/quality of its territory, similarly complicating empirical studies on the evolution of vocalizations (this is discussed briefly in REF. 2).

2. HANS SLABBERKOORN. “Singing in the wild: the ecology of birdsong” 2004. In PETER MARLER AND HANS SLABBERKOORN, eds., *Nature’s music: the science of birdsong*. (Elsevier Academic Press, various cities) pp. 178-205.

This much more recent review of environmental effects on vocal communication in birds cites WILEY AND RICHARDS (REF. 1), and references therein, heavily where it discusses the same issues, and at times fails to support claims that in WILEY AND RICHARDS were clearly marked as predictions. However, it is much easier to read, and encompasses much more: specifically, behavioral aspects of the effect of environment on transmission of vocalization. A couple of examples:

- * As I mentioned above in my discussion of REF. 1, a bird may make choices over how loud to sing. There is evidence that this corresponds to territory size. If singing is intended to repel other males, and territory sizes happen to be locally small, a bird may sing softer with the effect of not unnecessarily inciting a competitor further away in number of territories than would otherwise be the case.
- * WILEY AND RICHARDS (REF. 1) propose that in addition to reverberations and attenuation being looked at as *negative* effect of dense vegetation, they may also enable birds to judge their distance from the vocalizer. Slabberkoorn cites empirical evidence for this sort of assessment (this is known as “ranging”). He also cites work suggesting that some birds may take advantage

of reverberations in species where *length* of notes is apparently associated with fitness, by singing notes of narrow frequency-range, which will sound longer as a result of reverberation.

Both reviews discuss the effects of noise on birdsong, but I neglect this issue here. Slabberkoorn also discusses the effects of different weather conditions.

II. Experimental studies and short reviews

3. DR. P. MARLER. 1955. "Characteristics of some animal calls" *Nature* **176(4470)**: 6-8.

I came across this paper as a result of trying to track down the source for the prediction that open habitats should select for songs of higher frequencies and broader bandwidths. While it turned out that this paper did not make this prediction, it is interesting for another reason: it presages much of the discussion in later literature about issues surrounding the effects of habitat structure on bird vocalizations. The ethological contingencies discussed later in WILEY AND RICHARDS [1982, REF. 1] surface here as a discussion of the divergent aspects of vocalizations geared for easy detection of the location of the vocalizing bird, vs. concealment. Vocalizations geared for detection of location, such as songs for attraction of mates and discouragement of competitors, calls for attraction of chicks by chickens, and calls for recruitment of other birds to aid in defense, are characterized by wide frequency spectra, a relatively low frequency range centered within the range of maximum sensitivity for the bird, and rapid changes in both frequency and amplitude (i.e. for the latter, discontinuous sound). These maximize detectability of location via binaural detection of phase difference (strongest for lower frequencies), of intensity differences (which are more pronounced at higher frequencies, and thus the rapid and wide swings in frequency enhance detection of location), and of time differences (enhanced by discontinuous sound). By contrast, calls geared for concealment, such as begging calls of young and calls warning of the presence of a predator, are often relatively pure, of non-modulated high frequency, and continuous. [This also relates to the concerns of Boncoraglio and Saino [2007, REF. 9] that an hypothesis of acoustic adaptation in birds should take into account factors such as the presence of predators and other unwelcome "eavesdroppers."]

4. CYRIL M. HARRIS. 1966. "Absorption of Sound in Air versus Humidity and Temperature" *Journal of the Acoustical Society of America* **40(1)**: 148-159.

