Geographic variation in songs of the Bewick's wren: a search for correlations with avifaunal complexity

Donald E. Kroodsma

Department of Zoology, University of Massachusetts, Amherst, Massachusetts 01003-0027, USA

Summary. Song characteristics of the Bewick's wren (*Thryomanes bewickii*) are compared from nine localities in the western United States. Character shifts, i.e., a difference in means, are evident for all song characters: Arizona and Colorado songs are especially short and long, respectively (Figs. 1, 2); songs of insular (Santa Cruz Is.) and nearby mainland populations in California are very dissimilar (Table 1); excluding the insular population, the frequency range of song phrases is positively correlated with latitude (Fig. 3). Variance shifts, i.e., a difference in repertoire size or Coefficients of Variation (CV's) of measured song characters, are also present; most notably, Arizona males have exceptionally stereotyped songs, with small song phrase repertoires (Table 2) and low CV's. Population densities and/or habitat structure undoubtedly influence signal design, but correlations reported here suggest that the avifaunal complexity and the corresponding vocal milieu should also be examined rigorously as possibly important influences.

Introduction

The songs of most, if not all, bird species vary geographically. That variation may be very slight, as in species which apparently do not learn to sing (e.g., *Myiarchus* or *Empidonax* flycatchers: Lanyon 1960, 1978; Kroodsma, 1984), or it may be very pronounced, as in typical oscines which often learn local song variants (Mundinger 1982).

The significance of this macro-geographic variation is poorly understood, but several hypotheses have been advanced. The spatial variation could reflect nothing more than an accumulation of chance events, with random changes in song patterns taking place through time and over space (e.g. Wiens 1982). Founder effects, for example, undoubtedly influence geographic variation (Thielcke 1969; Mirsky 1976). If song is to function in either attracting mates or proclaiming territories, though, such random events should play a secondary role to at least two other forces, namely, (1) habitat structure and its influence on sound transmission (Morton 1975) and (2) the overall sound environment of the community and selection for specific distinctiveness (Marler 1960). Evidence for the influence of habitat structure on sound transmission has recently been provided by Morton (1975), Marten and Marler (1977), Bowman (1979, 1983), Gish and Morton (1981), and Wiley and Richards (1982); thus, the structure of vocal signals may vary adaptively among habitats. However, convincing evidence that the complexity of the avifauna and the attendant sound environment affect signal characters is still lacking (Thielcke 1969; Bremond 1977; Brown 1977; Miller 1982).

With this in mind I sought to determine whether I could find patterns of geographic variation which were consistent with the hypothesis that avifaunal complexity might be inversely related to vocal complexity of a given species (Marler 1960). If this hypothesis is true, one would predict relatively stereotyped songs in rich mainland avifaunas and more variable, less species-distinct songs in depauperate avifaunas of islands or more northern latitudes. I chose the Bewick's wren (*Thryomanes bewickii*) for study because this species occurs throughout the western continental United States and on the Channel Islands off the coast of California. For several song parameters I examined the means for "character shifts" and both reper-

144
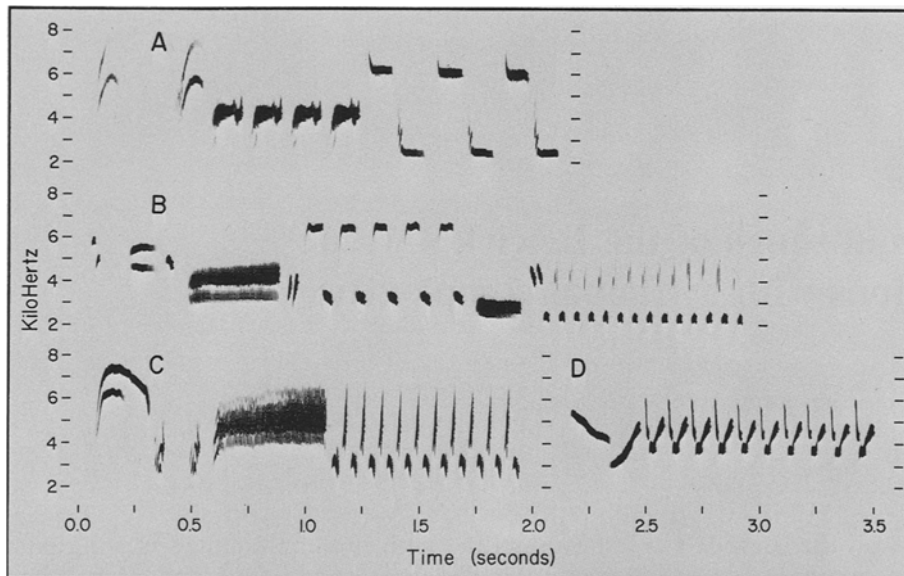
Fig. 1. Representative sonagrams from four western USA populations of the Bewick's wren:
A) Santa Cruz Island, California,
B) Grand Junction, Colorado,
C) Santa Barbara, California, and
D) Madera Canyon, Arizona

