

# UC Berkeley

## UC Berkeley Previously Published Works

**Title**

Human language diversity and the acoustic adaptation hypothesis

**Permalink**

<https://escholarship.org/uc/item/4zb5t7gm>

**Journal**

Proceedings of Meetings on Acoustics, 25(1)

**ISSN**

1939-800X

**Authors**

Maddieson, I  
Coupé, C

**Publication Date**

2015-11-02

**DOI**

10.1121/2.0000198

Peer reviewed

## 1. Introduction and background.

The phonetic structures of individual modern human spoken languages mostly differ as a function of differences that existed in earlier versions of those same languages. These characteristics are inherited through a process of cross-generational cultural transmission. But human languages must also be shaped by the evolutionary pressures that impact the behavior of all living creatures. This paper posits that there is an environmental effect on language diversity similar to that posited for other biological communication systems that depend on the acoustic channel.

Acoustic communication in the biological world varies for many reasons (Hauser 1996, Ryan & Kime 2002). These include the differing sound-producing mechanisms and capabilities that different organisms have, differences in the receiver characteristics (such as varying hearing ranges), differing functions of the ‘message’ to be conveyed (such as threat, attraction, contact, alarm), competition for bandwidth (the acoustic niche hypothesis, Krause 1987), and differing transmission conditions in the locales which different species inhabit. It has been argued that the last of these has measureable influence in shaping the acoustic structure of signals used by a variety of species. The hypothesis that this is so has come to be known as the Acoustic Adaptation Hypothesis (henceforward, AAH). The AAH has particularly been studied in birds (e.g. Chappuis 1971, Morton 1975, Seddon 2005, Boncoraglio & Saino 2007). This research has indicated that such factors as the typical density of vegetation in a species’ habitat correlate with both spectral and temporal properties of bird songs. In the spectral domain, Boncoraglio & Saino’s (2007) meta-analysis of multiple studies found that “*Maximum, minimum, peak frequency and frequency range [are] found to be significantly lower in closed compared with open habitats*”. The temporal structure of bird songs also correlates with habitat: for example, Badyaev & Leaf (1997) found that among a group of warblers “*species occupying closed habitats avoided the use of rapidly modulated signals and had song structures that minimized reverberation.*” Illustrative waveforms and spectrograms of contrasting song types are shown in Figure 1.

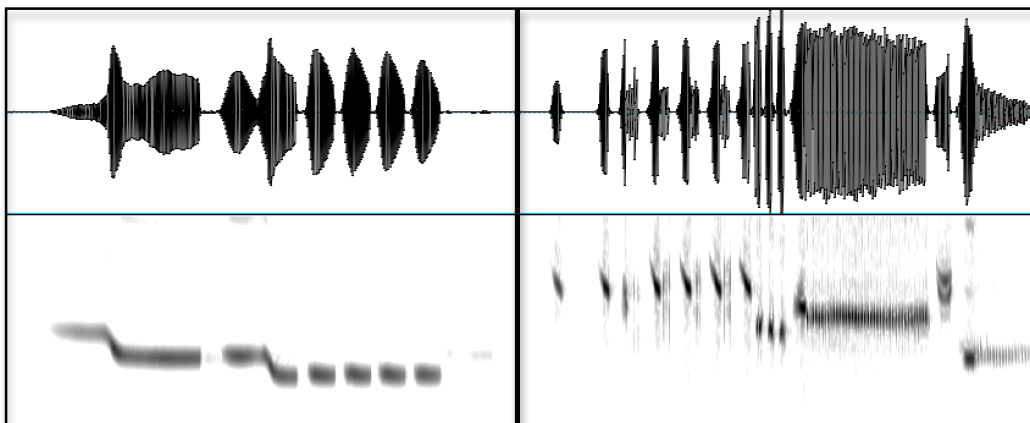


Figure 1. Waveforms and spectrograms (0-12 kHz) of song samples of Golden-Crowned Sparrow (*Zonotrichia atricapilla*, left, tallgrass habitat) and Savannah Sparrow (*Passerculus sandwichensis*, right, tundra habitat). Recordings copyright 1994-2013 David L. Martin, <http://naturebits.org>.

But not only bird song has been studied. For example, comparing calls of a range of cat species Peters et al (2009) found what they regard as support for the AAH, noting that “*spectral features of intense mew calls in the Felis taxa studied have evolved to reduce attenuation when propagating through their respective habitat types.*” They observed that “*mean dominant frequencies of intense mew calls of the Felis (sub)species living in open habitat types are significantly lower than those of the taxa living in dense types*”. The direction of this correlation may appear at odds with the results in the avian literature, but could be related to the fact that open habitat in this study means (semi-)desert rather than prairie.

Why might some such differences be attributable to the effects of the habitat itself? Acoustic signals naturally degrade in intensity as they radiate from their source. However, in addition to the attenuation due to increasing distance from the source (-6 dB for each doubling of the distance from a ‘spherical’ source), there are numerous other factors that affect the spectral and temporal profile of radiated acoustic signals. For our concerns, what is most important are the differential effects that these have. Atmospheric absorption is frequency-dependent on air temperature and humidity (Harris 1966, Piercy et al 1977, Bass et al 1984, Sutherland & Daigle 1998). Broadly, absorption at lower frequencies is greater with lower humidity and with higher temperature, but absorption attenuates all higher frequencies more than lower ones. Ground absorption is primarily a function of the hardness of the surface, but softer surfaces have a peak attenuation at a lower frequency than harder ones (Embleton 1996, Attenborough et al 2011). The presence of vegetation above ground also broadly speaking increases attenuation of higher frequencies due to absorption and scattering (Aylor 1972, Marten & Marler 1977, Marten et al 1977, Wiley & Richards 1978, Martens & Michelsen 1981, Martens 1982, Albert 2004).