This is one of the studies, not directly related to birds, on which the WILEY AND RICHARDS 1982 review [REF. 1] is based. Harris used an apparatus involving a closed chamber that can be filled with a gas of known concentration (e.g. air of known humidity) and controlled for temperature and pressure. A given bandwidth of sound was projected into the chamber. The physics of this experimental setup are somewhat beyond my understanding. Apparently, however, once the sound source is turned off, it is possible to record a decay curve for the sound, the slope of which determines the decay rate of the median frequency. Using this setup, Harris obtains attenuation rates for different frequencies at different temperatures and humidity levels (in dB/sec, convertible to dB/100 m using wavelength for the given frequency at the given temperature). Sound at higher frequencies is affected (attenuates) much more than at lower frequencies. For the levels of relative humidity (R.H.) and temperatures tested (R.H. of 30 to 80% and temperatures of 15 to 30°C), air of higher humidity and at higher temperature mediates less attenuation of sound than air at lower humidity and lower temperature. By extrapolation, this trend actually reverses at even lower relative humidities and temperatures (and this reversal is increasingly apparent at temperatures above 0°C for increasing frequencies above 1 kHz or so). I was hoping this article would allow me to determine to what extent Wiley's and Richards's predictions regarding the relevance of Atmospheric Absorption to attenuation of bird vocalizations

are merited. Harris's calculations of attenuation in dB/100 m are in addition to the 6 dB/doubling of distance from the source which is given for Spherical Spread in WILEY AND RICHARDS. Wiley and Richards discuss sound propagation over a distance of 50 to 200 meters, and, so, I have to say that such attenuation rates as ~1.6 dB/100 m for 2 kHz at R.H. of 30% and 15°C vs. ~5.2 dB/100 m for 4 kHz, as given by Harris, suggest a significant differential effect within the frequency range typical of songbirds given the parameters covered by Wiley and Richards.

5. DONALD AYLOR. 1971. "Noise reduction by vegetation and ground" *Journal of the Acoustical Society of America* **51(1 part 2)**: 197-205.

This is another of the studies, not directly related to birds, which is cited in WILEY AND RICHARDS. I discuss it only briefly. Aylor was (ostensibly) interested in outdoor noise reduction by plants, over which there had been debate in the literature, and some lack of understanding with respect to the effects of bare ground. Aylor projected random noise through a variety of vegetation, or above variously manipulated open ground, and measured attenuation. Of relevance to us, here, is that two vegetation types mediated more excess attenuation than others, within the frequency range used by songbirds. Densely planted corn mediated the greatest excess attenuation at that range, followed by brush in summer, followed by a clustering of brush in winter and various kinds of woods, which either showed very little excess attenuation at that frequency range, or none that was measurable. The corn was additionally tested at different densities, and increased density effected attenuation differentially for different frequencies, with higher frequencies disproportionately affected. However, for the 3 frequencies presented, the greatest differentiation was between 1 and 2 kHz, whereas the increased attenuation by increased plant density was very close, comparing 2 kHz and 4 kHz. This suggests to me that, within the frequency range typically used by songbirds, the effect of varying habitat should work roughly equally at all frequencies.

6. POUL HANSEN. 1979. "Vocal Learning: its role in adapting sound structures to long-distance propagation and a hypothesis on its evolution." *Animal Behavior* **27(4)**: 1270-1271.

This paper is cited by BONCORAGLIO AND SAINO [2007, REF. 9] as one of the origins of the Acoustic Adaptation Hypothesis. (This hypothesis conjectures that bird vocalizations evolve to maximize efficiency of transmission in the face of environmental acoustic constraints.) However, the term "acoustic adaptation" does not occur in the paper, and the hypothesis presented is much more ambitious. It is described as an *alternative* to natural selection, and posits that young male passerine birds of a given species *choose* which among the various adult male songs in their earshot they will learn, preferring those that are best propagated through the environment. I find this paper slightly ridiculous. Hansen suggests that as the environment 'filters' out elements of song that propagate poorly, young males will not pick up those elements, and thus will only incorporate in their songs those elements best suited to long-distance propagation. This neglects the possibility that songs may be used as short-distance signals as well—for instance, directed towards a male's bonded mate, or, in fact, towards his nestlings and fledglings. In addition, this hypothesis leaves out birds that have innate song. Not even all passerines are song-learners (although Hansen may not have known this in 1979. See "**Do the birds in these articles learn their song, or is their song innate?**" below). A further problem is that Hansen stipulates that young males should learn their songs at a time when the environment most closely resembles that in which they will be singing. However, the period of critical song-learning occurs at a couple weeks of age, and adult males typically sing more while they are searching for mates, several weeks before their young hatch. (I'm still trying to figure out to what extent this was known in 1979.) All in all, though, I cannot rule out the effect of learning (in oscine passerines) on songtype. Martens [JOCHEN MARTENS. 1996. "Vocalizations and speciation of Palearctic birds." In DONALD E. KROODSMA AND EDWARD H. MILLER, eds., *Ecology and evolution of acoustic*