toire sizes and coefficients of variation for "variance shifts" (see Miller 1982) from eight mainland populations and one island population.

Materials and methods

I sampled songs of the Bewick's wren at Point Reyes Bird Observatory, Calif.; Santa Barbara, Calif.; Madera Canyon, Ariz.; Grand Junction, Colo.; William Finley National Wildlife Refuge, Ore.; Basket Slough National Wildlife Refuge, Ore; Sauvie Island, Ore.; Klamath Falls, Ore.; and on Santa Cruz Is., Calif. Sample sizes are indicated in Table 2. The island avifauna contained relatively few species, at least in comparison to the immediate mainland avifauna at Santa Barbara (Yeaton 1974). Of eight mainland locations, the Arizona site undoubtedly had the richest avifauna (Lane 1965), though appropriate census data are neither available nor readily obtainable for all locations (see Discussion). Thus, while some predictions could be made for songs from Santa Cruz Island and Madera Canyon, none were possible for the remaining seven populations.

Songs were recorded on Uher 4000 Report-L's with 60 cm parabolic reflectors and Uher M514 microphones. Because male Bewick's wrens sing with "eventual variety" (i.e., AAA ... BBB ..., repeating one song type many times before proceeding to the next), I recorded individuals during an entire morning, or until recognizable song types began to appear for a third time in the sample. This is generally an effective means of obtaining the full repertoire of these wrens (Kroodsma 1972).Songs were graphed on a Kay Elemetrics Co. Sona-Graph 6061A, using the wide band filter.

I made fourteen measurements or calculations on a representative sonagram for each song type from each individual (Table 7 in Kroodsma (1972); available upon request from the author): 1) song duration (s); 2) total duration of trill portion of song; 3) total duration of note complex portion of song; 4) frequency range (high minus low frequency) of each phrase; 5) sum of frequency range x duration of trills (i.e., "trill area"); 6) sum of frequency range x duration of note complexes ("note complex area"); 7) sum of frequency range x duration of all phrases of the song ("song area"); 8) number of phrases per

song; 9) number of trills per song; 10) number of phrases per s; 11) number of syllables in trills; 12) number of syllables per s in trills; 13) syllable duration; and 14) interval between syllables (see Mulligan 1966 for definition of terms). In addition, estimates of the number of 15) song types and 16) component phrase types per individual were made for six locations.

There is some redundancy in parameters 1–14. For example, parameters 3 and 6, 8 and 9, and 1 and 7 are highly correlated (Spearman rank correlation coefficient ≥ 0.9); by selectively eliminating one parameter of the correlated pairs, I determined that five parameters (4, 5, 7, 10 and 11) were sufficiently independent so that they were not correlated with each other at $p < 0.05$. Trends and conclusions in this paper remain largely the same, however, whether the entire parameter set (1–14) or the reduced set (4, 5, 7, 10, 11) is used for analysis and discussion. For thoroughness, I therefore use all 14 parameters.

Results

For the most part, only the striking trends in the data or differences among locations are reported here. Because of their value in assessing the role of avifaunal complexity in influencing vocal characters, I examine especially carefully the data from species-rich Madera Canyon and species-poor Santa Cruz Island.