In addition to their differential frequency effects, environmental conditions also affect the temporal patterns of acoustic signals. Reflection and diffraction of sound waves from surfaces and objects in their path can result in the effective prolongation of a (part of a) signal as the direct and diverted signals arrive at the receiver. This is particularly destructive to sounds with rapid amplitude modulation, such a rapid trills in bird songs (Richards & Wiley 1980, Naguib 2003). Local eddies in the air due to wind or temperature gradients have similar consequences (Wilson et al 1999, Salomons 2001 Appendix I). Dabelstein et al (1993) discuss the sum of these effects in terms of a ‘blur ratio’ (see also Slabbekoorn 2004b).

These effects on frequency and amplitude can be viewed as a complex filter which is applied to the original sound produced, and which modifies what is available to a receiver of the signal. However, in addition to filtering, masking can also be relevant to environmental sound transmission (Brumm & Slabbekoorn 2005, Slabbekoorn 2004a). Rainfall, wind and flowing water can generate broad-band masking sounds, and other biological signals may compete for bandwidth. More recently, anthropogenic noise has become pervasive in many parts of the world, and this also contributes to masking effects.

Although not all studies looking for evidence of adaptation of biological acoustic signals to environmental conditions have found confirmation (Daniel & Blumstein 1988, Ey & Fisher 2009), the general consensus in the literature seems clearly to accept that the selective transmission of signal characteristics in different contexts plays a role in shaping some aspects of those signals (e.g. Hauser 1996, Bradbury & Vehrencamp 1988, Römer 2001, Winkler 2001, Ryan & Kime 2002).

## 2. The Acoustic Adaptation Hypothesis and human language.

Most discussions of the AAH are directed at accounting for (part of the) variation in acoustic signals across different species. But human communication varies considerably within our species — we speak different languages — and it is (part of) this variation that the present study aims to understand. We may therefore ask if within-species differences that correlate with environmental factors have previously been found. Without doing exhaustive research it is relatively simple to find examples. Hunter & Krebs (1979) examined songs of great tit (*parus major*) populations in widely dispersed sites from Morocco and Iran to Spain, Norway and the U. K. and found that birds inhabiting denser forest environments had songs with a lower maximum frequency, narrower frequency range and fewer notes per phrase than birds inhabiting more open woodland or hedgerows. Nicholls & Goldizen (2006) studied satin bowerbird (*Ptilonorhynchus violaceus*, Figure 2) populations along the east coast of Queensland, Australia, and found significant effects of variation in local habitat on song structure: “*Lower frequencies and less frequency modulation were utilized in denser habitats such as rainforest, and higher frequencies and more frequency modulation were used in the more open eucalypt-dominated habitats.*” Within-species effects have also been reported, inter alia, by Wasserman (1979), Anderson & Connor (1985), and Tubaro & Segura (1994). In addition, several studies have indicated that masking effects also impact bird song behavior. For example, both great tits (Slabbekoorn & Peet 2003) and song sparrows (*melospiza melodia*) (Wood & Yezerinac 2006) have been shown to shift to higher frequency ranges in the presence of mostly low-frequency urban background noise.



Figure 2. Satin bowerbird, *Ptilonorhynchus violaceus*. Photo credit Tim Laman

The idea that the AAH may have relevance to human linguistic differences seems to have first been proposed by social anthropologist Robert Munroe and collaborators (Munroe et al 1996). The original proposal was that people living in warm climates spend more time outdoors than those in cold climates. This means they are often communicating over larger distances under poorer transmission conditions, that is, outdoors rather than indoors. Hence, there is a need to adapt to optimize longer-distance transmission. Munroe et al interpret this (originally) as predicting that warm climate languages will show a preference for simple CV syllables. A series of papers debated this issue, with other factors besides climate, such as tree cover, sexual promiscuity and ‘baby-holding’ featuring in the discussion and an overall measure of sonority rather than a count of the percentage of CV syllables being presented as the preferred correlate (Ember & Ember 1999, Munroe & Silander 1999, Ember & Ember 2000, Munroe et al 2000, Fought et al 2004, Munroe et al 2009, Ember & Ember 2010, Munroe & Fought 2010). All these studies were based on analysis of a short wordlist consisting of from 38 to 200 words from a sample of no more than 60 languages, selected to represent the major cultural areas of the world as indexed in the Human Relations Area Files (based at Yale University, now online at <http://hraf.yale.edu>). It seems worth examining the possible application of the AAH to human languages on a wider scale.

Our proposal bears in mind that, overall, the filtering effects of the environment are more likely to degrade higher frequency sounds and are more likely to degrade rapidly changing sounds. Since consonants, especially obstruents, generally depend on higher frequency acoustic characteristics for their identification and often involve more rapid and salient amplitude changes than do vowels, we predict that human languages may display some adaptation with regard to how much they rely on consonants versus vowels in response to differing environments.