communication in birds. (Cornell University Press, Ithaca and London) pp. 221-240] gives examples that suggest that both learning and genetic differences can contribute to difference in songtype between closely related groups (even at levels below species) and that both, in fact, can serve as agents of speciation.

7. STEPHEN I. ROTHSTEIN AND ROBERT C. FLEISCHER. 1987. "Vocal dialects and their possible relation to honest status signaling in the Brown-headed Cowbird." *The Condor* **89(1)**: 1-23.

I attempted to track down the first formal mention of the "Acoustic Adaptation Hypothesis." This paper is the earliest mention I've found of the term "Acoustic Adaptation" (at least in an ecological context—"acoustic adaptation" is apparently also a psychological term, and there are psychological papers mentioning it dating back to the 1920s. Incidentally, the first mention I've found of the term "Acoustic Adaptation Hypothesis" is in REF 8, below [WILLIAMS AND SLATER, 1993]. I'm still at a loss as to where this term was coined).

The Acoustic Adaptation Hypothesis plays a relatively minor role in this paper. Rothstein's and Fleischer's purpose in this paper was to introduce and provide support for a new hypothesis for the rise and maintenance of dialects in bird vocalizations ("honest convergence"). The system they worked with is intriguing: a large, continuous, ecologically bounded population of Brown-headed Cowbirds (*Molothrus ater*) in the eastern Sierra Nevada (where they are invasive), which can be divided into three well-defined regions, each corresponding to a separate, temporally stable, male flight-whistle dialect. They discuss 5 hypotheses that may explain the rise of dialects. These are: 1. "History or isolation," which posits that geographical isolation alone, with no effect of selective forces, account for the different dialects; 2. "Genetic or local adaptation," which, as far as I can tell, is very similar to reproductive character displacement—females prefer males with local dialects to the effect of minimizing outbreeding; 3. "Acoustic adaptation"—the subject of this bibliography—"dialects arise and are maintained because the dialect vocalization transmits best through the local habitat"; 4. "Social adaptation," which posits that young males and immigrants benefit from imitating the local dialect. Hypothesis 4 is further divided into two possible subhypotheses: 4a. "Competitive mimicry," or "deceptive mimicry" or, as the authors prefer here, "deceptive convergence"—males benefit from imitating the (easy-to-learn) songs of dominant males. Temporal maintenance of dialects is not predicted here, because dominant males are expected to frequently change their song; 4b. "Honest convergence:" males benefit from imitating the local dialect, but this time the song takes time to learn. Hence, it is an honest signal of quality to the extent that quality is related to age, familiarity with the local environment, and ability to defend against neighboring males. Hypothesis 4a is rejected due to temporal stability of the dialects. Hypothesis 3, the "acoustic adaptation" hypothesis, is tentatively rejected here, because two of the dialects occur in similar habitat (riparian corridors in sagebrush, vs. pine forest in the third dialect), and because some flight-whistle dialects of Brown-headed Cowbirds (in other parts of their range) are known to extend through varying habitats. Due to significant dispersal between dialect areas and bilinguality, hypotheses 1 and 2 are rejected. Key to rejecting hypothesis 4b—the authors' new hypothesis, would be the capacity to show that songs are learned quickly. Evidence to the contrary in this case, in comparing songs of males of different ages, therefore lends support to the authors' hypothesis.

In my opinion, Brown-headed Cowbirds are a poor system in which to test the Acoustic Adaptation Hypothesis, because previous work, which the authors themselves cite, has shown that Brown-headed Cowbird vocalizations can be quite stereotyped.