Character shift

As expected, nearly all measured parameters revealed some degree of geographic variation. For example, based on either song duration or the number of component phrases, the songs of Arizona and Colorado males were readily distinguished from songs of Oregon and California males (see Figs. 1 and 2). Arizona songs were characterized by their relatively brief duration ($\bar{x} =$
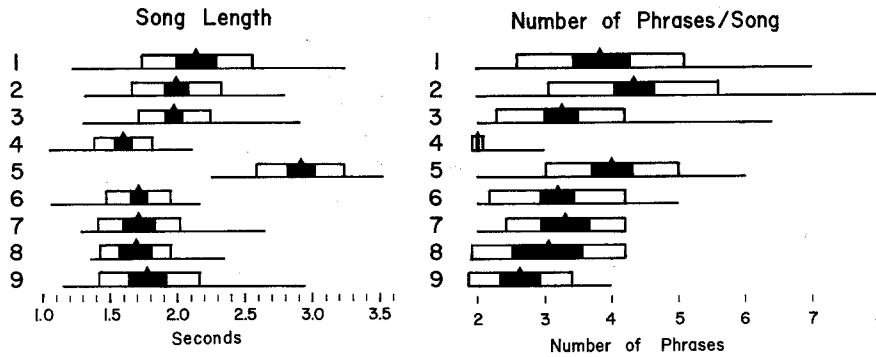
Fig. 2. "Dice-grams" for song duration and number of phrases per song at nine geographic locations. Sample mean is indicated by small triangle at midpoint of black bar, range of variation by horizontal line, two standard errors on each side of mean by blackened bar, and one sample standard deviation by the black plus white bar on each side of the mean. Locations are: (1) Roint Reyes, Calif.; (2) Santa Barbara, Calif.; (3) Santa Cruz Is., Calif.; (4) Madera Canyon, Ariz.; (5) Grand Junction, Colo.; (6) Finley Refuge, Ore.; (7) Basket Slough Refuge, Ore.; (8) Sauvie Island, Ore.; and (9) Klamath Falls, Ore.
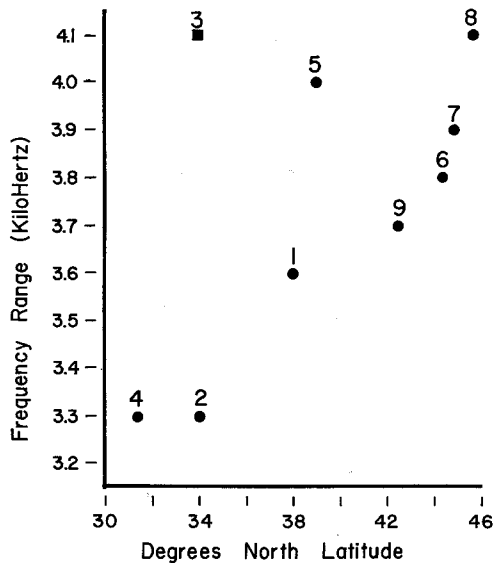

Fig. 3. Frequency range of song phrases in mainland populations (solid circles) at different latitudes (mainland populations, $r=0.85$, $p<0.01$). The frequency range of phrases recorded on Santa Cruz Island (3) is similar to that found among wrens at more northern latitudes. Locations are numbered as in Fig. 2

1.59 s, $n=70$, $s.e.=0.03$) but especially by the small number of phrases per song ($\bar{x}=2.01$, $n=70$, $s.e.=0.01$). Colorado songs were exceptionally long ($\bar{x}=2.92$ s, $n=40$, $s.e.=0.05$). California songs tended to be longer than Oregon songs, and except for Santa Cruz Island songs, consisted of more phrases/song (Fig. 2).

In the frequency range of the phrases, Arizona birds were again at the low extreme, with an average frequency range per phrase of only 3.29 kHz ($n=141$, $s.e.=0.11$). The songs of Santa Barbara

birds were also of a relatively narrow frequency range ($\bar{x}=3.35$ kHz, $n=334$, $s.e.=0.07$) when compared to some of the other, especially more northern populations. Overall, the frequency range of the phrases was highly correlated with latitude ($r=0.85$, $p<0.01$), if the Santa Cruz Island population was excluded from the sample (Fig. 3). The frequency range in phrases of this insular population was similar to that found in wrens at more northern latitudes.

