Character and Variance Shift in Acoustic Signals of Birds

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I. INTRODUCTION

Ecological and behavioral interactions among species commonly lead to co-evolution. Indeed, it could be claimed that most phenotypic characteristics include adaptations for coexistence with other species. Some of these adaptations are complex and highly specific, as between termites and their digestive symbionts. Others are relatively simple general-purpose adaptations, such as cryptic appearance and behavior of vulnerable prey species. The complexity and specificity of such coadaptations depend largely upon the extent to which individual fitness in coexisting species is influenced by their interaction, although numerous other factors may be involved. In this chapter I am concerned with those characteristics of sound signals which have evolved through interaction (or its absence) among related and unrelated species.

Concepts central to this chapter have been used extensively in evolutionary and ecological studies. A species may exhibit displacement (either contraction or divergent shift, or both) in its use of a limiting resource when syntopic with a
superior or more abundant competitor. Conversely, a species may show expansion (competitive release) or convergent shift, or both, when a competitor is rarer or absent. Such responses are probably facultative and nongenetic at first, and acquire a genetic basis over time (MacArthur and Wilson, 1967). The same processes are presumed to act upon morphological characters important in resource use. Thus, characters may exhibit divergent shift or reduced variation in competitive environments (Brown and Wilson, 1956; van Valen, 1965). Examples of divergent character shift and shift of character variance are shown in Fig. 1.

All of these ideas have been extended to animal signals [e.g., Marler, 1957, 1960; Smith, 1977; Thielcke (1973) and others use the term “contrast reinforcement” when referring to character displacement in bird sounds]. A good example of divergent shift in a visual signaling structure involves two damselfly species, *Calopteryx aequabilis* and *C. maculata*. Wing pigmentation is important in courtship in these species, and males of *C. maculata* use this cue to identify conspecific females, especially in areas of sympathy with *C. aequabilis* (Waage, 1975). Females of both species have dark and fairly similar wing pigmentation in allopatri, and diverge in sympathy (particularly *C. aequabilis*: see Fig. 2A; see also Waage, 1979).

Species often diverge unequally in sympathy. This is obvious for *C. aequabilis* and for chorus frogs: *Pseudacris feriarum* exhibits strong divergence in pulse rate of male advertisement calls in sympathy with *P. nigrita* (Fig. 2B) (Fouquette, 1975).

There are few clear examples of competitive release of signals or signaling structures. However, various authors have suggested that songs of birds in simple communities (e.g., on small or isolated islands) may differ in complexity from conspecific song in more diverse communities. For example, the Blue Tit (*Parus caeruleus*) has a more complex song on Tenerife, Canary Islands, than on the mainland (Figs. 3 and 4; see Section II,A,2).

The concepts of displacement and expansion implicate important and widespread selection pressures and have a broad diversity of applications. Hereafter, I distinguish shifts in location and variance of acoustic characters as character shift and variance shift, respectively. Variance shift includes shifts in complexity and information content of sounds. Either or both kinds of shift can result from acoustic relations among syntopic species.

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1Necessary criteria for invoking divergent shift have been reviewed by Grant (1972). These include knowledge of character states in allopatri and sympathy, and of why differences exist; accentuated differences in sympathy can result for many reasons unrelated to competition or interference between species.

2This is the conventional view. Thomson (1980) and others point out that a resource need not be limiting to population size for niche shifts to take place.
Fig. 1. (A) Cumulative plots of shell length of mud snail species (Hydrobia) in sympatry (symp.) and allopatry (allop.) in Denmark. The size of particles ingested by these deposit feeders varies directly with body size, as estimated by shell length. (After Fig. 1 of Fenchel, 1975; based on raw data of T. Fenchel.) (B) Relationship of the coefficient of variation in mandible size in workers of an ant species (Veromessor pergandei), to species diversity (in nats) of sympatric granivorous ant species. Size of seeds handled by workers of V. pergandei varies with mandible size. Thus, colonies with different-sized workers prey upon a great diversity of seeds and upon a large fraction of available seeds. (After Fig. 2 of Davidson, 1978; based on raw data of D. W. Davidson.)
II. EVOLUTIONARY ORIGINS OF SPECIES SPECIFICITY

A. Selective Pressures and Constraints Affecting Species Specificity

1. Hybridization

The concept of character displacement as applied to sound signals developed from Peter Marler’s writings in the 1950s, particularly on the issue of whether or not the structure of animal signals is arbitrary. Many songbird species emit calls when they perceive predators, and these calls have physical features which make callers difficult to locate. This suggests that the characteristics are not arbitrary, but have evolved under selective forces favoring nonlocatability (Marler, 1955). It is a short step to consider that the structure of more complex sounds, like songs, is also adaptive, especially considering their importance to mate attraction and pair-bond formation in the presence of related species.

But see Shalter (1978).
Reproduction between heterospecifics is generally assumed to lower their fitness, since no or few hybrids are typically produced, and these may be inviable, sterile, or have reduced fertility (Dobzhansky, 1970; Mayr, 1963). Such effects should lead to divergence in characters like song, which function as pre-mating isolating mechanisms in mate attraction and pair formation. But what fraction of species-specific acoustic characters has evolved in sympatry as a direct result of selective pressures surrounding hybridization, and what fraction has evolved in allopatry?

With Müller (1942), Mayr advocates the view that "the greatest part of the genetic basis of the isolating mechanisms is an incidental by-product of the genetic divergence" between species which took place during their allopatric origins (Mayr, 1976, p. 133). Nevertheless, he acknowledges that behavioral (and other prezygotic) isolating mechanisms might be readily strengthened in sympatry, especially in taxa like birds whose mating is behaviorally complex (MacArthur and Wilson, 1967; Mayr, 1942, 1963, 1976; Mecham, 1960). Conversely, Fisher (1958), Dobzhansky (1937), and others view isolating mechanisms as adaptations serving to reduce hybridization: "Their evolutionary functions are . . . limitation or prevention of . . . gene exchange between species" (Dobzhansky et al., 1977, p. 172). Furthermore, "sexual isolation in animals may very well be bolstered by making the species' traits easily recognizable to conspecific individuals" (Dobzhansky, 1951, p. 211). Thus, both schools agree that character differences at the level of reproductive behavior may be reinforced when species become sympatric, though they disagree about the extent of reinforcement.

The degree of elaboration of acoustic isolating mechanisms can only be estimated with knowledge about the incidence of hybridization and its costs to individual fitness, the nature of gene flow to and from areas of sympathy, the stage of speciation when isolating mechanisms are acquired, the heritability of relevant ethological (acoustic) characters, and the kinds of nonselective processes and selective pressures unrelated to hybridization which lead to species specificity (Bigelow, 1965; White, 1978). Nevertheless, it is reasonable to
assume that signals used early in mate attraction and courtship are under the greatest selective pressure from related species, if any signals are, because they deter interbreeding with minimal loss of time and energy (Liley, 1966; Nuechterlein, 1981). Because such sounds are typically complex, variable, and strongly differentiated among related species of birds, they must be the most effective as acoustic isolating mechanisms. For precisely the same reasons, they are the most difficult to judge adaptedness of.