### **3. The data analyzed**

The present study takes basic phonological data from the substantial sample of languages in the LAPSyD database (Maddieson et al 2013) and correlates this with environmental data from global surveys of climate and ecology. LAPSyD contains data on the inventories of consonants and vowels for each language included, as well as information on syllable structure and the role, if any, of tone or stress. For this study the following linguistic variables were examined:

- *Number of Basic Vowel Qualities*
- *Total number of distinct Vowels*
- *Total number of distinct Consonants*
- *Complexity of permitted consonant strings in syllable Onset and Coda*
- *An Index of “Consonant-heaviness” combining the last two factors*

The indexes reflecting the complexity of the maximal permitted syllable onsets and codas are calculated as shown in Table 1. Both range over the values 0-3 but these values are assigned differently for the onset compared to the coda. For the coda, the index simply reflects the number of consonants that are permitted in the maximal syllable. For the onset, since the universal syllable type is CV, the value 0 is assigned to a language that allows only one consonant in onset position. Furthermore, two-consonant onsets are

separated into the more common Obstruent + Sonorant type (value 1) and the rarer Obstruent + Obstruent type (value 2). English words illustrating the syllable types in question are shown in the table, but of course English allows both simple and complex syllables and has a summed value for maximal onset and coda complexity of 6. Hawaiian, which permits no more than one consonant in onset and none in coda has a summed index of 0. Chamorro, like Hawaiian an Austronesian language, allows onsets with a sonorant in second position and a single coda consonant, so has an index of 2.

Table 1. Onset and Coda values — score for maximum allowed in language

| <i>Onset</i> |                       |         | <i>Coda</i> |                     |            |
|--------------|-----------------------|---------|-------------|---------------------|------------|
| Value        | Description           | Example | Value       | Description         | Example    |
| 0            | Single onset C        | 'see'   | 0           | No coda C           | 'see'      |
| 1            | Obstruent + Sonorant  | 'sleep' | 1           | Single coda C       | 'seat'     |
| 2            | Obstruent + Obstruent | 'skip'  | 2           | Two coda consonants | 'salt'     |
| 3            | 3 or more onset C's   | 'strip' | 3           | 3 or more coda C's  | 'twelfths' |

The index of Consonant-heaviness is the sum of two values, namely, the sum of the Onset and Coda scores plus a scaled value for the total number of distinct consonants in the language. The Onset + Coda score ranges from 0 to 6, whereas the consonant inventory size ranges from 6 to 156 with a median of 21 and a mean of about 22.7. In order to make the contribution of these properties approximately equal, the number of consonants is divided by 5.

LAPSyD currently contains data on 706 languages. Since it is more likely that environmental effects will be apparent in the case of languages spoken in a smaller area over a longer period of time, the widespread 'colonial' languages such as English, Spanish, Russian, Mandarin Chinese, and Portuguese were eliminated from consideration, together with other languages in the set with a speaker population of over 5 million according to estimates published in Lewis et al (2015). This excludes Hindi, Egyptian Arabic, Vietnamese, Bengali, Italian, German, Japanese, Javanese, Korean, Telegu and Tamil.

For each language retained, an estimate of the area in which it is spoken was obtained from the *World Language Mapping System (WLMS)*, a collaboration between Global Mapping International (2016) and SIL International which generates the language maps used in *The Ethnologue* (Lewis et al 2015). This procedure requires forcing an alignment between languages as identified in LAPSyD and the classification given in *The Ethnologue*. Inevitably, the specific description included in LAPSyD will not always correspond to the properties of a language as identified in *The Ethnologue*.

Ecological and climatic data was obtained from the International Steering Committee for Global Mapping (<http://www.iscgm.org>) and other organizations, such as the UN FAO Sustainable Development Department, the Geospatial Information Authority of Japan, and the Climate Research Unit of the University of East Anglia. The following primary variables were examined:



- mean annual temperature (exemplified in Figure 3)
- mean annual precipitation
- percent tree cover (maximal seasonal extent)
- elevation above sea level
- rugosity (i.e. roughness of land surface)