In order to obtain an index of the degree of geographic variation over distance, I compared the song characters (1) between the island and nearby mainland wren populations, T.b. nesophilus and T.b. correctus, respectively, separated by approximately 30 km of the Santa Barbara Channel; (2) between two populations of a subspecies (T.b. eremophilus) separated by roughly 850 km, and (3) among three populations of another subspecies (T.b. calophonus), over 150 km in the Willamette Valley of Oregon (Table 1). No major barriers prevent dispersal within the Willamette Valley, and the difference in songs from the Finley refuge to Sauvie Island is a good base against which the other tests may be compared. The songs of these three Oregon populations were very similar, with only one parameter differing at $p<0.001$. Songs of the two T.b. eremophilus populations (Ariz. and Colo.) differed markedly, with the means of ten of the 14 measured song parameters differing at $p<0.001$. Despite the relatively short distance from Santa Cruz Island to the mainland, nine of the 14 song parameters differed at $p<0.001$. In a comparable distance on the mainland (between the Finley and Basket Slough refuges, Oregon), I found

Table 1. Results from tests of difference between means of measured song parameters at selected geographic localities. One, two, and three asterisks indicate $p < 0.05$, $p < 0.01$, $p < 0.001$, respectively. Analysis of variance was used for parameters 1–14, the Mann-Whitney U test for parameters 15 and 16

Song parameters	Combinations of geographic locations compared		
	Santa Barbara Santa Cruz Is	Madera Canyon Grand Junction	Finley refuge Basket Slough ref. Sauvie Island
1. Song duration	—	***	—
2. Total trill duration of song	***	***	**
3. Total note complex duration of song	***	***	***
4. Frequency range of phrases	***	***	—
5. Total trill area of song		***	*
6. Total note complex area of song	***	***	**
7. Song area	***	***	—
8. Number of phrases per song	***	***	—
9. Number of trills per song	***	***	—
10. Number of phrases per second	***	—	—
11. Number of syllables per sec in trills	*	—	—
12. Number of syllables in trills	—	*	—
13. Syllable duration	***	—	—
14. Interval between syllables	—	***	—
Summary: Number of measured parameters different			
$p < 0.05$	10	11	4
$p < 0.01$	9	10	3
$p < 0.001$	9	10	1
15. Song types in individual repertoires	—	*	no test
16. Phrases in individual repertoires	*	—	—

Table 2. Song and phrase type repertoires for males from six locations in the western United States. Data are medians, with sample sizes and ranges in parentheses

	Point Reyes Calif	Santa Barbara Calif	Santa Cruz Is. Calif	Madera Canyon Ariz	Grand Junction Colo	Finley Refuge Ore
Song types/individual	14.5 (2, 12–17)	20 (4, 16–22)	17.5 (4, 17–20)	17.5 (4, 16–19)	10 (4, 9–11)	16 (31, 13–20)
Phrase types/individual	46 (2, 47–65)	87.5 (4, 66–93)	56 (4, 52–69)	35.5 (4, 32–38)	40.5 (4, 33–47)	50 (7, 43–63)

none of the 14 song parameters different at $p < 0.001$. Thus, the isolation of the insular population by the Santa Barbara Channel has had a strong effect on many of the song characters.

Variance shift

Song and phrase repertoires. One index of song variability is the number of different song or phrase types within the repertoire of an individual (Table 2). The number of song types ranged from a low of nine in Colorado to a high of 22 at Santa Barbara. California birds tended to have larger song type repertoires than Oregon birds. The small

sample from Point Reyes, where one bird sang only 12 song types, is probably atypical. Of the two inland *T.b. eremophilus* populations, Colorado birds had smaller song repertoires (range, 9–11) than Arizona birds (range, 16–19). I found no appreciable difference in song repertoire sizes between Santa Barbara and Santa Cruz Island.