Hybridization and introgression between Blue-winged and Golden-winged warblers (Vermivora pinus and V. chrysoptera) are well documented (Berger, 1958; Gill, 1980; Mayr, 1942; Parkes, 1951; Short, 1962, 1963). These have resulted from range modifications in both species since the late 1800s, particularly in V. pinus, whose range now overlaps extensively that of the more northern V. chrysoptera. The species show minor ecological differences in nesting habitat and foraging characteristics, but their nesting territories often overlap locally (Confer and Knapp, 1981; Ficken and Ficken, 1968a,b,c; Gill and Murray, 1972a; Murray and Gill, 1976; Parkes, 1951). In addition, male V. pinus arrive on the nesting grounds each spring before male V. chrysoptera (Ficken and Ficken, 1968a,b,c; Murray and Gill, 1976). Each species possesses two kinds of learned songs (I and II) which are generally considered to have epigamic and intrasexual functions, respectively, and each male sings only one version of each (Gill and Lanyon, 1964; Gill and Murray, 1972a,b; Kroodsma, 1981; Chapter 1, Volume 2). Altogether, songs of the two species include about seven types of components [termed A-G by Gill and Murray (1972a,b); other sonagrams are in Bondesen (1977), Ficken and Ficken (1967), Kroodsma (1981), Lanyon and Gill (1964), and Meyerriecks and Baird (1968)]. Song I should be the most sensitive indicator of shift resulting from maladaptive hybridization. In V. pinus this generally has two components (A, B), each occurring once, and in V. chrysoptera there are three to five repetitions of one component (C). Some component variants are unique to one or the other location, but no systematic trends emerge. Both A and B in song I of V. pinus are essentially identical in allopatry (Long Island, New York) and sympatry (Michigan) with V. chrysoptera (Gill and Murray, 1972b; Lanyon and Gill, 1964). The only suggestion of shift lies in the absence of component C from song of sympatric V. pinus, and the greater variation in song I patterns of V. pinus in allopatry than in sympatry (Table I). These data alone need not imply variance shift, and may just represent geographic variation (Gill and Murray, 1972a). Nevertheless, various lines of evidence suggest that isolating mechanisms are under reinforcing selection, for hybrids have low fitness, and positive assortative mating and back crossing prevail (Ficken and Ficken, 1968a; Gill and Murray, 1972a). Furthermore, V. pinus and

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7Signals which occur later in mate attraction and courtship sequences should become increasingly divergent with time, however (Alexander, 1968).
TABLE I
Forms of Type I ("Epigamic") Songs of Blue-Winged and Golden-Winged Warblers (Vermivora pinus and V. chrysoptera) in Allopatry and Sympatry

<table>
<thead>
<tr>
<th>Component sequence in song</th>
<th>AB/ABDB&lt;sup&gt;a&lt;/sup&gt;</th>
<th>ABA</th>
<th>AAA</th>
<th>ACB</th>
<th>AC</th>
<th>CCCC</th>
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<tr>
<td>V. pinus</td>
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<tr>
<td>allopatric</td>
<td>6</td>
<td>0</td>
<td>1</td>
<td>7</td>
<td>1</td>
<td>0</td>
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<td>V. pinus</td>
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<tr>
<td>sympatric</td>
<td>46</td>
<td>2</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
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<tr>
<td>V. chrysoptera</td>
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<tr>
<td>sympatric</td>
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<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>20</td>
</tr>
</tbody>
</table>

<sup>a</sup> Data are from Gill and Murray (1972a,b), and include songs classified spectrographically and by ear. Identity of singers was therefore often judged by gross plumage phenotype. See remarks of Short (1969).

V. chrysoptera have rapid courtship and a brief nesting season, which should favor species-specific displays in mate attraction (Ficken and Ficken, 1968a,b). The weak evidence for shift in epigamic song of these species suggests that song is sufficiently unimportant as an isolating mechanism, or is already sufficiently effective (different), that its further evolutionary change is unnecessary (or immeasurable?). Furthermore, song type I varies much less geographically than does II, at least in V. pinus (Kroodsma, 1981). In any case, song is only part of a suite of isolating mechanisms in V. pinus and V. chrysoptera, which are very different in plumage and which have prominent visual displays, especially at close range (Baird, 1967; Ficken and Ficken, 1962, 1968b; Meyerrieckes and Baird, 1968).

An instructive contrast with the preceding example is provided by the Indigo and Lazuli buntings, Passerina cyanea and P. amoena. Like the Vermivora species, males of these species have distinctive species-specific plumage, and hold type A territories whose occupancy they advertise with learned song (Emlen, 1972; Emlen et al., 1975; Rice and Thompson, 1968). Passerina amoena is broadly distributed in western North America, and P. cyanea in the east; ranges overlap in the Great Plains, where hybridization and interspecific territoriality occur (Emlen et al., 1975; Sibley and Short, 1959). Song components in allopatric populations differ, and have been described in detail by Emlen (1972), Rice and Thompson (1968), and Thompson (1968, 1969, 1970, 1972, 1976). The species also differ in song in several other ways in allopatry: P. cyanea songs tend to be longer, slower in cadence, and more complex in temporal organization. In an area of hybridization near Chadron, Nebraska, songs of
the two species contain various proportions of typical allopatric song components. Thus, components typical of allopatric *P. cyanea* comprised 14–100% of songs of four (phenotypic) *P. cyanea*, and 0–100% of songs of 14 (phenotypic) *P. amoena* (Emlen *et al.*, 1975, Table 1). Song cadence of the minority species there, *P. cyanea*, is faster than it is in allopatry. No other significant interpretable differences were found. Only indirect evidence of selection against hybridization could be sequestered: hybrids were uncommon; introgression was virtually undetectable; five birds collected in an ecologically suboptimal area were probably hybrids; and two “impure” pairings suffered delayed breeding as compared with four others. In brief, there is no evidence of contraction or divergent shift in song, despite intensive and detailed study, and even though various lines of evidence suggest that it should occur. This may be because hybridization is minimized through interspecific territoriality, which sets signaling needs met by convergent character shift (convergence in song cadence of *P. cyanea* and sharing of song syllables, in sympatry).

The preceding examples concern well-studied species that can hybridize and whose complex song is probably an effective isolating mechanism. Even so, no strong patterns suggesting contraction or divergent shift in song characteristics are apparent. These results are typical of intensive studies on various taxa and suggest that differences among related species are generally not strongly reinforced as isolating mechanisms (e.g., Grant, 1975; Heth and Nevo, 1981; Martens, 1975; Selander and Giller, 1961; Thielecke *et al.*, 1978; Watson and Littlejohn, 1978). In any case, interpretation is a major problem even with strong evidence of shift among related species. Such species are most likely to interfere with one another acoustically because of their relatedness, which imparts generally high similarity in habitats, activity rhythms, acoustic characteristics, sound functions, and so on. Consequently, shift is perhaps most likely to occur among related species, but for reasons unrelated to hybridization. [den Boer (1980) argues similarly, for high ecological similarity within groups of Carabidae (Coleoptera).]

2. Other Considerations of Species Specificity

The view that species-specific characteristics of song evolved to reduce hybridization fits nicely with the observation that songs differ greatly among species, even among closely related species with very similar external characteristics (e.g., sympatric species of *Empidonax* [Johnson, 1963, 1980; Stein, 1958, 1963] and *Phylloscopus* [Marler, 1957, 1960]). It also makes sense of the observation that song is much more highly species-specific than simple calls are (Güttinger and Nicolai, 1973; Marler, 1957; Thielecke, 1970). The broad correlation among relatedness, similarity in appearance and in simple calls, and differences in complex songs, suggests that character shift is important and perva-
It is a truism that species differ" phenotypically, and that differences vary directly with the complexity (dimensionality) of the characteristics under consideration. Songs must therefore vary more among and within species, and correspondingly must have higher species specificity than simple calls, on this basis alone. Furthermore, long-distance acoustic advertisement by birds is often under the dominant influence of sexual selection, which can cause rapid evolutionary change and marked divergence among species. Such divergence should be particularly marked if song is learned, since learning increases interindividual variation upon which sexual selection can work. Thus, strong differences among long-distance complex sounds of related species are to be expected, even in the absence of ecological, behavioral, or reproductive interactions. Simple calls should be more similar across species than should songs, but this by itself does not imply that selection has promoted greater species specificity in the latter than in the former. Also, evidence for evolution or adaptive alteration of signals to reduce interaction among species must be much stronger than simple listings of species differences, although such are often interpreted as adaptations in that sense (see also Section III).

The need for species specificity has also been used to explain examples of variance shift. Thus, in depauperate avifaunas where species recognition is not a problem, song may be more complex than in richer bird communities. The most widely cited examples of this trend are species in the Canary Islands (Lack and Southern, 1949; Marler, 1960; Marler and Boatman, 1951; Marler and Hamilton, 1966). For example, song of central European Parus caeruleus generally consists of just two simple, sequentially graded series, each of a single note type (Fig. 3). Songs on Tenerife, Canary Islands, are composed of at least two note types; these are more structurally complex than in central Europe, have a much more complex sequential organization, and vary more among individuals (Fig. 4) (Becker et al., 1980). Similarly, nonsong calls of the Goldcrest (Regulus regulus) "are of bewildering variety" compared with those in British populations (Marler and Boatman, 1951, p. 95).