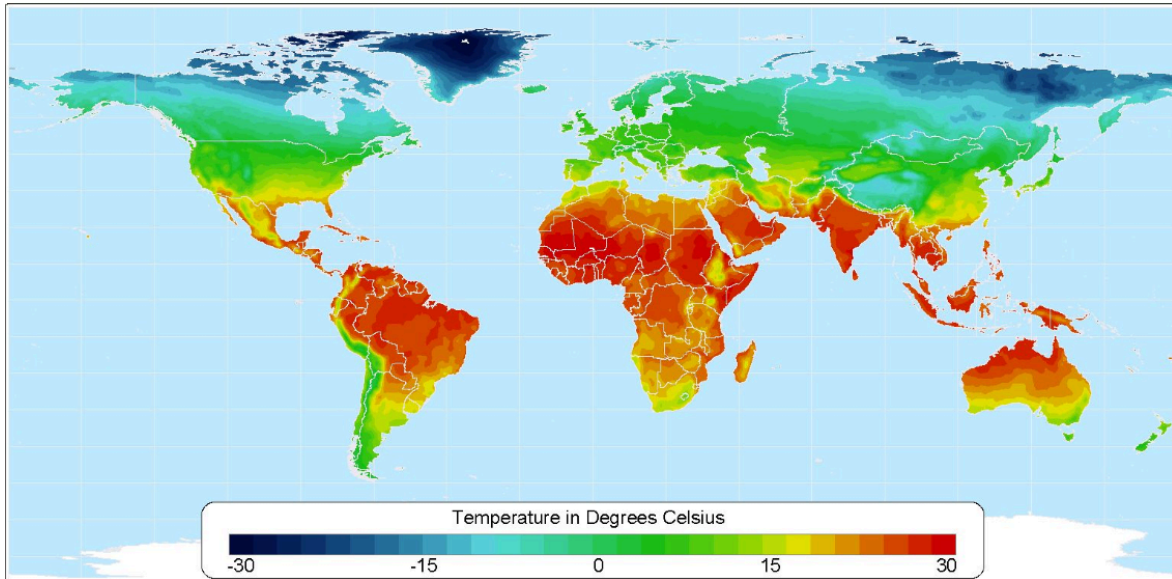


Figure 3. Global mean annual temperature map; data from Climate Research Unit, University of East Anglia.

These data are typically provided as mean values in quadrants with a dimension of 15 minutes of latitude and longitude. The values of these variables in the quadrants that correspond most closely to the area for each given language were averaged and used in the next step of the analysis. A few languages were unable to be matched satisfactorily with an area in WLMS or with viable ecological data or had some missing data in LAPSyD and so were eliminated from consideration. This left 663 languages in the set. These are widely distributed across the six global geographical/genetic language groups as defined in LAPSyD (Table 2).

Table 2. Distribution of language sample.

| Area                        | number of languages |
|-----------------------------|---------------------|
| Europe, West and South Asia | 99                  |
| East and South-East Asia    | 119                 |
| Africa                      | 152                 |
| North America               | 78                  |
| South America               | 119                 |
| Oceania                     | 96                  |
| Total                       | 663                 |

Europe, West and South Asia includes all of the former USSR. North and South America

are divided at the Isthmus of Tehuantepec. East and South-East Asia is divided from Oceania by Wallace’s Line. All members of a language family with a majority located in a given area are included in that area even if geographically distant.

#### 4. Results

As a preliminary step the possible existence of a simple linear correlation between each of the five phonological traits listed earlier and each of the five environmental factors was checked. Analysis was performed with the JMP Pro package (SAS Institute 2013). Results are shown in Table 3. Highly significant correlations ( $p < .0001$ ) are indicated by \*\*\*, less strong relationships by \*\* ( $p < .001$ ) or \* ( $p \approx .05$ ) and non-significant ones by *n.s.* Mean annual temperature and precipitation, and percent maximum tree cover are all strongly related to both the number of consonants and the degree of consonant clustering in syllable onsets and codas, as well as (obviously) with the index combining both of these traits. Higher values of these environmental factors correlate with lower numbers of consonants and less clustering. Higher elevation correlates with more consonants. Rugosity also shows some correlation with consonantism, greater rugosity going together with more use of consonants. In general, the size of vowel inventories does not show any interesting relationship to the environmental factors.

Table 3. Linear correlations between phonological and environmental factors.

|             | Temp.       | Precip.     | Tree cover  | Elevation   | Rugosity    |
|-------------|-------------|-------------|-------------|-------------|-------------|
| Basic V     | <i>n.s.</i> | <i>n.s.</i> | <i>n.s.</i> | <i>n.s.</i> | <i>n.s.</i> |
| Total V     | <i>n.s.</i> | <i>n.s.</i> | *           | <i>n.s.</i> | <i>n.s.</i> |
| Total C     | ***         | ***         | ***         | ***         | *           |
| Onset+Coda  | ***         | ***         | ***         | <i>n.s.</i> | **          |
| C-Heaviness | ***         | ***         | ***         | ***         | **          |

Naturally enough, several of the environmental factors are correlated with each other: higher precipitation, for example, is likely to encourage the growth of more trees, and — other things being equal — higher elevation predicts lower mean temperature. A principal components analysis of these variables was conducted to examine their co-variation. The loadings of the ecological variables on the first two principal components, which together account for more than three-quarters of their variance, are shown graphically in Figure 3. Tree cover and annual precipitation are very close in the two-dimensional space. Otherwise, the first component broadly opposes precipitation, temperature and tree cover to elevation and rugosity; the second component primarily opposes temperature to the other variables, with rugosity the most highly (positively) weighted factor.

The first principal component is highly correlated with all the linguistic variables involving consonant inventory size and the structure of onsets and codas, but not with vowel inventory. The second principal component is *not* significantly correlated with any of the linguistic variables. Recall that the consonant-heaviness index combines the information on consonant-inventory and syllable structure. There is a highly significant correlation ( $p < .0001$ ) between this index and Principal Component 1, which is graphed on the scatterplot in Figure 5. This relationship accounts for almost 20% of the variance in the use of consonants in the languages in our sample.



