

# Grading, Discreteness, Redundancy, and Motivation- Structural Rules

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I. Introduction .....	183
A. Differentiating between "How," "Why," and "What" Birds Communicate .....	183
B. Assumptions Derived from Ethology, Linguistics, and Information Theory .....	185
C. Is Communication a Sharing of Information, Manipulation, or What? .....	187
II. The Motivation-Structural Rules Model .....	187
A. Background .....	187
B. The Motivation-Structural Rules Model .....	188
C. Motivation-Structural Code and the Functions of Vocalizations .....	190
III. Grading, Discreteness, and Redundancy .....	191
A. Distance and the Motivation-Structural Code .....	191
B. Grading and Discreteness .....	192
C. Redundancy in Passerine Songs .....	196
IV. Summary Remarks .....	209
References .....	210

## I. INTRODUCTION

### A. Differentiating between "How," "Why," and "What" Birds Communicate

Interest in the evolutionary origins and adaptiveness of avian vocalizations has increased in the last decade. This interest is forcing a reexamination of old concepts and assumptions so that descriptions of how birds communicate can be

183

tied to the ultimate question of why they vocalize. We sometimes make assumptions when describing how birds are communicating that make it difficult or impossible to interpret these data from an evolutionary perspective. MacKay (1972, p. 3) sensed this when he stated "how can we avoid foreclosing empirical issues, and missing essential points. . . ., by our choice of conceptual apparatus and working distinctions? . . . in a new field, we must expect our concepts to need constant refinement, and must be alert for signs that something important is escaping us because our customary ways of looking at the phenomena have a significant 'blind spot'."

The ultimate question, "why," can be answered when we know the fitness benefits gained by the sender. Traditionally, the information in and function of vocalizations were assessed by studying the reactions of receivers and to do otherwise was considered anthropomorphic or nonoperational (Marler, 1961, 1967; but see Smith, 1977, p. 287). Communication involves the change in the sender and receiver during and immediately after their interaction, but the change of interest to the evolutionary biologist is the average increase in inclusive fitness the interaction brings to the sender. Selection does not favor a bird "sending" unless there is, on the average, a fitness benefit. Granted, there is value in studying "how" birds communicate but there is danger that, in the interpretation of the data, only fitness benefits shared by the sender and receiver will be brought out. How, what, and why questions should not be separated if the evolutionary history of communication is to be a focus.

Smith (1974, p. 1018) suggests that communication should be mutually beneficial to sender and receiver because:

In the evolution of communication within a species, one normal constraint usually is that the exchange of information must be useful to both the communicator and the recipient. The behavioral patterns evolved by the communicator enable him to transmit information that increases the probability of a social response suited to his needs. A recipient evolves the tendency to respond to this information only when the response suits his needs, which often differ, at least superficially, from those of the communicator. When their needs are not compatible, lack of selection pressure for the recipient to respond appropriately usually removes any advantages for the communicator, or at best yields an evolutionarily unstable situation of misinforming, to which recipients are always counter-adapting.

Smith emphasizes the mutual benefits of communication in his own work (see Smith, 1977) but, nonetheless, suggests the framework for an evolutionary approach in the quote above. What are the sender's needs, how do they differ from the receiver's, is there misinforming, and how are recipients counteradapting? An evolutionary approach involves only a change in emphasis: from downplaying these questions to focusing on them when interpreting data.

However, more than a change in emphasis is needed before communication studies conform to an evolutionary perspective more consistently. We must

critically examine some assumptions. I do this by presenting them in their historical perspective below before discussing discreteness, redundancy, and motivation-structural rules in communication.

## B. Assumptions Derived from Ethology, Linguistics, and Information Theory

In ethology, displays are defined as behaviors specially adapted for social signal functions (Moynihan, 1956). These adaptations included stereotypy and exaggeration, characteristics serving to make them conspicuous against background noise. Displays could be named, counted, and compared among species (Moynihan, 1970; Wilson, 1972), and variations in them were considered unimportant until recently (Barlow, 1977). Displays are said to appear and disappear over evolutionary time depending on their effectiveness in providing information in interactions (Moynihan, 1970). The form and number of displays characteristic of a species were often compared between species in making taxonomic judgements. Displays were viewed as species-typical characteristics with little attention given to how selection acting at the individual or genic level promoted particular displays. There was an interest in the evolutionary origins of displays from nondisplay precursors. Some visual displays and their precursors were extensively studied (e.g., Morris, 1956) but the precursors for particular vocalizations were not obvious and the ethological display concept did not provide an explanation for the origins of particular vertebrate vocalizations (Smith, 1977, p. 325).

The display concept was used as the logical background for hundreds of "vocalizations of" papers that listed vocalizations as stereotyped and named entities. Often the vocalization names were based on the apparent function of the sound or were given onomatopoeic names. Sounds were named so that they could be discussed, usually at the level of the species (e.g., the *caw*) but no adaptive significance was attached to their physical structure: a *caw* was considered to be arbitrary in structure like words are. I believe that people are uncritically comfortable with the concept of arbitrariness in animal sound structures due to our use of arbitrary sounds in speech. In Section II, I present some ideas that suggest that sound structures are not arbitrary.