The suggestion that complex songs should characterize impoverished avifaunas can be readily assessed with other island-mainland comparisons. Consider the Savannah Sparrow (Ammodramus sandwichensis), which nests commonly throughout much of North America and experiences a broad spectrum of avian communities and sound environments. Most males have only one song type (rarely two: J. B. Gollop, unpublished data), and are often polygynous in the well-differentiated population on Sable Island, Nova Scotia, where they are the only native breeding passerine (McLaren, 1972; Stobo and McLaren, 1975; limited polygyny also occurs elsewhere: Weatherhead, 1977, 1979; Welsh,
Thus, sexual selection and the near absence of other species could rapidly generate song complexity there. Individual song elements on Sable Island are not more complex than on the mainland (Fig. 5) (Chew, 1979, 1981; J. B. Gollop, unpublished data). However, five of six males on Sable Island had nine note types per song, and the sixth had ten ($\bar{Y} = 9.2$). Birds in the much more complex breeding avifauna near Churchill, Manitoba, had fewer note types per song: nine had seven, eighteen had eight, and one had nine ($\bar{Y} = 7.7$). This trend supports a correlation between avifaunal and song complexity, but is countered by data for communities of intermediate complexity: two males from the Ogilvie Mountains, Yukon Territory, had nine, one had ten, and five had eleven note types per song ($\bar{Y} = 10.4$; Fig. 5); and songs from birds in southern Ontario, mainland Nova Scotia, and Saskatchewan, show no systematic relationship of number of note types to avifaunal complexity (Chew, 1979, 1981; J. B. Gollop, unpublished data; see also Bradley, 1977).

Why should such an apparently simple test case yield such equivocal results? One reason is that the hypothesis being tested was inadequate: divergent predictions can pertain to variance shift. Thus, it can be advanced that complex songs
should evolve in simple communities because of the release from normalizing pressure for species specificity; alternatively, complex species-specific sounds should evolve in complex communities to facilitate rapid, unequivocal species identification [on the Canary Islands, "Songs of several species are shorter and simpler . . . than those of their British counterparts" (Lack and Southern, 1949, p. 615)]. Another reason is that evolutionary changes in complexity can result from diverse selective and nonselective processes unrelated to community structure, including learning and sexual selection. One of these is simply sampling error and subsequent drift, resulting from low numbers of colonists, small population size, etc. Another has been suggested by Thielcke (1973), as the "withdrawal-of-learning" hypothesis. Consider the colonization of an island by a songbird species. Colonists are likely to be few in number and to include young birds, males of which have uncrystallized song. If these mature with insufficient exposure to species-typical song, their uncrystallized song could become characteristic of the population, and song of island adults could come to resemble that of mainland juveniles. This is the likelyest explanation for the complex song form

![Sonagrams of songs of eight male Blue Tits (Parus caeruleus) from Tenerife, Canary Islands. (Originals provided by H.-H. Bergmann; analyzing filter bandwidth, 300 Hz.)](image-url)
Fig. 5. Sonagrams of songs of six male Savannah Sparrows (*Ammodramus sandwichensis*) from Ogilvie Mountains (Yukon), Sable Island (Nova Scotia), and Churchill (Manitoba). Songs typically begin with several notes such as “1,” as in the bottom panel. Only the last note in each introductory series is shown in the top five panels. “Note types” are single or compound notes which may be repeated immediately, and are distinguished by numbers. Subsequent repetitions are considered as separate note types (e.g., 1, 3, 7, and 10 in the top panel). Note types do not correspond across panels. (Analyzing filter bandwidth, 300 Hz.)
in *Parus caeruleus* on Tenerife and in the Dark-eyed Junco (*Junco hyemalis*) on Guadalupe Island, off Baja California (Becker et al., 1980; Mirsky, 1976). It may also explain some instances of interspecific song learning (e.g., Kroodsma, 1972).

It is clear from this and the preceding section that character and variance shift are not unitary concepts. Shift-like patterns can result from diverse processes, some related to hybridization and selection for enhancement of isolating mechanisms, and some not. Furthermore, there is no obvious reason to expect variance and character shift to covary.

The diversity of potential causes makes it difficult to explain which forces lead to shift and maintain it in any particular case. Nevertheless, two broad sets of forces can be distinguished, one concerned with general costs to interference, and the other with costs to species misidentification (including costs of hybridization). Thus, selection promoting shift can stem from costs of lengthier, more frequent, or louder signaling in biologically noisy environments. Colonists or minority species in noisy environments may be under selective pressure to change simply because of the difficulty in being heard, irrespective of the similarity of their sounds to those of other residents, or the presence of related species. Change can also be promoted by the presence or absence of related species with similar sounds, because of danger of hybridization, or because time and energy are wasted through inappropriate responses by and to heterospecifics, or both.

Character shift can have diverse causes, but its mechanisms are probably quite uniform. Sound characteristics which encode species identity are usually important for recognition of conspecific mates or competitors. These characteristics are under normalizing selection *within* populations, for effective and efficient communication (see Carson, 1978; Hubbs, 1960; Manning, 1977; Paterson, 1978, 1980; Templeton, 1980). Thus, a male songbird with a deviant song may take a long time to attract a mate or may attract a low-quality mate, regardless of the ambient sound environment. In an altered sound environment, those males with only a slightly deviant but still recognizable song will be favored. Character shift should thus evolve gradually toward increased distinctiveness. Because most acoustic signals are complex and highly redundant, shift probably does not have to proceed very far before a new mode is established.

Variance shift should be uncommon, if intrapopulational normalizing selection on characteristics encoding species identity is widespread. This is because further reduction of population variance may be unnecessary even if a new sound

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*The aberrant insular song type . . . may be as constant . . . as the mainland song," however (Hansen, 1979, p. 44; italics added).
*A distinction between "reproductive" and "competitive" character displacement is often noted (e.g., Huey and Pianka, 1974; White, 1978), but their effects are usually inseparable, as these and earlier remarks indicate (Wilson, 1965).
environment favors it, and increased variance is selected against, for the reasons stated, even in a permissive sound environment.

3. Social and Ecological Influences on Species Specificity

The evolutionary importance of species specificity, and hence the variation and complexity of acoustic isolating mechanisms, is set by numerous interrelated factors. Some of these factors derive from the social functions of different sounds and the relative importance of sound in communication; others come from characteristics of the prevailing bioacoustic environment.

Sounds which are broadcast over large areas are more likely to come under pressure to diverge or contract from those of other species than are short-range sounds. Sound function also affects this likelihood. Thus, sounds emitted by unmated males to attract mates should diverge or contract more, or more quickly, than sounds with a similar broadcast area but which just function to space out males; and both of these kinds of sounds should respond more quickly than short-range sounds with equivalent functions. Such simple pair-wise examples could be multiplied but of course various factors operate simultaneously in any real situation, with inseparable effects. Consider a species in which unmated males broadcast over large areas to attract females. Following Marler (1957), we predict that such signals are more species-specific than: (i) short-range signals with different functions but equivalent importance to fitness; (ii) signals with the same broadcast area but with smaller effects on fitness; and (iii) signals with equivalent functions and effects on fitness in a different species, but with a smaller broadcast area. The latter prediction has several sources. First, acoustic interference from related and unrelated species is weak over small broadcast areas. Second, visual signals become increasingly important over short display distances, and these weaken the necessity for shifts in acoustic characteristics, or even make them unnecessary. Finally, intraspecific acoustic interference can be severe for species which display at high densities; this promotes evolutionary simplification of acoustic signals and increased reliance upon visual signals. Highly polygynous species often fall in this category, and sexual selection in such species is so strong that extreme conformity with this prediction is expected.

The Calidridinae (Scolopacidae) illustrate some of these points. The Ruff (*Philomachus pugnax*) is a traditional lek species. Males have complex and striking visual epigamic displays on lekking hills, but are utterly silent there (Hogan-Warburg, 1966; van Rhijn, 1973). The Buff-breasted Sandpiper (*Tryngites subruficollis*) is also a lek species, but leks are transient, males are separated on them by much greater distances than in *Philomachus*, and males display with flutter-jumps and wing extensions. These displays are visible over considerable distances because of the white undersurface of the wings. During courtship over short distances, males use elaborate visual displays and emit soft, simple “tick” sounds (Myers, 1979; Oring, 1964; Parmelee *et al.*, 1967; Sutton,
Males of the polygynous Sharp-tailed and Pectoral sandpipers (*Calidris acuminata* and *C. melanotos*) are even more widely dispersed during courtship but otherwise have a social system similar to that of *Tryngites* (exploded lek). A major display of males is a low flight with characteristic flight path, wing action, throat expansion, and repeated trains of simple, loud calls (Flint and Kishchinskii, 1973; Pitelka, 1959). Males of most monogamous calidridine species are typically dispersed even more during courtship. Even their simplest long-distance calls are more complex than those of *C. melanotos* (analyses of sounds of *C. acuminata* are not available), and only some gross motor characteristics of display flights have potential signal value (height above ground and fluttering actions of the wings, mainly). Thus, calidridines exemplify some simple relationships among mating system, broadcast area, prominence of visual displays, and complexity of acoustic displays.