8. J. M. WILLIAMS AND P. J. B. SLATER. 1993. "Does Chaffinch *Fringilla coelebs* song vary with the habitat in which it is sung?" *Ibis* **135**: 202-208.

I wanted to look at some papers that tested the Acoustic Adaptation Hypothesis (AAH). This is the earliest paper I tracked that actually used the term. Right off the bat it is interesting, because it claims that one stipulation of the AAH is that a bird be capable of song learning, which should give it the advantage of adapting its song to its habitat. This places Williams's and Slater's version of the AAH squarely with HANSEN 1979 [REF. 6, above], and contrasts sharply with Boncoraglio's and Saino's later version of the AAH [REF. 9, below], which makes no mention of song learning. Clearly, a shift had taken place in the definition of the hypothesis in the interim.

Williams and Slater claim their study does not support the AAH. However, their premises are completely flawed. The idea for their study originates in a suggestion by a previous group (Jenkins and Baker) that differences in song between Chaffinches in Europe and Chaffinches in New Zealand are the result of adaptations of the New Zealand birds to "dense coniferous forests." European Chaffinches typically occur in deciduous forest. Williams and Slater decided to test for differences in song in European Chaffinches between two habitats: open scrub, and coniferous forest. They tested the predictions that songs in coniferous forests would be characterized by lower frequencies, slower note-repetition rates, and will resemble the songs of New Zealand Chaffinches in two further characteristics suggested by Jenkins and Baker to be the result of adaptation for denser vegetation. What both groups seem to have completely failed to take into account is that the effect of "dense" coniferous vegetation relative to open habitat on bird vocalizations has been predicted to be non-existent within the frequency range typical of passerines [WILEY AND RICHARDS, 1982—REF. 1]. One also wonders why Williams and Slater did not compare Chaffinch song in coniferous forest and in their more typical deciduous forest habitat. Needless to say, their predictions did not pan out!

Of further significance, the confusion about what constitutes "closed" and what constitutes "open" habitat makes me wonder if the meta-analysis carried out by Boncoraglio and Saino (2007, REF. 9) might have been biased by mistaken designation of habitat structure in any of the studies they chose to analyze. (Boncoraglio and Saino did not include this study in their analysis, because it does not report test statistics of nonsignificant variables.)

9. GIUSEPPE **BONCORAGLIO** AND NICOLA **SAINO**. 2007. "Habitat structure and the evolution of bird song: a meta-analysis of the evidence for the acoustic adaptation hypothesis." *Functional Ecology* **21**: 134-142.

After scouring the literature and finding 40 articles that tested aspects of the Acoustic Adaptation Hypothesis (AAH) via comparisons between bird populations or species in differing habitats, Boncoraglio and Saino selected the 26 of these articles whose statistical approaches allowed meta-analysis. They used meta-analysis to test two predictions of the AAH: 1, that birds in closed habitats sing at lower frequencies than birds in open habitats, and 2, that inter-element intervals are longer in songs of birds from closed habitats. (It is noteworthy that prediction 1 is in some conflict with WILEY AND RICHARDS [1982, REF 1—see above], who predicted that, at least as far as attenuation is concerned, the effects of turbulence in open habitats can equal those in forest. Empirical evidence does agree with prediction 1 [cited in SLABBERKOORN, REF. 2]. However, I'm still trying to figure out where the *prediction* originates.) Their main conclusions were that, depending on the specific frequency measure, prediction 1 is supported to varying extents. Prediction 2 is not supported, although it was the only measure of song-speed/note repetition rate that they were able to test, given the available studies in the literature. The authors discuss their results in the context of the AAH, but also make a strong appeal for a theory of acoustic adaptation that incorporates other elements besides habitat—such as energetic costs of signalling, and the effect of predators/brood parasites (which may select for vocalization characteristics that render the singer difficult to locate—characteristics often directly opposed to those predicted by the AAH).