Marler (1955) first countered the view that the physical structure of bird sounds is arbitrary by arguing that some sounds are structurally designed to provide clues to the sender's location while others are not. Recent studies on the adaptations of sounds for long-distance transmission have further reduced the veracity of the assumption that vocalizations have arbitrary physical structures (Morton, 1975; Marten *et al.*, 1977; Waser and Waser, 1977; Wiley and Richards, 1978).

Ethology has not produced a conceptual model or unifying theoretical framework for analyzing animal communication (Smith, 1977, p. 18). Ethologists used concepts derived from linguistics and information theory that were not based on evolutionary theory. From linguistics, zoosemiotics has, inadvertently, come to be used as a one-word equivalent of the study of animal communication (Sebeok, 1977, p. 1055). Information theory provided a mathematical framework within which a series of terms (e.g., channel, entropy, bits) were rigorously definable; even "information," a term that might better have remained ambiguous, was defined as the reduction of uncertainty. Game theory may replace information theory, even in the field of man-computer speech interfacing (Thomas, 1978). These nonevolutionary concepts led ethologists to separate the process of communication from other aspects of the biology of animals, aspects that provide the sources of natural selection acting on vocalizations and communication. The concept that senders provide and share information, and that displays contribute to the "orderliness" of interactions, pervades notable works on communication (e.g., Smith, 1977) with little consideration that these assumptions need verification or, at least, explanation.

An example will clarify what I have just said. Chickadees (*Parus* spp.) utter *chip* sounds that are termed "contact notes" when the birds forage in flocks during the winter. Contact note is a name given to the sound ascribing its function, to keep flock members together. We have an explanation for the sound: flock members share information about their locations and thereby stay in proximity, and receivers and senders are benefited because hawks cannot easily approach a flock undetected (Morse, 1973). But this explanation is a series of untested assumptions and is too general and vague to produce testable hypotheses. The *chip* is chevron-shaped when analyzed on a spectrograph, and when this sound structure is compared across many species the information conveyed is general: something of interest has been perceived by the sender (Morton, 1977). Therefore, another interpretation of contact notes is possible. The sender may *chip* when it discovers food or when it is moving rapidly from perch to perch, but the sender is benefited in either case if the movement of others away from the sender is slowed or if the *chip* attracts them toward the sender. For receivers, if food resources are sufficiently rich, responding to *chips* is advantageous in a trade-off between loss of foraging time and the predator detection benefit to being a flock member. This approach, emphasizing the importance of the sound's structure and differences in fitness benefits between sender and receiver, provides us with a series of testable hypotheses about the function of chips. This approach also places the communication within an ecological setting: food richness becomes important to our understanding of receivers' positive responses to these "contact notes." The study of communication thus becomes integrated with other aspects of biology.

### C. Is Communication a Sharing of Information, Manipulation, or What?

Why is it that cooperation among communicators, sharing beneficial information, is assumed by so many researchers? Above, I suggested that this might be due to a sort of "cryptic anthropomorphism" wherein human speech has influenced our thinking about animal communication. However, it is also likely that communicating birds do have the appearance of sharing information or cooperatively communicating. But, the evolutionary process leading to this appearance may have little to do with mutually beneficial information between sender and receiver. The appearance of cooperation in communication may be analogous to the appearance of cooperation in pairbonding. What used to be thought of as a cooperative, mutually beneficial series of behaviors resulting in reproduction "for the good of the species" is now viewed more as a contest between the sexes, and terms such as mate testing and anticuckoldry behavior are used to describe the "cooperating" effort of mating (e.g., Trivers, 1972).

Wallace (1973) suggested that vocalizations might be used to misinform. His model showed how signals that successfully misinform receivers may improve the signaler's relative fitness to the point where the entire population eventually consists of misinformers. Now, the formerly manipulative signal is used by all and has become a convention. The human observer may not find the original manipulative function and the signal's origins may be undetectable. However, if Wallace is correct, we should be able to detect new cases of misinformation for new forms should continue to arise.

Dawkins and Krebs (1978) suggested that the word "communication" as used by ethologists should be abandoned in favor of "manipulation." This may be an overemphasis of the fitness benefits derived from misinforming. Is a convention, in the sense described above, still a form of misinforming? Conventions and manipulative signals are vague terms and probably not readily distinguishable empirically but have conceptual value if they are viewed as components of communication. But perhaps Darwin's (1872) term, "vocal expression," is less biased than communication and might better indicate that the researcher is concerned with the evolutionary history together with the immediate process of communicating.