These observations of relationships are strengthened by observations on a related lek species, the Great Snipe (*Capella media*), which is nocturnal. The reduced emphasis on visual signaling in *C. media* is accompanied by complex and prominent vocal displays (Ferdinand, 1966; Ferdinand and Gensbøl, 1966; Lemnell, 1978).

Generalization is difficult, however. Complex species-specific song occurs in short-range courtship in various species of grassfinches (Estrildidae), in which visual signaling with plumage and posture is also important (Hall, 1962; Zann, 1976a,b). Many species of birds that communicate frequently and importantly over short distances have complex graded systems of vocal communication, whether or not plumage is strongly modified for visual signaling (e.g., ducks, quails, jays, phalaropes, jacanas, rails: Abraham, 1974; Anderson, 1978; Berger and Ligon, 1977; Hardy, 1979; Hope, 1980; Howe, 1972; Huxley and Wilkinson, 1977; Jenni *et al*., 1974; Mace, 1981). Therefore it may be possible only to elucidate relationships among the factors discussed above, for closely related species.

Dispersion, density, and stability of species' spacing patterns all affect signal functions and are all strongly affected by ecological forces. Such forces include seasonality, spatial and temporal characteristics of resource distribution, predation, species richness, and trophic level. The effects of these factors on spacing patterns are intertwined with their effects on social structure, activity budgets, and so on, which influence signaling characteristics in turn. Numerous perspectives on such interrelationships are available, and further treatment here is unnecessary (e.g., Bradbury and Vehrencamp, 1977; Crook, 1965; Crook *et al*., 1976; Emlen and Oring, 1977; Geist, 1978; Jarman, 1974; Lill, 1974; Waser and 10Hall (1962, p. 41) states that "The extent of the song differences . . . is . . . much less than might be predicted on the basis of what is known of the more familiar passerines," but sonographic evidence there and in Zann (1976a) is not supportive.
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Wiley, 1979; Wittenberger, 1979; Wittenberger and Tilson, 1980, and references therein). Frequency and rate of occurrence, magnitude, direction, and predictability of ecological variations will determine the extent to which adaptive shifts occur. Variations of particular significance for shifts in acoustic signals lie in characteristics of spacing, of the overall bioacoustic environment (reflected in avifaunal composition), and of the presence of related species. All of these vary importantly with ecological factors like productivity. For example, spatial variations in productivity yield heterogeneity in a species' breeding density and spacing pattern. Highly productive areas may accommodate many species, including related species at high density; conversely, regions of low productivity may be inhabited by fewer species at lower densities (and probably distributed less uniformly). It is straightforward to consider comparable variations over time. Some of the most significant of these for adaptive shifts are year-to-year fluctuations in avifaunal composition and breeding density. Sustained shifts are unlikely to evolve where these and related ecological characteristics differ strongly from year to year. Additionally, the physical environment plays an important role in selecting for certain sound characteristics (see Bowman, 1979; Gish and Morton, 1981; Hunter and Krebs, 1979; James, 1981; Chapter 5, this volume).

In summary, character and variance shifts are most likely to evolve in long-distance signals of species which inhabit structurally simple environments that are temporally and spatially stable in physical characteristics, in those factors which set spacing patterns, and in high avifaunal complexity (including related species). Of course this is just a specific prediction related to general concepts about evolution in changing environments, and many other relevant considerations exist (Levins, 1968; Roughgarden, 1979).

In this section I have outlined some examples and principles which emphasize the complexity of selective forces favoring shift and the difficulty in documenting it. Some of the difficulty arises from the practical difficulties in estimating fitness differentials through field research, but most is due to the anticipated rarity of measurable shift because of variation in the kind and magnitude of selective pressures, and the importance of visual signaling.

B. Minimizing Interference and Achieving Species Specificity

1. Behavioral and Ecological Adjustments

Individuals can adaptively modify their acoustic signals, and this must impede evolutionary response to natural selection promoting contraction or divergent shift. For example, when isolated from mates, Common Quail (Coturnix cour-


nix) emit more frequent separation crows in a noisy than in a quiet environment (Potash, 1975); male Ovenbirds (Seiurus aurocapillus) tend to sing incomplete songs when at moderate distances from their mates, but give full songs at greater distances (Lein, 1981); males of various songbird species avoid singing when neighbors are singing (Gochfeld, 1978; Kroodsma and Verner, 1978; Wasserman, 1977); White-rumped Shamas (Copsychus malabaricus) imitate one another during agonistic interactions, whereas mates avoid singing similar song structures (Kneutgen, 1969); subordinate male Long-billed Marsh Wrens (Cistothorus palustris) tend to follow and match song types of dominants during countersinging (Kroodsma, 1979); and so on. Given the widespread occurrence of these and other facultative adjustments in intraspecific communication, it is easy to envision responses which minimize acoustic interference with heterospecífics. Some data indicate simply that individuals tend to signal when heterospecífics are silent [Cody and Brown, 1969; Ficken et al., 1974; for other taxa, see Littlejohn and Martin (1969), Samways (1977), and Samways and Broughton (1976)]. There are few comparable observations on facultative spatial adjustments. However, male gray treefrogs (Hyla versicolor) space out so that sound pressure levels at each calling position are no higher than about 93 dB (Fellers, 1979; see also Thiele and Bailey, 1980; Whitney and Krebs, 1975). A simple mechanism like this may operate widely, with minor ecological consequences.

Selection which favors unequivocal intraspecific signaling promotes improved discrimination by receivers, as well as increased species specificity in signals. In birds, improved discrimination is probably learned through unrewarding or aversive interaction with heterospecífics; it is unlikely to result directly from genetically determined tuning of the auditory system, as occurs in anurans and acoustic insects (Capranica, 1976; Elsner and Popov, 1978).

Altered responsiveness to sound signals has been documented in sympatric species of birds. Song discrimination by sympatric Vermivora chrysoptera and V. pinus in Michigan has been studied by Gill and Murray (1972a) (see Section II.A.1). V. pinus males responded to playbacks of heterospecific song type I on 4 of 18 trials, and V. chrysoptera responded on 2 of 14 (totaling ½; see further). In allopatry, V. pinus (Maryland) responded on 7 of 9 trials, and V. chrysoptera (West Virginia) on 1 of 17 (Ficken and Ficken, 1969). V. pinus males thus responded to song type I of V. chrysoptera less often in sympathy than in allopatry. Other data that support the suggestion that responsiveness is less in sympathy come from playback experiments on song types I and II. Males of both species in sympathy responded more often to playbacks of heterospecific song type II than I, as predicted: V. pinus responded to II on 6 of 10 trials (versus ½), and V. chrysoptera on 9 of 12 (versus ¾; Gill and Murray, 1972a, p. 287). Overall, then, there were ½ (18.8%) responses to heterospecific I and ½
Western Grebes (*Aechmophorus occidentalis*) occur in dark and light phases, which act as good species (Ratti, 1979). Individuals emit simple advertising calls early in "courtship"; these are usually single calls in light-phase birds and double in dark-phase birds. Observational data and playback experiments reveal a strong tendency for birds to reply or otherwise respond to calls of their own color phase, particularly in sympatry (Nuechterlein, 1981) (Table II).