However, equating songs which are not of equal complexity, e.g., those of Arizona with those of Colorado, gives an unrealistic picture of "repertoire" size (see Kroodsma 1982b for a more thorough discussion of this problem). Another measure of repertoire size is the total number of different phrases used by the individual. Although the same

problem can arise here, a phrase is closer to the basic building block of the song and therefore more likely reflects the diversity of sounds which a given bird produces. As with song types, California birds tended to have larger phrase repertoires than Oregon birds. Even though Arizona males had larger song type repertoires than Colorado males, they actually averaged fewer different song phrases per male, because the songs were much simpler. Despite comparable song type repertoires, Santa Barbara birds had phrase repertoires which were 56% larger than those on Santa Cruz Island; this was due largely to the greater number of phrases per song in the mainland populations.

In all populations, neighboring males shared nearly identical song types. There was no measurable increase or decrease in the degree of song sharing among neighbors. Thus, vocal variation in song types or phrases among individuals was roughly the same within all populations. These data indicate that song learning from neighboring males (Kroodsma 1974) plays an equally important role in song development among all populations.

Coefficients of Variation

A character shift in learned signals might be expected for a number of reasons among locations (see Discussion), but the variance of measured characters better indicates how stereotyped the vocal displays are. I determined the Coefficient of Variation (CV) for each of the 14 parameters for the nine geographic locations. For each song parameter, I ranked the nine locations by the CV; then, based on the 14 ranks for each location, I determined the median rank for that location. Form least to most variable, the ranks were: Madera Canyon, 2; Grand Junction, 3.5; Sauvie Island, 4.75; Finley Refuge, 5; Santa Barbara 5; Santa Cruz Island, 5; Basket Slough, 6; Klamath Falls, 7.5; Point Reyes, 8. (If I included only the five independent parameters, the ranks were 2, 4, 4, 3, 6, 5, 6, 5, and 8, respectively. Note that Madera Canyon and Point Reyes were still least and most variable, respectively, while rankings of the other locations, especially the mainland and island California populations, did not change appreciably. Further discussion will therefore be based on the entire data set of 14 parameters.)

The short, simple songs from southern Arizona were by far the most stereotyped, ranking either lowest or second lowest in the CV's for 11 of the 14 measured song parameters. The relatively long and complex songs from Colorado were also quite

stereotyped, ranking either lowest or second lowest in the CV's for six of the 14 parameters. In spite of the significant differences in character shift from Santa Barbara to Santa Cruz Island (Table 1), there was no appreciable variance shift; the ranking of the CV's was the same (5) for each location.

Discussion

Two of the most striking features of these data are (1) the simple and highly stereotyped songs of wrens from the rich avifauna of Madera Canyon and (2) the positive correlation between frequency range of mainland song phrases and latitude, with the island song phrases similar to mainland phrases of more northern latitudes. Each of these intriguing correlations might be considered support of Marler's (1960) sound environment hypothesis, and is discussed in succession below.

The Arizona songs had the lowest Coefficients of Variation and typically consisted of only two phases; individual males had the smallest phrase repertoires of any population sampled. It is tempting to conclude that these results are an effect of a very diverse avifauna (Lane 1965) occurring in this part of Arizona. However, if these stereotyped songs were really a result of selection for species-distinctiveness in a rich avifauna, one should likewise expect to find a relaxation of this distinctiveness and increased CV's from Santa Barbara to Santa Cruz Island. No such shift occurred. The CV's were comparable for these two locations, and the phrase repertoire of individuals from Santa Cruz Island was not greater than but only two thirds of the nearby mainland wrens. No other continent-wide patterns were evident in either the CV's or phrase repertoires.