This is a short, easy-to-read, highly conservative study. The fact that the authors present repeated significant effects of habitat structure on frequency characteristics of bird song after several manipulations and calculations to correct for possible bias, and at the same time present their case that this effect is not overwhelming, lends, I think, highly to their transparency and credence. However, I have several serious concerns: in addition to their prediction 1, they make several other predictions in their Discussion which directly conflict with WILEY AND RICHARDS. Most notably, they predict that higher reverberation in closed habitats should select against frequency-modulation. This is in direct contrast to WILEY AND RICHARDS. Refinement of the AAH since 1982 may explain this conflict. An AAH prediction new to me here is that closed habitats should select for narrower bandwidths, for more effective propagation.

A final note is that, briefly scanning the list of studies they used in their meta-analysis, in the majority of studies where it is quickly discernable, the “closed habitat” was forest. As I’ve already discussed above for WILEY AND RICHARD [1982], coniferous forest is not predicted to affect song over the frequency range typical for passerines.

10. ELIZABETH P. **DERRYBERRY**. 2009. “Ecology shapes birdsong evolution: variation in morphology and habitat explains variation in White-crowned Sparrow song” *The American Naturalist* **174(1)**: in press.

This is a very recent study on the relationship between habitat structure and bird vocalizations, and additionally between morphology and bird vocalizations. It investigates the effect of bill size and of density of habitat on trill rate (note-repetition rate) in the song of White-crowned Sparrows—one of the best-studied songbirds, and one whose song was very intensively studied by Luis Baptista. Derryberry compares recordings made by Baptista in 1970 with recordings made in 2005, matched as best as possible to original locations. Using variation in bill morphology in the birds recorded in 2005, and habitat changes as measured using aerial photos from 2005 and 1970, she finds both that increasing bill size and increasing habitat density are accompanied by a decrease in trill rate. The morphological results are in agreement with work by others. More to the point here, the effects of habitat density changes found here are in agreement with previous *predictions*—this is the first study (apparently) to address this issue empirically within the framework of evolutionary time.

In addition to the significance of the study, the introduction of the article is also an excellent resource for previous work both on the effects of habitat structure and of bill morphology on bird vocalizations.

III. The experimental papers I presented in class

11. DARREN **IRWIN**. 2000. “Song variation in an avian ring species.” *Evolution* **54(3)**: 998-1010.
12. D. E. **IRWIN**, M. P. THIMGAN, AND J. H. **IRWIN**. 2008. “Habitat structure and the evolution of bird song: a meta-analysis of the evidence for the acoustic adaptation hypothesis.” *Journal of Evolutionary Biology* **21**: 435-448.

These two papers are part of a whole series of papers by the groups of Trevor Price and Darren Irwin on the ring-species system of the Greenish Warbler, *Phylloscopus trochiloides*, which consists of a series of interbreeding subspecies surrounding the Tibetan Plateau, with the two subspecies in the northern end not interbreeding, and overlapping in range.

The first paper I assigned as optional background. It tests several hypotheses for divergence in song between the subspecies, including sexual selection, ecological effects (simplified by the

assumption that latitude correlated with habitat), and a combination of the two. Irwin found a strong cline going from south to north in the characters of song he tested. He found a weaker east to west cline. He therefore concluded that both ecological and intersexual forces must have played a role in song divergence.

The second paper in a way carries the premise of the first forward, by also examining call notes, in addition to song. In contrast to the case for song, Irwin et al. found the two northern subspecies differed considerably in their call notes, which goes against an argument for acoustic adaptation, given that the two subspecies occur in similar habitat.

IV. Questions raised in class

How “fast” do birds hear? More generally, what do birds hear?

When studying evolutionary aspects of bird vocalizations, it is important to consider what birds can hear, because much bird vocalization is communicated to other birds.