The trends discussed above should typify species which are not interspecifically territorial. Opposite trends are predicted for species which hold mutually exclusive territories. A few male Reed Warblers (*Acrocephalus scirpaceus*) which were interspecifically territorial with Marsh Warblers (*A. palustris*) also had mixed song. These males sang at the rapid tempo characteristic of *A. palustris* during interspecific singing encounters, and one uttered more *palustris* song while singing with them than when singing alone (Lemaire, 1977). In sympatry, males of *Passerina cyanea* and *P. amoena* respond equally strongly to playbacks of conspecific and heterospecific song (see Section II,A,1). Males in allopatric populations respond strongly to conspecific song, but very weakly to heterospecific song (Emlen, 1972; Emlen et al., 1975; Thompson, 1969), a trend also approximated in some *Acrocephalus* species (Catchpole, 1978). Emlen et al. (1975, p. 172) "hypothesize that sympatric buntings 'learn' to misidentify congeners as a result of individual behavioral experiences," and that such "learned misidentification" is adaptive when it is more costly to share a territory with an ecologically, genetically, or morphologically similar heterospecific or hybrid than to exclude them. Similar considerations probably also

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**Table II**

<table>
<thead>
<tr>
<th>Color phase of female whose stimulus call was used</th>
<th>Dark</th>
<th>Light</th>
</tr>
</thead>
<tbody>
<tr>
<td>Percentage (and sample size) of males advertise-calling or approaching in response to stimulus calls</td>
<td></td>
<td></td>
</tr>
<tr>
<td>In sympathy (Oregon)</td>
<td>66(38)</td>
<td>3(33)</td>
</tr>
<tr>
<td>In allopatry (Manitoba)</td>
<td>68(40)</td>
<td>48(40)</td>
</tr>
</tbody>
</table>

* Data are from Nuechterlein (1981).

(68.2%) to II in sympatry [see also Gill and Lanyon (1964) on allopatric *V. pinus*].
apply to other pairs of related species (Becker, 1977; Falls and Sijj, 1959; Kroodsma, 1973; Thieleke, 1972).

Individuals of most bird species can probably adjust to acoustic interference facultatively and (or) through learning. Local adjustments in aggressive and sexual behavior must be particularly advantageous for species that inhabit complex communities, are widespread or ecologically generalized, and have high vagility or weak philopatry. Mechanisms for such adjustments already exist at the level of intraspecific acoustic signaling. It is likely that these are just taken over for interspecific functions, and that responses in sympathy are simply weakened or strengthened through local contingencies of reinforcement (see Miller, 1967, 1968).

Acoustic interference among species can also be reduced by ecological differences in spatial or temporal characteristics of signaling. The permissive role played by ecological differences is illustrated by Australian lyrebirds (*Menura*), which mimic species that breed and vocalize at a different season (Robinson, 1973, 1974, 1975). It is improbable that acoustic interference ever effects substantial ecological differences (see also Orians and Collier, 1963). However, even ecologically similar species can reduce acoustic interference by using conventional encounter sites, or calling sites which differ in ecologically irrelevant ways, as in some anurans and insects (Littlejohn, 1977; MacNally, 1979; Parker, 1978; Saltho and Mecham, 1974). The two sibling species of Western Grebes may minimize interbreeding partly through local segregation of nesting colonies (Ratti, 1979; but see Nuechterlein, 1981), and different species of weaver finches (*Ploceus cucullatus* and *P. nigerrimus*) nesting in the same tree may likewise show clustering of nests (Crook, 1964). For species which advertise at low population densities, it may be unimportant to space out once a minimal distance from the nearest caller is exceeded. This probably applies mostly to large species, carnivorous species, and species in low-productivity environments (Harestad and Bunnell, 1979).

To summarize, high acoustic interference need not lead to character or variance shift in signal structure. Selection promoting shifts must often be blunted by nonevolutionary, facultative responses in signal form and reception, and by true evolutionary responses in spacing or timing which have minor ecological consequences.

True evolutionary convergence in social signals can be achieved by convergent character shift or expanded character variance. Where individuals that react aggressively and display effectively to ecologically similar heterospecífics have increased fitness, convergent signals (or mimicry) and interspecific territoriality could evolve (Cody, 1969, 1973; Marler, 1960; Moynihan, 1968; Rice, 1978a,b). This seductive outline has few supporting data, and has been severely criticized (Becker, 1977; Brown, 1977; Murray, 1971, 1976). In any case, the significance of adequately documented examples of convergence for the concepts of character and variance shift is obvious.
2. Shifts in Character Location (Character Shift)

a. How Are Sound Characteristics Likely to Diverge? Species may be under pressure to diverge even in relatively dissimilar signals if the signals occupy the same frequency band or are emitted at the same time and place. Signals which occupy the same frequency band can become distinct through differentiation of temporal features. Such differentiation is probably only opposed when physiological limits to sound production and reception are approached (Ewing, 1979; Littlejohn, 1977), or when temporal characteristics are closely adapted to environmental conditions. For example, the rate of trilling cannot increase freely in vegetated and other closed habitats because trills are so susceptible to reverberation (Richards and Wiley, 1980; Chapter 5, this volume). Despite such constraints, the evolution of sound distinctiveness based on temporal features is probably achieved fairly easily. The same is true of amplitude characteristics, though details of amplitude are unimportant in long-range communication (when acoustic interference among species is generally highest) because they degrade so quickly over distance (Wiley and Richards, 1978; Chapter 5, this volume). In contrast, divergence in the frequency domain is opposed by several factors.

First, attenuation of a signal is closely tied to its frequency spectrum, and this relationship is strongly affected by many environmental characteristics (Wiley and Richards, 1978; Chapter 5, this volume). Thus, the frequency spectrum of calls (especially long-distance calls) is generally closely adapted to optimal (often maximal) transmission in the prevailing environment, and there is probably strong selection against changes in it (Bowman, 1979; Hunter and Krebs, 1979; James, 1981). Indeed, adaptive differences in the frequency spectrum of song exist even among local populations of White-throated Sparrows (Zonotrichia albicollis) in habitats with different sound-transmission properties (Wasserman, 1979). Further evidence for the selective importance of effective transmission lies in the prevalence of dawn chorusing in numerous bird species, when conditions are best for long-distance acoustic signaling but when acoustic interference is greatest (Henwood and Fabrick, 1979). In addition, there is no evidence of partitioning of the audible frequency spectrum in complex anuran communities, despite their relatively simple calls (Littlejohn, 1977).

Second, calls should occupy a frequency band in which conspecifics have high auditory sensitivity. This conservative force may be strong in lower vertebrates (Hopkins and Bass, 1981; but see Myrberg and Spires, 1980), but may not be particularly important for homeotherms, where most sound processing occurs in

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12Adaptation of amplitude characteristics to local environments is suggested by Gish and Morton (1981), however. If individuals are under selection to conceal their distance from conspecifics while singing, it can be done most effectively if callers can retain degradable source characteristics in long-distance calls (see also Chapter 6, this volume).
the central nervous system (Nottebohm, 1976): auditory sensitivity functions are remarkably similar across bird species and typically correspond only roughly to frequency spectra of the same species' sounds (Cohen et al., 1978; Dooling, 1980; Dooling et al., 1978; Sachs et al., 1978; Chapter 4, this volume).

Finally, effecting a shift in frequency of a sound signal must usually entail a change in the size of sound-producing structures, which varies directly with body size across species in most taxa [see Bowman (1979), Eisenberg (1976), Hutterer and Vogel (1977), McGrath et al. (1972), Martin (1972), and Würdinger (1970); but not across Vireo solitarius subspecies: see James (1981)]. Frequency shifts may also necessitate changes in tracheal length, which can influence resonance frequency (Hinsch, 1972; Chapter 2, this volume). The ability of a population to respond to selective pressures favoring a shift in the frequency spectrum of its sounds is impeded further by the relationships among age, size, sound frequency, and auditory sensitivity. Within species, sound frequency declines with age (Schleidt and Shalter, 1973; Schubert, 1976a,b; Würdinger, 1970; Ehret, 1980) and bears an inverse relationship to body size among adults (Lanyon, 1978; Schubert, 1976a). In addition, cochlear microphonics for precocial and altricial species suggest increasing sensitivity to higher frequencies with age (Gates et al., 1975; Golubeva, 1978; see also Brown and Grinnell, 1980; Brzoska et al., 1977, Fig. 7).

When a species exhibits shift in acoustic signals, temporal features and time-varying characteristics of frequency are likely to change first. Major changes in frequency spectra of sounds are probably harder to effect, especially for long-distance signals, and changes in amplitude characteristics are easily achieved but are relevant mainly for short-range signals. The precise way in which shift comes about will be hard to predict. This depends on which characters are undergoing shift, and the effect of their change on receivers. But a general prediction can be made. Consider two species which are under equal pressure to diverge in a song character \( Y \), and which differ slightly in \( Y \) to begin with. In general, the evolutionary cost or difficulty of change is proportional to \( (\Delta Y / Y) \), so the species with the largest measure on \( Y \) should diverge most.