In depauperate avifaunas, it is conceivable that the frequency range might expand in the absence of competing sounds from other species. Such expansions are evident in foraging niches (e.g. Yeaton 1974) and could also occur in use of the audible frequency spectrum. The frequency range of mainland song phrases was highly correlated with latitude, and the island songs were considerably greater in frequency range than the adjacent mainland. The usual positive correlation of body size with latitude would tend to produce a lower mean or minimum frequency in songs at northern latitudes (Morton 1977; Bowman 1979); here I found no differences in the minimum frequency but an increase in mean frequency with latitude. In addition, there is no appreciable difference in body size between insular and mainland California birds (Power 1980). There is, though, a rough negative

correlation of species diversity with latitude in these mainland wren habitats (consider data from Lane 1965; VanVelzen 1979, plot 111; VanVelzen and VanVelzen 1982, plots 150, 158; Anderson 1970; Yeaton 1974), and the island avifauna is simpler than that of the adjacent mainland (Howell 1917; Diamond 1969; Yeaton 1974). However, I am reluctant to attempt a more rigorous analysis of this possible correlation with species abundance for two reasons. First, different census techniques and plot sizes of the above investigators do not allow rigorous comparisons. Second, even if census approaches were standardized, it is unknown how much contact with another species might be necessary for this postulated effect (see Miller 1982). Would species number or diversity (including an equitability component to compensate for rare species) be more appropriate, and would alpha or beta diversity be more desirable to use? Or perhaps "community song diversity", a measure of the overall variety of songs in a community, would be more useful.

These are intriguing correlations, but they cannot implicate cause and effect; thus, while they are in some aspects consistent with Marler's (1960) hypothesis, these data are not a test of that hypothesis. It is possible, for example, that frequency range and variability of signals could be a result of different properties of sound transmission in the respective habitats or of a different optimum (not necessarily maximum) distance for sound transmission in populations of different density (Lemon et al. 1981). The Santa Cruz Island chaparral is more arborescent than the mainland chaparral, and Bewick's wrens occur in higher density in island than mainland chaparral habitats (Yeaton 1974). Each of these factors could be related to increased frequency ranges in island songs (Hunter and Krebs 1979), yet with present knowledge it is impossible to predict exactly what would be the effects on the songs. Perhaps Arizona habitats are more homogeneous, and sound transmission properties of these habitats select for a limited array of highly stereotyped songs (W.I. Boarman, R.I. Bowman, personal communication). I am skeptical, however, that the structural environment will completely explain these correlations.

Similarly, while another correlational study (Hunter and Krebs 1979) concluded that great tit (*Parus major*) song structure (maximum frequency, frequency range, and number of notes/song) was explained largely by tree density and territory size, this may not be the whole story. In a stepwise multiple regression analysis, the number of other bird species commonly singing in each habitat type

did not explain a significant *additive* portion of the variance in song characters, even though both the maximum frequency and frequency range were highly correlated with species diversity ($r = -0.70$ and -0.71, respectively, $p < 0.03$; for this analysis I used data from tables in Hunter and Krebs 1979, using a corrected value of 0.76 rather than 0.97 for frequency range of notes from birds in English woodlands: M.L. Hunter, Jr., personal communication). Such a regression analysis does not indicate, though, whether tree density and territory size explain significantly *more* of the variance than the avifaunal complexity. In addition, a fourth song character, the frequency range of the individual notes (not the entire song, as above), was highly correlated with the number of competing songsters ($r = -0.82$, $p < 0.01$), but *not* with either tree density or territory size ($r = -0.34$ and -0.49, respectively). While Hunter and Krebs found that differences in the *amount* of song produced among the different habitats did not explain differences in song characters, it is perhaps more likely that the *variety* and *quality* of songs rather than the overall quantity would be more influential.

Other data from the literature, while bearing on these issues, are also largely inconclusive. For example, song frequency is correlated with latitude in several other species (Lanyon 1960; Chappuis 1969; Nottebohm 1975), but no cause and effect relationship has been established. Other studies have demonstrated character but not necessarily variance shifts among isolated populations in depauperate avifaunas. Mirsky (1976) found that songs of dark-eyed juncos (*Junco hyemalis*) on Guadalupe Island are more complex and span a wider frequency range than on the mainland. The larger insular juncos (Miller 1941) would tend to produce songs of a lower mean frequency, but frequency ranges (and probably mean frequency) were actually greater in the larger juncos. The expanded frequency range and increased variability appears consistent with the avifaunal complexity hypothesis. Among western flycatchers (*Empidonax difficilis*), in which songs are probably not learned and are therefore less flexible in evolutionary time (Kroodsma 1982a), larger body size among the Channel Island birds has led to a lower mean song frequency (Johnson 1980). On the other hand, Bitterbaum and Baptista (1979) found no frequency differences among mainland and Channel Island house finch (*Carpodacus mexicanus*) songs. Finally, the earlier conclusions of Marler (1960; Marler and Boatman 1951) regarding songs of the chiffchaff (*Phylloscopus collybita*) on Tenerife and the Azores have been challenged by