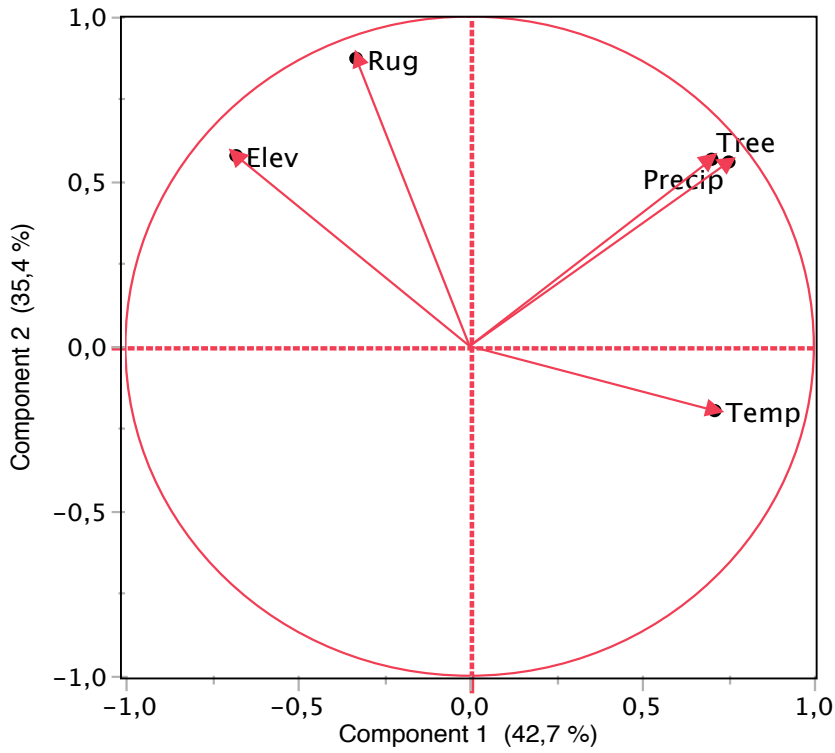


Figure 4. Loading plot for principal components of ecological variables discussed.

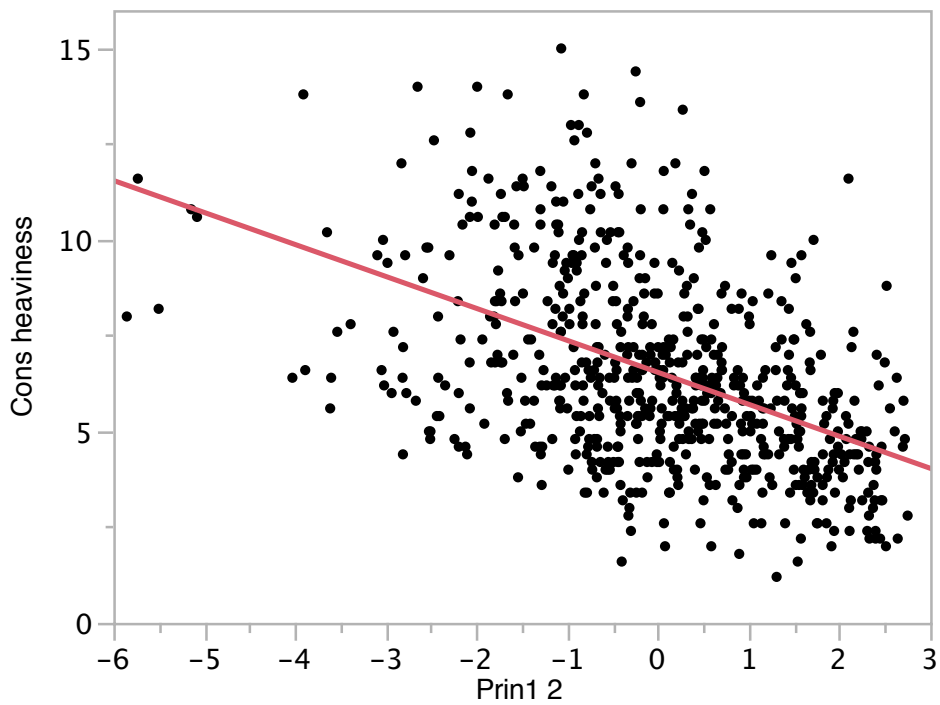


Figure 5. Linear fit (red) between principal component 1 and consonant-heaviness index,  $R^2 = .196$ ,  $p < .0001$ . Four languages with values above 16 due to very large consonant inventories are not shown on the plot but are included in the analysis.

## 5. Discussion and Conclusions

Our analysis shows that considered both singly and in a joint analysis, characteristics of the the syllable structure and consonant inventory correlate to a significant degree with properties of the environment in which languages are spoken. Broadly speaking, languages spoken in areas with higher annual precipitation and greater tree cover demonstrate a lower reliance on the use of consonants in their sound patterns, in terms both of the number of consonant contrasts distinguished and in the role consonants play in syllable structures. Higher temperature contributes in the same direction, while higher elevation and greater rugosity contribute somewhat to more rather than less use of consonants. This finding seems quite parallel to research results examining environmental correlations with bird song characteristics. These generally have found that birds inhabiting areas with denser vegetation tend to use lower frequencies and simpler temporal structures (i.e. less rapid amplitude fluctuations) than those in more open areas. Lower reliance on consonant distinctions and use of simpler syllable structures seem quite comparable traits in human languages. Figure 6 shows waveforms and spectrograms of the English words “strict” and “away”. The first is ‘consonant-heavy’ and involves relatively rapid major changes in amplitude and consonants that are primarily acoustically distinct from each other in the higher frequency regions, the second consists only of vocalic elements with little change in amplitude or in frequency distribution. If these two words are filtered using a low-pass filter with a cut-off at 1000 Hz “strict” is not intelligible but “away” still is; even though the latter signal contains energy at higher frequencies, this is not critical to identifying the word.