During my presentation, I made an unreferenced claim that birds can hear more detail per unit time than can humans. Dr. Connor was interested whether there was research supporting/testing this claim. My uncited claim turns out to be partly merited and partly not. Applicable here are a paper and a review by Robert Dooling [The paper: ROBERT J. DOOLING, MARJORIE R. LEEK, OTTO GLEICH, AND MICHEAL L. DENT. “Auditory temporal resolution in birds: Discrimination of harmonic complexes.” *Journal of the Acoustical Society of America* **112(2)**: 748-759; The review: ROBERT DOOLING. “Audition: can birds hear everything they sing?” 2004. In PETER MARLER AND HANS SLABBERKOORN, eds., *Nature’s music: the science of birdsong*. (Elsevier Academic Press, various cities) pp. 206-225]. Robert Dooling writes that it has often been speculated that birds hear with greater temporal resolution than humans, based on their complex vocalizations, which often include modulations of frequency and/or amplitude too rapid to be discernible to the human ear, and this view has been pushed using studies, among others, comparing the cochlear structure of birds with humans. However, direct experimental evidence failed to find that birds resolve a variety of temporal characteristics better than humans, or other vertebrates in general. The failure of all of these studies lies in the fact that they all relied on temporal differences that revolve around changes in amplitude envelope [which I (simplistically?) understand as crude overall changes in intensity]. In his 2002 paper, Dooling employs “Schroeder complexes,” which are synthetic waves that are constant in amplitude envelope and spectrum (“the distribution of energy over frequency”), but whose complex harmonic pattern can be manipulated to the exclusion of envelope and spectrum. The higher the fundamental frequency of these complexes, the shorter the time between iterations, which gives the listener a shorter amount of time to discern any randomly introduced changes in harmonic structure. Birds, it turns out, can discern these changes at much higher frequencies than humans. Human discrimination of these changes dropped precipitously between 200 and 300 Hz, whereas Zebra finches, for instance, were able to discern them at a frequency of at least 1 kHz. So, birds can hear more detail per unit time than can humans, but not more *amplitude*-based details.

And, on the score of amplitude, one more note on what birds hear: MARLER [1955, REF 3] cites a German paper [J. Schwartzkopff. 1950. *Z. vergl. Physiol.* **32**: 319] that provides experimental evidence that Chaffinches rely mostly on differences in (perceived) intensity of vocalization to locate other chaffinches. This is in sharp contrast to experimental evidence cited in WILEY AND RICHARDS [1982, REF 1] that Ovenbirds (*Seiurus aurocapillus*) do not use amplitude modulation to recognize their own species, despite the fact that the distinctive amplitude pattern of Ovenbird song features prominently in human recognition of it [J. B. FALLS. 1963. “Properties of bird song eliciting responses from territorial

males.” *Proceedings of the International Ornithological Congress* **13**: 259-271—this reference is difficult to find. I tracked it down recently, but have not yet managed to lay my hands on it]. Dooling’s review lends support to the latter view of bird perception, by noting that birds have been shown to be less discriminating of differences in sound intensity than humans. In any case, the point is, it is important not to assume that characteristics of sound that are distinctive to *us* are also distinctive to *birds*.

How loud do birds sing? (question raised by Dr. Connor)

I won’t answer this fully, since I still haven’t managed to learn as much about this as Dr. Connor had learned by the date of my presentation. References about loudness of singing, and variation between birds in this regard, are cited in SLABBERKOORN [2004, REF. 2]. Dr. Connor mentioned 90 dB as a generally suitable approximation.

I do want to mention, however, that according to WILEY AND RICHARDS [REF. 1], sound intensity cannot be traced back all the way to its source, but only as close as a distance r to the source, where $r = 2a^2/\lambda$, with a being the radius of a “cylinder piston source,” and λ being the wavelength. For small birds this apparently translates to a distance of a few centimeters.

What is the applicability of the effect of vegetative structure on efficient transmission of vocalizations if birds are sitting on perches on top of the vegetation when they sing? (question raised by Dr. Connor)

One quick note on this: Derryberry (REF. 10, above) briefly discusses this. Males may be singing to other perched males. However, they may also be singing to their mate/offspring within, and therefore *across* the vegetation.