Thielcke (1969) and Becker et al. (1980), who felt that the insular songs were no more variable than those in some mainland populations.

In conclusion, several factors must influence the characteristics of vocalizations produced by a songbird at any given place and time. Chance phenomena undoubtedly play a role (e.g., Thielcke's 1973 "withdrawal of learning" via the founder effect). The effects of habitat structure on signal design have been amply demonstrated (e.g., see Bowman 1979, 1983; Gish and Morton 1981; Wiley and Richards 1982). In theory, the songs of sympatric songsters undouptedly set broad limits on signal design for a given species, though it is unclear whether these theoretical limits on the diversity of signals are ever approached in nature. Verifying possible interspecific influences will certainly be far more difficult than documenting how sounds attenuate in different habitats, for the effects may be more subtle and experiments impossible to design. Only careful study of both character and variance shifts in communities of differing avifaunal (and therefore vocal) complexity which occur in habitats of *known* acoustic properties will begin to reveal those interspecific influences. There are enough hints and questions in existing data sets that, until such a feat is accomplished, it may be unwise to dismiss the hypothesis that the complexity of the sound environment (*sensu* Marler 1960) may have an important bearing on signal design.

References

Anderson SH (1970) Ecological relationships of birds in forests of western Oregon. Ph D thesis, Oregon State University, Corvallis

Becker PH, Thielcke G, Wüstenberg K (1980) Versuche zum angenommenen Kontrastverlust im Gesang der Blaumeise (*Parus caeruleus*) auf Teneriffa. J Ornithol 121:81–95

Bitterbaum E, Baptista LF (1979) Geographic variation in songs of California House Finches. Auk 96:462–474

Bowman RI (1979) Adaptive morphology of song dialects in Darwin's finches. J Ornithol 120:353–389

Bowman RI (1983) The evolution of song in Darwin's finches.

In: Bowman RI, Berson M, Leviton AE (eds) Patterns of evolution in Galapagos organisms. AAAS, Pacific Division, San Francisco, Calif, pp 237–537

Bremond J-C (1977) Acoustic competition between song of the wren (*Troglodytes troglodytes*) and the songs of other species. Behaviour 65:89–97

Brown RN (1977) Character convergence in bird song. Can J Zool 55:1523–1529

Chappuis C (1969) Un cline vocal chez les oiseaux palearctiques: variation tonale des vocalizations, sous differentes latitudes. Alauda 37:59–71

Diamond JM (1969) Avifaunal equilibria and species turnover rates on the Channel Islands of California. Proc Natl Acad Sci USA 64:57–63

Gish SL, Morton ES (1981) Structural adaptations to local habitat acoustics in Carolina Wren songs. Z Tierpsychol 56:74–84

Howell AB (1917) Birds off the islands of the coast of southern California. Pac Coast Avifauna 12:1–127

Hunter ML Jr, Krebs JR (1979) Geographical variation in the song of the Great Tit (*Parus major*) in relation to ecological factors. J Anim Ecol 48:749–785

Johnson NK (1980) Character variation and evolution of sibling species in the *Empidonax difficilis-flavescens* complex (Aves: Tyrannidae). Univ Calif Publ Zool 112:1–151

Kroodsma DE (1972) Singing behavior of the Bewick's Wren: development, dialects, population structure, and geographical variation. Ph D thesis, Oregon State University

Kroodsma DE (1974) Song learning, dialects, and dispersal in the Bewick's Wren. Z Tierpsychol 35:352–380