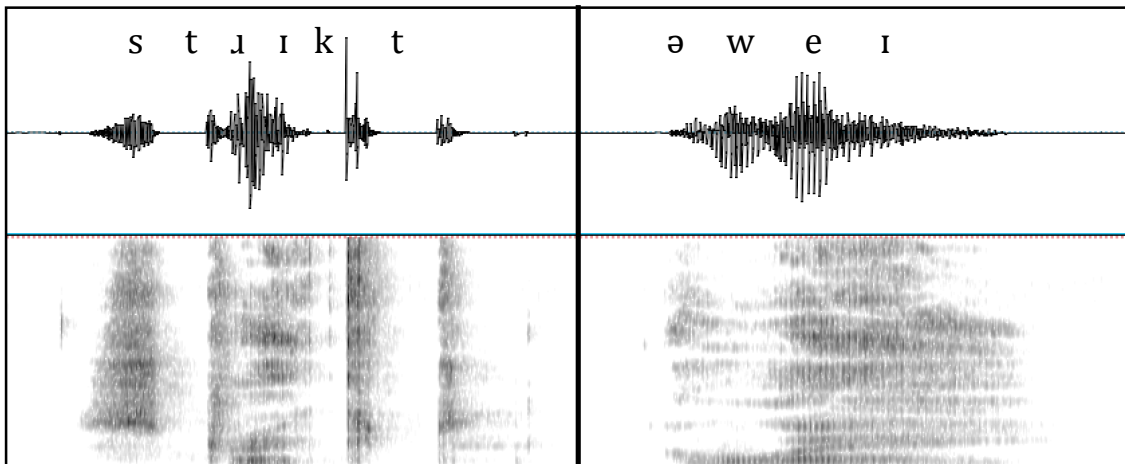


Figure 6. Waveform and spectrograms (0-20 kHz range) of English words “strict” and “away”

There are some important differences between our research and the bioacoustic tradition of work on acoustic adaptation which inspires it. Our study uses continuous variables to represent the environmental factors examined whereas the bioacoustic tradition is based on categorical distinctions between habitat types. It would be interesting to see if large-scale studies of, say, bird-song using continuous variables would sharpen the ability to detect this type of adaptation. On the other hand, factors that must be taken into consideration for some non-human species, such as the height above ground of the

generator and recipient of an acoustic signal, are of little concern for human communication since we became essentially a ground-dwelling species a long time ago. Signals generated from an elevated perch or in the forest canopy naturally have much reduced effects from interaction with the ground surface.

Finally, we recognize the possibility that the correlations we are finding could be artifacts created by distributions of linguistic traits in fact attributable to other causes. We are evaluating whether patterns of language contact, language family affiliation, demographic factors such as the size of speaker populations or human migration history, among others, could provide explanations for what appears at first sight an environmental effect (see Coupé 2015, Coupé & Maddieson 2016). So far, this does not seem to be the case.

We are also planning to go beyond this work, which is based solely on static characteristics of the languages, by examining the relative frequency of sound types in running speech across a sizable cross-language sample. One language that permits complex syllables or has a large inventory of consonants may not exploit these resources at all frequently, while another relies on them constantly. If the AAH applies to human languages, stronger correlations between ecological and climatic variables and relative frequency of sound types are to be expected than are found with static measures. Indeed, the original proposal by Munroe et al (1996) linking AAH and human language was predicated on the relative (lexical) frequency of simple structures. Examination of running speech would be a truer test of the strength of this linkage.

## References

- Albert, D. G. 2004. *Past Research on Sound Propagation Through Forests*. US Army Corps of Engineers, Cold Regions Research and Engineering Laboratory, Hanover NH.
- Anderson, M. E. & R. N. Connor 1985. Northern Cardinal song in three forest habitats in Eastern Texas. *Wilson Bulletin* 97: 436-449.
- Attenborough, K., I. Bashir & S. Taherzadeh. 2011. Outdoor ground impedance models. *Journal of the Acoustical Society of America* 129: 2806-2819.
- Aylor, D. 1972. Noise reduction by vegetation and ground. *Journal of the Acoustical Society of America* 51: 197-205.
- Badyaev, A. V. & E. S. Leaf. 1997. Habitat associations of song characteristics in *Phylloscopus* and *Hippolais* warblers. *The Auk* 114: 40-46.
- Bass, H. E., L. C. Sutherland & J. Piercy. 1984. Absorption of sound by the atmosphere. *Physical Acoustics: Principles and Methods, Volume 17*. Academic Press, Orlando: 145-232.
- Boncoraglio, G. & N. 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.
- Bradbury, J. W. & S. L. Vehrencamp 1988. *Principles of Animal Communication*. Sinauer, Sunderland.
- Brumm, H. & H. Slabbekoorn. 2005. Acoustic communication in noise. *Advances in the Study of Behavior* 35: 151-209.
- Chappuis, C. 1971. Un exemple de l'influence du milieu sur les émissions vocales des oiseaux: l'évolution des chants en forêt équatoriale. *Terre et Vie* 25, 183-202.
- Coupé, C. 2015. Testing the Acoustic Adaptation Hypothesis with GIS and spatial regression models. Meeting on 'Causality in the Language Sciences', Max Planck