### b. Analysis of Character Shift

Most putative examples of divergent character shift in signals rest on a few variables for two related species. Some clear examples of such shift are in Section I, and more will be documented, especially for simple, special-purpose, low-dimensional signals. There are some general problems with this approach. First, low-dimensional sound signals are uncommon in general, and are certainly uncommon among birds. Second, sounds are probably adapted to the overall acoustic environment, and not just to sounds of related species; in any case, the joint effect of low community complexity with respect to related species and (acoustic) niche complementarity renders the likelihood of simple compensation among related species very low. Finally, compen-
sation can be achieved through reduced variance as well as by divergent character shift (Fig. 6C). Indeed, the potential for evolutionary change of variance may profoundly affect the possibility of character shift (Slatkin, 1980). All these considerations make the simultaneous examination of location and variance essential, except for extremely simple sounds (Section II,B,3,b).

3. Shifts in Character Complexity and Dispersion (Variance Shift)

a. Measurement of Variation and Complexity. The Fox Sparrow (Zonotrichia iliaica) is a monogamous species whose breeding range extends across North America. It consequently breeds in bird communities with very different levels of complexity, and its song characteristics also vary: in the simple terrestrial avifauna of Newfoundland, males average only 1 song type per male (Blacquiere, 1979); in Utah and Idaho, they average 3 (Martin, 1977). Syllable diversity per song (no. of syllable types/no. of syllables) varies accordingly, averaging 0.78 in Newfoundland and 1.00 in Utah and Idaho [based on data in Blacquiere (1979) and Martin (1977); see also Martin (1979)]. These observations suggest that the species has simpler emissions in simple sound environments. However, the trends are opposite for song complexity as estimated by song length (number of syllables) and number of syllable types, which are, respectively, 11.7 and 9.1 in Newfoundland, and 8.2 and 8.2 in Utah and Idaho (data sources are as above). Clearly, opposite interpretations could be placed on these trends.

The preceding example illustrates the importance of the way in which complexity is defined in assessing variance shift. There are numerous ways to construe and define complexity, not all of which are applicable when studying variance shift. Two different questions must be addressed: in what characters should complexity be estimated?, and, how should complexity be estimated? (See also Chapter 5, Volume 2.)

Characteristics chosen for measurement depend on the level of integration in which a worker is interested. In bird songs, the smallest unit recognized is usually a temporally continuous utterance (syllable). Even at this level, simple and compound measures on frequency (F), amplitude (A), and time (T) must be evaluated. For example, the simple song of the Grasshopper Warbler (Locustella naevia) is a sequence of rapid, rhythmical repetitions of two alternative types of pulses, and may last up to 2 min. The second pulse in each couplet is about 6 msec long and has a characteristic amplitude envelope and signs of frequency modulation (Brackenbury, 1978). Given this typical sort of situation for even very simple syllables, it is clear that a single, uniquely derived measure of syllable complexity cannot exist: any such measure will reflect complexity in several domains (F, A, and T) among which interaction can occur. Thus, similar estimates of complexity for two syllable types may be due to different contribu-
tions from the three domains, different patterns of covariation, etc. Complexity at higher levels of integration can obviously be even more varied, and a single comprehensive measure of complexity (e.g., song complexity) will be even more elusive. In practice, measures of sound complexity must be based upon chosen characteristics. It is imperative that the level of integration is explicit (e.g., syllable, phrase, . . . . , song, song repertoire), and desirable that complexity be assessed in various ways and for each domain separately, as far as possible.

There are numerous ways to view, measure, and represent variation and complexity (see also Chapter 5, Volume 2). For continuous variables, conventional measures are standard deviation (or standard error, or variance) and coefficient of variation (CV). The latter is used when variables being compared have different means, on the assumption that the magnitude of the CV is independent of the mean (this assumption is rarely tested in ethology). There have been numerous univariate statistical treatments of continuous variation in bird sounds (e.g., Bergmann, 1976; Johnson, 1980; Konishi, 1964; Marler and Isaac, 1960a,b, 1961; Payne and Budde, 1979; Shiovitz, 1975; Smith et al., 1980). Multivariate statistics of variation are also available (van Valen, 1974, 1978) but none has been used in ethological studies, to my knowledge.

Variation and complexity can also be expressed through various diversity and information-theoretic measures, for both continuous and discrete data. These are treated in many texts and review papers (e.g., Colgan, 1978; Hazlett, 1977; Pielou, 1975, 1977). Some (notably the Shannon–Wiener information measure, $H'$) have been widely used in the analysis of signaling, and may prove useful in studying variance shift. For example, predictability and redundancy are important attributes of animal sounds which may be modified in sympatry, and both have formal expressions derivable from $H'$. Other approaches can be applied to sequential complexity: recurrence intervals, time-series analyses, formal grammars, etc.

There is a plethora of quantitative methods available for documenting and analyzing structural variation, and none is natural and “best.” The variation and complexity in sound properties being assessed may be expressed differently according to the measure chosen. For example, “diversity” indices are not all

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13Barlow (1977, p. 101) suggests a converse measure of stereotypy $ST = \frac{P}{(SD + 0.01P)}$, which has the undesirable property of being a curvilinearly decreasing function of CV.

14Reliability and repeatability of measurements on sonagrams are low. Measurement error and bias are particularly likely to lead to spurious differences in variation between frequency and temporal measures, and between brief and long calls in temporal measures. This matter merits close scrutiny, since sonagrams are the main display used for measurement. Alternative forms of sound analysis are probably necessary for adequate study of continuous variation in sound characteristics, especially for brief sounds with rapid frequency shifts.

15Routledge (1980) suggests that the Simpson index is preferable to the Shannon–Wiener index for estimating ecological α diversity and for enabling comparison of diversity estimates.
concordant and emphasize or measure different properties of a collection (Hurlbert, 1971; Routledge, 1979). Similarly, "redundancy" may be evaluated in a correlational or a sequential sense. The most important procedure in evaluating variation and complexity is the specification of their level and nature appropriate to the hypothesis being tested.

b. Ecological Analogs. It is easy to analogize sound characteristics with ecological roles, and hence acoustic with ecological space. The analogy provides conceptual and analytic approaches from ecology for studying overlap and variation in sound signals.

Hypothetical utilization functions \( u \) for resource \( j \), by species 1 and 2 are shown in Fig. 6A. The means of \( u \) are separated by distance \( d \), and the overlap between the species is determined by this value and the standard deviation \( \sigma \) (estimated by \( w \)). The unidimensional overlap value, \( \alpha_{12} \), is estimated as \( C \exp \left[-d^2/2 \left(w_1^2 + w_2^2\right)\right] \), where \( C \) is a normalization constant \( = f(w_1, w_2) \) (May, 1974). It is straightforward to extend this to multidimensional overlap, assuming a common covariance matrix (Harner and Whitmore, 1977). This assumption, however, is probably rarely met with for acoustic variables, and more

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16This expression is not generally used in ecology, where multistate categorical resources are recognized and overlap across them is measured (Hurlbert, 1978; May, 1975).
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complex computations involving the substitution of \( \alpha \) into the formula for the \( p \)-variate normal density are necessary (G. Sugihara, personal communication). In any case, overlap as measured in these ways obviously depends simultaneously on location and dispersion, and in the simplest case varies inversely with the ratio \( d/w \) (Fig. 6B and C). Overlap (\( \alpha \)) declines as \( d/w \) increases, and declines most rapidly at \( d/w = \sqrt{2} \) (Fig. 6B). Even where \( d = 0 \), \( \alpha \) is less than 1.0 if \( w_1 \neq w_2 \) (Fig. 6D, upper).

This approach is applicable to sound characteristics, but two further points must be made. First, overlap must generally have unequal effects on species. Thus, the rarer of two species will be affected most by their overlap (Fig. 6D, lower). The same effect is present if two species are equally abundant, but their overlapping sound signals have different effects on fitness (e.g., the signals have different functions, or they have equivalent functions with different quantitative effects on fitness, or some combination of these). Second, overlap \( per se \) may not be necessary for acoustic signals to be under pressure to diverge or contract. Sounds which are similar to one another (small \( d \)) but are nonoverlapping may still cause some confusion in receivers, and lead to reduced fitness of similar-sounding emitters.