Kroodsma DE (1982a) Learning and the ontogeny of sound signals in birds. In: Kroodsma DE, Miller EH (eds) Acoustic communication in birds, vol 2. Academic Press, New York, pp 1–23

Kroodsma DE (1982b) Song repertoires: problems in their definition and use. In: Kroodsma DE, Miller EH (eds) Acoustic communication in birds, vol 2. Academic Press, New York, pp 125–146

Kroodsma DE (1984) Songs of the alder flycatcher (*Empidonax alnorum*) and willow flycatcher (*Empidonax traillii*) are innate. Auk 101:13–24

Lane JA (1965) A birdwatcher's guide to southeastern Arizona. L&P Photography, Santa Ana, Calif

Lanyon WE (1960) The Middle American populations of the Crested Flycatcher, *Myiarchus tyrannulus*. Condor 62:341–350

Lanyon WE (1978) Revision of the *Myiarchus* flycatchers of South America. Bull Am Mus Nat Hist 161:429–627

Lemon RE, Struger J, Lechowicz MJ, Norman RF (1981) Song features and singing heights of American warblers: maximization or optimization of distance? J Acoust Soc Am 69:1169–1176

Marler P (1960) Bird songs and mate selection. In: Lanyon WE, Tavolga WN (eds) Animal sounds and communication. Am Inst Biol Sci Publ 7:348–367

Marler P, Boatman DJ (1951) Observations on the birds of Pico, Azores. Ibis 93:90–99

Marten K, Marler P (1977) Sound transmission and its significance for animal vocalizations. I. Temperate habitats. Behav Ecol Sociobiol 2:271–290

Miller A (1941) Speciation in the avian genus *Junco*. Univ Calif Publ Zool 44:173–434

Miller EH (1982) Character and variance shifts in acoustic signals of birds. In: Kroodsma DE, Miller EH (eds) Acoustic communication in birds, vol 1. Academic Press, New York, pp 253–295

150

Mirsky EN (1976) Song divergence in hummingbird and junco populations on Guadalupe Island. Condor 78:230–235

Morton ES (1975) Ecological sources of selection on avian sounds. Am Nat 109:17–34

Morton ES (1977) On the occurrence and significance of motivation-structural rules in some bird and mammal sounds. Am Nat 111:855–869

Mulligan JA (1966) Singing behavior and its development in the song sparrow (*Melospiza melodia*). Univ Calif Berkeley Publ Zool 81:1–76

Mundinger P (1982) Microgeographic and macrogeographic variation in acquired vocal patterns. In: Kroodsma DE, Miller EH (eds). Acoustic communication in birds, vol 2. Academic Press, New York, pp 147–207

Nottebohm F (1975) Continental patterns of song variability in *Zonotrichia capensis*: some possible ecological correlates. Am Nat 109:605–624

Power DM (1980) Evolution of land birds on the California Islands. In: Power DM (ed) The California islands: proceedings of a multidisciplinary symposium. Sta Barbara Mus Nat Hist

Thielcke G (1969) Geographic variation in bird vocalizations.. In: Hinde RA (ed) Bird vocalizations. Their relation to current problems in biology and psychology. Cambridge University Press, Cambridge, pp 311–342

Thielcke G (1973) On the origin of divergence of learned signals (songs) in isolated populations. Ibis 115:511–516

VanVelzen WT (1979) Forty-second breeding bird census. Am Birds 33:54–114

VanVelzen WT, VanVelzen AC (1982) Forty-fifth breeding bird census. Am Birds 36:49–106

Wiens JA (1982) Song pattern variation in the Sage Sparrow (*Amphispiza belli*): dialects or epiphenomena? Auk 99:208–229

Wiley RH, Richards D (1982) Adaptations for acoustic communication in birds: sound transmission and signal detection. In: Kroodsma DE, Miller EH (eds) Acoustic communication in birds, vol 1. Academic Press, New York, pp 122–181

Yeaton RI (1974) An ecological analysis of chaparral and pine forest bird communities on Santa Cruz Island and mainland California. Ecology 55:959–973