- Institute for Evolutionary Anthropology, Leipzig, April 13-15 2015.
- Coupé, C. & I. Maddieson. 2016. Quelle adaptation acoustique pour les langues du monde? *Actes du 13ème Congrès Français d'Acoustique*, Le Mans, April 11-15 2016.
- Dabelsteen, T., O. N. Larsen & S. B. Pedersen. 1993. Habitat-induced degradation of sound signals: Quantifying the effects of communication sounds and bird location on blur ratio, excess attenuation, and signal-to-noise ratio in blackbird song. *J. Acoust. Soc. Am.* 93: 2206-2220.
- Daniel J. C. & D. T. Blumstein 1988. A test of the acoustic adaptation hypothesis in four species of marmots. *Animal Behaviour* 56: 1517–1528.
- Ember, C. R., & M. Ember. 2010. Climate, econiche, and sexuality: Influences on sonority in language. *American Anthropologist* 109: 180–185.
- Ember, C. R., & M. Ember. 2000. High CV score: Regular rhythm or sonority? *American Anthropologist*, N.S. 102: 848–851.
- Ember, M., & C. R. Ember. 1999. Cross-language predictors of consonant-vowel syllables. *American Anthropologist* 101: 730–742.
- Embleton, T. F. W. 1996. Tutorial on sound propagation outdoors. *J. Acoust. Soc. Am.* 100: 31-48.
- Ey, E. & J. Fischer. 2009. The “Acoustic Adaptation Hypothesis” — a review of the evidence from birds, anurans and mammals. *Bioacoustics* 19: issue 1-2.
- Fought, J. G., R. L. Munroe, C. R. Fought, & E. M. Good. 2004. Sonority and climate in a world sample of languages. *Cross-Cultural Research* 38: 27–51.
- Global Mapping International. 2016. World Language Mapping System, Version 17. [http://www.worldgeodatasets.com/files/9313/0400/5767/WGDS\\_WLMS.pdf](http://www.worldgeodatasets.com/files/9313/0400/5767/WGDS_WLMS.pdf)
- Harris, C. M. 1996. Absorption of sound in air versus humidity and temperature. *J. Acoust. Soc. Am.* 40:148-159.
- Hauser, Marc. 1996. *The Evolution of Communication*. MIT Press, Cambridge, MA.
- Huisman, W. H. T., M. J. M. Martens & W. van Asseldonk. 1987. Measured and modeled temperature effects on outdoor sound transmission. *Proc Inst Acoustics* 9: 63-70.
- Hunter, M. L. & J. R. Krebs. 1979. Geographical variation in the song of the Great Tit (*Parus major*) in relation to ecological factors. *Journal of Animal Ecology* 48: 759-785.
- Krause, B. 1987. Bioacoustics, habitat ambience in ecological balance. *Whole Earth Review* 57: 14–18.
- Lewis, M. P., G. F. Simons & C. D. Fennig (eds.). 2015. *Ethnologue: Languages of the World, Eighteenth edition*. Dallas, Texas: SIL International. Online version: <http://www.ethnologue.com>
- Maddieson, I., S. Flavier, E. Marsico, C. Coupé & F. Pellegrino. 2013. LAPSyD: Lyon-Albuquerque Phonological Systems Database. Proceedings of Interspeech 2013, Lyon.
- Marler, P. & M. Tamura. 1962. Song “dialects” in three populations of white-crowned sparrows. *The Condor* 64: 368-376.
- Marten, K., & P. Marler. 1977. Sound transmission and its significance for animal vocalization. I. Temperate habitats, *Behav. Ecol. Sociobiol.* 2: 271-290.
- Marten, K., D. Quine, & P. Marler. 1977. Sound transmission and its significance for animal vocalization. II. Tropical forest habitats. *Behav. Ecol. Sociobiol.* 2: 291-302.
- Martens, M. J. M. & A. Michelsen. 1981. Absorption of acoustic energy by plant leaves. *Journal of the Acoustical Society of America* 69: 303-306.
- Martens, M. J. M. 1992. Sound propagation in the natural environment, animal acoustic communication and possible impact for pollination. In M. Cresti & A. Tiezzi (eds.) *Sexual Plant Reproduction*. Springer, Berlin.