Overlap between most bird sounds cannot be realistically assessed by univariate analysis, because of their complexity. Consider another simple ecological analogy, where species 1 and 2 overlap on resource axes \( i \) and \( j \). The species' two-dimensional overlap is determined by the direction and strength of the correlations between the separate utilization functions (Fig. 7).

Overlap and possible interference between heterospecifics cannot be predicted on the basis of overlap between the species to which they belong. This is because a species may have small or large \( \sigma \) (corresponding to a "specialist" or "generalist," in ecological terms), which has no fixed relationship to how specialized or generalized individuals are. Overlap in sound signals and resource use affects individual fitness, so it is clearly necessary to consider within- and among-individual components of variation [cf. within- and between-phenotype components of variance recognized by Roughgarden (1972)]. In general, we predict that competing species in sympatry will show reduced population and individual variances (the latter assumes that some level of individuality is favored, and that a species' variance is reduced; see Chapter 8, Volume 2).

To interpret the relationships of individual and population variation to sympatry, it is necessary to establish baseline measures. I do this here by analyzing variation in simple calls of two species. The Black-legged Kittiwake (\( Rissa tridactyla \)) emits a loud, stereotyped, and individualistic call when at the nest site, or when approaching and landing there. The species is densely colonial, and individuality in the landing call is important in communication within mated pairs. Kittiwake colonies include few other species, so landing calls need not encode species identity. These conditions provide for high individuality which
Fig. 7. Relationship of one-dimensional overlap between utilization curves of two species (1, 2), on resource axes $i$ and $j$, to two-dimensional overlap. The direction (and strength, not varied in this figure) of correlations between separate resource utilization functions determines whether higher-dimensional overlap is low (A) or high (B). (After Fig. 7.8 of Pianka, 1978.)

can be estimated by the percentage variation among groups, $100s_A^2/(s^2 + s_p^2)$, where $s_A$ is the added variance component among groups (here, among birds) in one-way analysis of variance (model II) [this approach has been used extensively by Jenssen (1979); see also Chapter 8, Volume 2].

Kittiwake calls include five distinct temporal components ($a - e$), and show strong differences among individuals in tonality, noise, and other spectral features (Fig. 8) (Wooller, 1978). Analysis of variance on the durations of temporal components reveals a range in percentage variation among groups of 30–68 (30–58 for males, 37–68 for females; Table III). These figures point to components $b$ and $d$ as having the highest variation among birds (for each sex), hence as being likely variables to encode individuality. Furthermore, the analysis establishes estimates against which others can be compared. Landing calls are fairly complex and occur at short range, so they are supplemented by visual sources of information. A logical comparison is with a species which differs on both points.

The American Woodcock (Scolopax minor) presents a simpler situation. Like kittiwakes, the American Woodcock faces no problems of species misidentification. Males emit nasal peent calls during mate-attraction displays at dusk (Mendall and Aldous, 1943; Sheldon, 1967). The calls are structurally simple, and because of their long transmission distance and crepuscular emission, are not accompanied by visual display components (Fig. 8). In brief, the peent call is a very low dimensional display, so would be expected to be more individualistic than the landing call of the kittiwake. Here though, advantages to individuality lie in attraction of females and repulsion of competing males. Individuality in peent calls may enable woodcock to be accurately censused, so considerable research on this matter has been done (Beightol and Samuel, 1973; Bourgeois,
Character and Variance Shift in Acoustic Signals

1977; Bourgeois and Couture, 1977; Samuel and Beightol, 1972, 1973; Thomas and Dilworth, 1980; Weir, 1979; Weir and Graves, 1981). Data of Bourgeois (1977) indicate substantially higher percentage variation among male woodcock than among kittiwakes, as predicted (range 65–90%; Table III). Again, some variables are much more individualistic than others.

Approaches which address questions about both character location and dispersion may prove to be valuable in exploring shift. A simple situation which can be

TABLE III

Percentage Variation among Groups for Landing Calls of Black-legged Kittiwake (Rissa tridactyla) and Peent Calls of Male American Woodcock (Scolopax minor)

<table>
<thead>
<tr>
<th>Variable (duration of components)</th>
<th>R. tridactyla</th>
<th>S. minor</th>
<th>Variable</th>
</tr>
</thead>
<tbody>
<tr>
<td>e, male</td>
<td>29.8</td>
<td></td>
<td></td>
</tr>
<tr>
<td>e, female</td>
<td>36.8</td>
<td></td>
<td></td>
</tr>
<tr>
<td>a, male</td>
<td>43.4</td>
<td></td>
<td></td>
</tr>
<tr>
<td>c, male</td>
<td>48.9</td>
<td></td>
<td></td>
</tr>
<tr>
<td>c, female</td>
<td>56.0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>d, male</td>
<td>56.8</td>
<td></td>
<td></td>
</tr>
<tr>
<td>b, male</td>
<td>57.6</td>
<td></td>
<td></td>
</tr>
<tr>
<td>a, female</td>
<td>58.6</td>
<td></td>
<td></td>
</tr>
<tr>
<td>d, female</td>
<td>60.8</td>
<td></td>
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</tr>
<tr>
<td>b, female</td>
<td>68.0</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>65.3</td>
<td>F3</td>
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</tr>
<tr>
<td></td>
<td>66.8</td>
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<tr>
<td></td>
<td>68.1</td>
<td>FC</td>
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<td></td>
<td>71.6</td>
<td>FD</td>
<td></td>
</tr>
<tr>
<td></td>
<td>86.6</td>
<td>total no. of pulses</td>
<td></td>
</tr>
<tr>
<td></td>
<td>88.7</td>
<td>total duration</td>
<td></td>
</tr>
<tr>
<td></td>
<td>89.6</td>
<td>T</td>
<td></td>
</tr>
<tr>
<td></td>
<td>90.4</td>
<td>rate of FM (= 1/DP)</td>
<td></td>
</tr>
</tbody>
</table>

a Letters a to e represent temporal components recognized by Wooller (1978) (see Fig. 8).

b Analyses were based on 50 calls by each of 25 males and 25 females, raw data on which were provided by R. D. Wooller.

c Analyses were based on seven to ten calls by each of eight males, from data in Tables 1 to 4, and Appendix Tables 1 to 5 of Bourgeois (1977).

d Measurements were taken on sonagrams for which the bandpass filter was 300 Hz, and intensity contours differed by 6 dB (area of maximal intensity, 36–42 dB). $F_p$, minimal frequency at the start of the 24- to 30-dB contour; $F_{C_{50}}$, frequency 5 mm after the start of the 36- to 42-dB contour, and centered vertically; $F_C$, frequency in the center of the 36- to 42-dB band; $F_D$, frequency 5 mm before the end of the 36- to 42-dB contour, and centered vertically; $T$, duration of the 36- to 42-dB band; and $DP$, mean duration of ten pulses in the center of a call [see Fig. 5 of Bourgeois (1977) and Fig. 1 of Bourgeois and Couture (1977)].
Fig. 8. Representative landing calls of four Black-legged Kittiwakes (Rissa tridactyla; upper, A--D) and peent calls of two male American Woodcock (Scolopax minor; lower, A and B). Each call is shown as wide band (300 Hz, on left) and narrow band (45 Hz, on right) sonagrams, and as an oscillogram (below). Time markers below the representations are expressed in milliseconds. Lettering (a--e) for R. tridactyla indicates temporal measurements discussed in the text and Table III (e = interval to next call; after Fig. 4 of Wooller, 1978). This figure was made from tape recordings of R. tridactyla in England, by R. D. Wooller, and of S. minor in Quebec, by J.-C. Bourgeois.
analyzed more comprehensively is needed. I do not know of an adequate data set for birds, but one exists for two sibling species of fiddler crabs, *Uca panacea* and *U. pugilator*. These species are syntopic in parts of Florida, and *U. pugilator* is in the minority. *Uca panacea* occurs from Florida to Texas, and *U. pugilator* occurs from Florida to Massachusetts. Courting males attract females to their burrows by waving the major cheliped. When a female is near, males vibrate the claw rapidly against the substrate (*U. pugilator*) or first walking leg (*U. panacea*) (Pawlik *et al.*, 1980; Salmon *et al.*, 1978).