Is “zero decibels” a convenient reference set to the threshold of human hearing? (question I raised)

Dr. Connor protested against this, noting that you can have negative decibels. I’m having difficulty tracking down the original work that led to the setting of “0” decibels (due to a combination of running out of time for this assignment and being limited as to online references available to SFSU students). However, secondary sources suggest that there is some merit to what I originally understood. According to HyperPhysics (C. R. Nave. 2005. <http://hyperphysics.phy-astr.gsu.edu/hbase/HFrame.html>; an online resource designed for K-12 teachers), “[s]ound level measurements in decibels are generally referenced to a standard threshold of hearing at 1000 Hz for the human ear.” This is translatable to $\sim 10^{-12}$ watts/m². According to a Wikipedia article [Ack! I used the “W” word!] on auditory threshold, such thresholds are determined based on a pre-specified percentage of time that a response is elicited in subjects. The reference cited is a textbook. Had I worked more consistently on this assignment over the semester, perhaps I would have gotten hold of the textbook and tracked down the original work. As it is, further elucidation will have to await further effort on my part.

Do the birds in these articles learn their song, or is their song innate? (question raised by Julie Miller)

This is important to ask for a variety of reasons. Some of the first allusions to the effects of environmental forces on the evolution of bird vocalizations assumed the capacity to learn song (see, for example, HANSEN 1979 and WILLIAMS AND SLATER, 1993, REFS. 6 and 8, above). On the other hand, the ability to evolve songtypes culturally might obscure the potential effects of genetic evolution.

Greenish Warblers (*Phylloscopus trochiloides*), the subjects of the articles I presented in class, are oscine passerines. Passerines, or “Perching Birds” comprise the most speciose order of birds (more than 50% of birds are in the order Passeriformes. There are, roughly, 29 or so orders of birds). Passeriformes is divided into 2 lineages, oscines (“songbirds,” although sometimes all of Passeriformes are referred to as “songbirds,” confusingly) and suboscines. Suboscines consist of about 10 families, all restricted to the New World. In 1985 Kroodsma published evidence that birds in the suboscine family Tyrannidae had innate song [DONALD E. KROODSMA. 1985. “Songs of the Alder Flycatcher (*Empidonax alnorum*) and Willow Flycatcher (*Empidonax traillii*) are innate.” *The Auk* **101**: 13-24]. In a controlled experiment, he raised nestlings of the birds in the lab, exposing them either to conspecific or heterospecific adult song. All individuals acquired a normal adult song of their own species. In addition, Kroodsma mentioned unpublished work by E. S. Morton, who hand-raised a Barred Antshrike (*Thamnophilus doliatus*, a suboscine then placed in the family Formicariidae) that developed apparently normal adult vocalizations. Previous research had shown that exposure to proper adult song is critical to proper song formation in a variety of oscine birds (some cited in the Kroodsma 1984 article). Isler et al. [MORTON L. ISLER, PHYLLIS R. ISLER, AND BRET M. WHITNEY. 1998. “Use of vocalizations to establish species limits in antbirds (Passeriformes: Thamnophilidae).” *The Auk* **115**(3): 577-590] review other evidence that suboscines in general do not learn song. (This evidence includes lack of anatomical structures in the brain associated with song learning in oscines, widespread lack of geographic variation in song in many suboscine species, and correlation of differences in song with genetic breaks where variation does occur.) The evidence for innate song in suboscines is therefore very strong.

In a strange review [JOCHEN MARTENS. 1996. “Vocalizations and speciation of Palearctic birds.” In DONALD E. KROODSMA AND EDWARD H. MILLER, eds., *Ecology and evolution of acoustic communication in birds*. (Cornell University Press, Ithaca and London) pp. 221-240], Martens chronicles several systems of Old World oscines where genes and culture seem to influence to varying degrees the maintenance (or lack of maintenance) of dialects. (He includes discussion of some species of *Phylloscopus*.) He implicates cultural evolution in speciation in some cases, and hypothesizes that some dialects may arise via isolation or reduction in population density leading to lack of song templates for young birds.

So, my answer to Julie’s question, in the case of the Greenish Warbler, is that I’m guessing *both* genetics and culture play a role in acquisition of song. [However, I haven’t yet looked into the extent to which other, non-song, vocalizations may or may not be innate.]