- Morton, E. S. 1975. Ecological sources of selection on avian sounds. *The American Naturalist* 109: 17-34.
- Munroe, R. L., & M. Silander. 1999. Climate and the consonant-vowel (CV) syllable: Replication within language families. *Cross-Cultural Research* 33: 43-62.
- Munroe, R. L., & J. Fought. 2010. Response to Ember and Ember's "Climate, Econiche, and Sexuality: Influences on Sonority in Language" *American Anthropologist* 109: 784-785
- Munroe, R. L., C. Fought & J. Fought. 2000. Rhythmicity or Sonority: Response to Ember and Ember's "Cross-Language Predictors of Consonant-Vowel Syllables" *American Anthropologist, N.S.* 102: 844-848.
- Munroe, R. L., J. G. Fought & R. K. S. Macaulay. 2009. Warm climates and sonority classes: Not simply more vowels and fewer consonants. *Cross-Cultural Research* 43: 123-133.
- Munroe, R. L., R. H. Munroe & S. Winters. 1996. Cross-cultural correlates of the consonant-vowel syllable. *Cross-Cultural Research* 30:60-83.
- Naguib, M. 2003. Reverberation of rapid and slow trills: Implications for signal adaptations to long-range communication. *Journal of the Acoustical Society of America* 113: 1749-1756.
- Nemeth, E., H. Winkler & T. Dabelsteen. 2001. Differential degradation of antbird songs in a Neotropical rainforest: Adaptation to perch height? *J. Acoust. Soc. Am.* 110 : 3263-3274.
- Nicholls, J. A. & A. W. Goldizen. 2006. Habitat type and density influence vocal signal design in satin bowerbirds. *Journal of Animal Ecology* 75: 549-558
- Peters, G. & M. K. Peters. 2010. Long-distance call evolution in the Felidae: effects of body weight, habitat, and phylogeny. *Biological Journal of the Linnean Society* 101: 487-500.
- Peters, G., L. Baum, M. K. Peters, & B. Tonkin-Leyhausen. 2009. Spectral characteristics of intense mew calls in cat species of the genus *Felis* (Mammalia: Carnivora: Felidae). *Journal of Ethology* 27: 221-237.
- Piercy, J. E., T. F. W. Embleton & L. G. Suthorland. 1977. Review of noise propagation in the atmosphere. *J. Acoust. Soc. Am.* 61: 1403-1418.
- Richards, D. G. & R. H. Wiley. 1980. Reverberations and amplitude fluctuations in the propagation of sound in a forest: Implications for animal communication. *The American Naturalist* 115: 381-399.
- Römer, Heiner. 2001. Ecological constraints for sound communication: from grasshoppers to elephants. In F. G. Barth & A. Schmid (eds). *Ecology of Sensing*. Springer, Berlin: 59-78.
- Ryan, M. J. & N. M. Kime. 2002. Selection on long-distance acoustic signals. In A. M. Simons, A. N. Popper & R. R. Fay (eds) *Acoustic Communication*. Springer, New York: 225-274.
- Salomons, E. M. 2001. *Computational Atmospheric Acoustics*. Kluwer, Dordrecht.
- SAS Institute. 2013. JPM Pro, version 11. SAS Institute, Cary NC.
- Seddon, N. 2005. Ecological adaptation and species recognition drives vocal evolution in neotropical suboscine birds. *Evolution* 59: 200-215.
- Slabbekoorn, H. 2004a. Habitat-dependent ambient noise: Consistent spectral profiles in two African forest types. *Journal of the Acoustical Society of America* 116: 3727-3733.
- Slabbekoorn, H. 2004b. Singing in the wild: the ecology of birdsong. In P. Marker & H. W. Slabbekoorn (eds). *Nature's Music: The Science of Birdsong*. Academic Press,

- Amsterdam: 178-205.
- Slabbekoorn, H., & M. Peet. 2003. Birds sing at higher pitch in urban noise. *Nature* 424: 267.
- Slabbekoorn, H., & T. B. Smith. 2002a. Bird song, ecology and speciation. *Philosophical Transactions of the Royal Society of London, Series B* 357: 493–503.
- Slabbekoorn, H., & T. B. Smith. 2002b. Habitat-dependent song divergence in the Little Greenbul: An analysis of environmental selection pressures on acoustic signals. *Evolution* 56: 1849–1858.
- Sutherland, L. C. & G. A. Daigle. 1998. Atmospheric sound propagation. In M. J. Crocker (ed.) *Handbook of Acoustics*. John Wiley & Sons, New York: 305-329.
- Tubaro, P. L. & E. T. Segura. 1994. Dialect differences in the song of *zonotrichia capensis* in the southern pampas: A test of the Acoustic Adaptation Hypothesis. *The Condor* 96: 1084-1088.
- Waser, P. M. & C. H. Brown. 1986. Habitat acoustics and primate communication. *American Journal of Primatology* 10:135-154.
- Wasserman, F. E. 1979. The relationship between habitat and song in the White-throated Sparrow. *The Condor* 81: 424-426.
- Wiley, R. H., & D. G. Richards. 1978. Physical constraints on acoustic communication in the atmosphere: implications for the evolution of animal vocalizations. *Behavioral Ecology and Sociobiology* 3: 69-94.
- Wilson, D. K., J. G. Brousseau & K. E. Gilbert. 1999. Acoustic scattering and the spectrum of atmospheric turbulence. *Journal of the Acoustical Society of America* 105: 30-34.
- Winkler, H. 2001. The ecology of avian acoustic signals. In F. G. Barth & A. Schmid (eds). *Ecology of Sensing*. Springer, Berlin: 79-104.
- Wood W. E., & S. M. Yezerinac. 2006. Song sparrow (*Melospiza melodia*) song varies with urban noise. *The Auk* 123: 650–659.