The pulse repetition rate in *U. panacea* is about 24 Hz in allopatri and sympathy, but in *U. pugilator* is 9.4 in sympathy and 11.6 in allopatri, suggestive of divergent shift [analyses discussed here and below are based on Tables 1 and 2 of Salmon *et al.* (1978) and raw data of M. Salmon]. *Uca pugilator* shows slightly less variation among males in sympathy than in allopatri, as predicted (54.5 versus 58.7%), but the trend is strongly reversed for the majority species, *U. panacea* (51.1 versus 40.9%; based on one-way analyses of variance). Other analyses yielded the following results:

1. *Uca pugilator* exhibits a reduced population variance in sympathy, as predicted, but *U. panacea* does not.

2. Individual males are not less variable in sympathy than in allopatri, for either species, contrary to prediction. The data plotted in Fig. 9 are in the predicted direction, but are not statistically significant.

In summary, there is a suggestion of divergent character shift and reduced population variance in sympathy for the minority species, *U. pugilator*, but no evidence of reduced individual variation in either species. This example was discussed at some length because it involves sibling species with limited learning.

Fig. 9. Relationship of variation in pulse repetition rate within male fiddler crabs (*Uca*), to sympathy (symp.) and allopatri (allop.). The right vertical scales in each diagram refer to the cumulative frequency plots. The coefficient of variation (CV) was used for *U. pugilator* because pulse repetition rate differed between allopatri and sympathy; the CV's are statistically independent of means for this data set. (Based on Tables 1 and 2 of Salmon *et al.*, 1978, and raw data of M. Salmon.)
abilities and simple acoustic signals, all of which increase the likelihood of adaptive adjustments of variances and means. The analytic results of this and the preceding example are promising; research on variance components in chosen sounds across communities could yield insight into the bioacoustic community structure of birds.

III. CONCLUDING COMMENTS

In this chapter I have suggested that shift is not a unitary phenomenon, that two components of shift be recognized and dealt with analytically, and that shift be appreciated as a special case of coevolution. Shift in acoustic signals of birds is probably less common and important than generally thought: high dimensionality of most avian sound signals and multimodality of much avian signaling reduce the necessity for divergent shift or contraction; the physical environment is important in selecting for physical characteristics of sounds, and the social environment is important in selecting for various forms of sound complexity; spatial and temporal fluctuations in ecological factors yield variations in avifaunal characteristics to which close adaptation of sound signals is unlikely; facultative responses must often effectively reduce acoustic competition and interference; and sounds of syntopic species are usually sufficiently different anyway, adaptive adjustment being unnecessary.

Based on these considerations, we predict that measurable shift is most likely in low-dimensional, long-range, unlearned sound signals of species in fairly simple and constant environments, where richness and evenness of the avifauna are high. Shift should be especially pronounced in long-range sounds used in mate attraction and (secondarily) territorial advertisement, in avifaunas which include many related species. Temporal features and characteristics of frequency modulation are most likely to undergo shift.

The mere documentation of species differences which conform with predictions in the last paragraph is inadequate for the inference of shift, however (Green and Marler, 1979). Consider the Red-headed and Downy woodpeckers (*Melanerpes erythrocephalus* and *Picoides pubescens*), which are broadly sympatric and simply drum with the bill on a substrate in long-distance signaling. Some of the likely important dimensions of this simple sound are duration, number of pulses, pulse repetition rate, and pulse interval, several of which differ strongly between the species (Table IV) (Crusoe, 1980). The simplest explanation of these trends is that the species evolved differently; there is no basis for invoking shift or other evolutionary accommodation. In any case, considering variation in avian community characteristics, examination of only two species might generally be pointless. The study of signal structure at the community level has begun for anurans (Hödl, 1977; Rand and Drewry, 1972) and mormyrid fish (Hopkins, 1980, 1981). Steiner (1979) notes that those spe-
TABLE IV
Characteristics of a Low-Dimensional Sound Signal (Drumming) in the Broadly Sympatric Red-Headed and Downy Woodpeckers (Melanerpes erythrocephalus and Picoides pubescens)\textsuperscript{a}

<table>
<thead>
<tr>
<th>Variable</th>
<th>M. erythrocephalus</th>
<th>P. pubescens</th>
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</thead>
<tbody>
<tr>
<td>Pulses per drum</td>
<td>14.7 ± 0.18</td>
<td>14.8 ± 0.21</td>
</tr>
<tr>
<td>Pulse train duration (dsec)</td>
<td>6.4 ± 0.08</td>
<td>8.7 ± 0.14</td>
</tr>
<tr>
<td>Pulse repetition rate (Hz)</td>
<td>20.8 ± 0.04</td>
<td>16.0 ± 0.09</td>
</tr>
<tr>
<td>Pulse interval (msec)\textsuperscript{b}</td>
<td>47.9 ± 0.04</td>
<td>63.0 ± 0.11</td>
</tr>
<tr>
<td>Sample size</td>
<td>559</td>
<td>306</td>
</tr>
</tbody>
</table>

\textsuperscript{a} Data are listed as $Y \pm SE$, and are based on data in Crusoe (1980).

\textsuperscript{b} Data are based on 7655 pulse intervals from 559 drums of M. erythrocephalus and 4217 intervals from 306 drums of P. pubescens.

cies of odontocete whales which have the widest distribution in the western North Atlantic have the most different calls, and those with narrow distributions (and which presumably encounter fewer other species) have less different calls (Table V). Similar approaches at the community level should also be applied to birds (Leroy, 1978, 1979).

A major hindrance to understanding the adaptedness of sounds to the bioacoustic environment is our ignorance of the behavioral significance of sounds and sound variants in the lives of different species. Without detailed studies of form, function and context, we cannot assume that sound qualities like constancy, predictability, and complexity have similar evolutionary significance across species or even populations [e.g., see Morton’s discussion of song of Carolina Wrens (Thryothorus ludovicianus) at different latitudes, in Chapter 6, this volume]. Nor can we assume that even major classes of sounds like song have comparable significance among related species. The study of character and vari-

TABLE V
Summary of Mahalanobis' Distance between Whistles of Five Species of Delphinidae (Odontoceti) from the Western North Atlantic\textsuperscript{a}

<table>
<thead>
<tr>
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<tbody>
<tr>
<td>Lagenorhynchus acutus</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Stenella plagiodon</td>
<td>3.1</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Stenella longirostris</td>
<td>2.8</td>
<td>1.8</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tursiops truncatus</td>
<td>7.6</td>
<td>6.2</td>
<td>7.1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Globicephala melaina</td>
<td>10.3</td>
<td>12.4</td>
<td>16.2</td>
<td>20.0</td>
<td></td>
</tr>
</tbody>
</table>

\textsuperscript{a} Mahalanobis' distance $D^2$ is the square of the Euclidean distance in $D$-space. Here, $D = 6$ for the variables beginning frequency, terminal frequency, maximal frequency, minimal frequency, duration, and number of changes between increasing and decreasing frequency. After Steiner (1979).
ance shift in bird sounds should begin with information on sound morphology, on the communicative contexts and significance of different sound types, and on the relationships of sound types and variants to fitness budget (e.g., Beer, 1975, 1976, 1980; Green, 1975; Lein, 1978, 1980, 1981; Smith, 1977). These matters should be examined across classes (age, sex, reproductive status, etc.), and considered against variations in species' ecological characteristics. The dynamics of acoustic interaction among species are diverse in kind, strength, predictability, and importance, and shifts are of correspondingly varied form and significance.

I feel that much evolutionary discussion surrounding character and variance shift, reproductive isolation, and species-specific attributes pays insufficient attention to the diversity of nonselective and natural selective processes underlying such patterns. For example, we have detailed knowledge of species-specific characteristics of short-range calls in some species of Anatidae and Phasianidae, through the fine research by Gottlieb and his colleagues (Gottlieb, 1979, and references therein; Miller, 1978; Miller and Gottlieb, 1976; see also Shapiro, 1980). Yet, we have no comprehensive understanding of whether or how species specificity in such calls (and responsiveness to them) has been selected for as such, why it is encoded in the characteristics it is, and so on. Character and variance shift, and related concepts, have been viewed as good evolutionary explanations for many observed natural patterns, but "the trouble about good answers is that people tend to look at problems in terms of answers they already know and which they expect or hope to find" (Birch, 1979, p. 197).

ACKNOWLEDGMENTS


REFERENCES


8. Character and Variance Shift in Acoustic Signals


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