## II. THE MOTIVATION-STRUCTURAL RULES MODEL

### A. Background

My suggestion that the physical structures of vocalizations have significance for understanding vocal expression in vertebrates was published earlier (Morton, 1977). There I suggested that vocalizations given by living species, particularly

those used in close range, follow a structural code that was established long ago in the evolutionary history of terrestrial vertebrates. I suggested that in evolutionarily older vertebrates, such as amphibians and reptiles, which continue to grow after sexual maturity, call frequency may directly reflect body size. Thus large individuals tend to have dominant frequencies lower than those of small individuals (e.g., Martin, 1972; Zweifel, 1968). Vocalizations have subsequently been shown to operate as effective size indicators in *Bufo bufo* (Davies and Halliday, 1978) and *Physalaemus pustulosus* (Ryan, 1980). This is also likely in crocodylians (J. Lang, unpublished data). In the amphibians just mentioned, the lower-frequency calls of larger males function to repel smaller males or form the basis upon which females choose larger mates. In several *Hyla* species smaller males remain silent but position themselves near larger males that are calling to attract females (Fellers, 1979). These smaller males are, in effect, parasitizing the sound of large size to obtain matings.

The sounds used by aggressive birds and mammals are low in frequency, whereas fearful or appeasing individuals use high-frequency sounds (Morton, 1977). Size symbolism provides an explanation for the evolutionary origin of these vocalizations. But since size in homeothermic vertebrates is constant at maturity, relative to amphibians and reptiles, the use of low- or high-frequency sounds does not directly reflect differences in size between communicating individuals. Instead, the sounds are generally thought to reflect differences in motivation. I term the code suggesting the relationship between sound frequency and motivation, motivation-structural rules.

## B. The Motivation-Structural Rules Model

The model predicts that vocalization structures follow a simple code with two physical dimensions, one dimension pertains to sound quality and ranges from harsh or atonal to pure-tone-like, the second dimension pertains to sound frequency. The two dimensions may vary independently but are often synchronized such that the lowest-frequency sounds are harsh while higher-frequency sounds are tonal.

Figure 1 illustrates the relationship between sound structures and motivation showing the "endpoint" (lowest harsh and highest tonal) sounds with the intermediate sounds grading between the endpoints in structure and depicting a variety of intermediate vocal expressions. An aggressive motivation is expressed through a low, usually harsh, vocalization and a fearful or appeasing motivation with a high, tonal sound. If a sound increases in frequency, it expresses lowered aggressive tendencies; if it falls, it expresses increased aggressive tendencies.

I emphasize that Fig. 1 simply shows a sampling of sound structures at various motivational stages from aggressive to fearful, to illustrate the structural coding

## 6. Grading, Discreteness, Redundancy, and M-S Rules

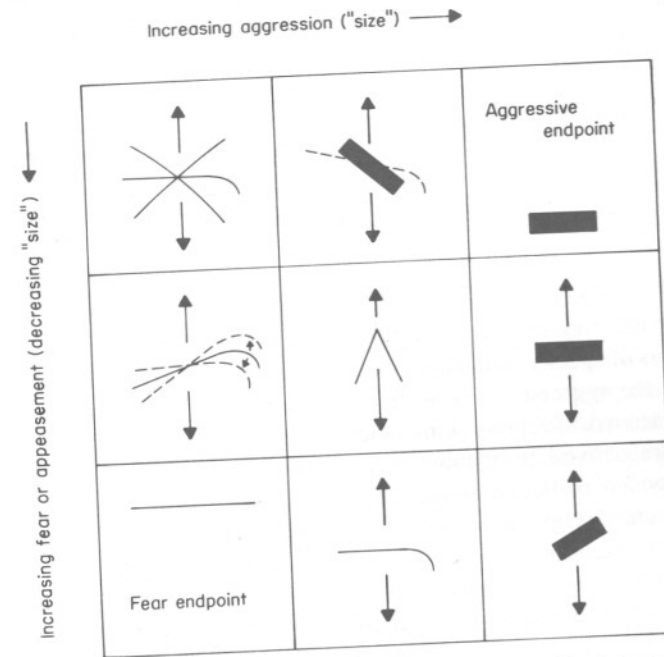


Fig. 1. A diagrammatic representation of sound structures to illustrate the motivation-structural code. Each block shows a hypothetical sound spectrogram (vertical scale, frequency; horizontal scale, time), with thin lines depicting a tonal sound and thick lines, harsh or broadband sounds. The arrows mean that the frequency of the depicted sound may vary up or down, approaching either the low- or high-frequency endpoints.

In the upper left block, motivation is weakly tending toward fear if the thin line slopes upward (its frequency rises) or weakly toward aggression if the slope is downward. In the middle left block, closer to the fear endpoint, sounds rise variously upward, between the dashed lines, and are tonal. The three blocks on the aggressive (right) side of the diagram are all broadband but the frequency is rising in the "distress" call, where fear and aggression are interacting. The central block depicts a chevron since the motivation and its sound structure are not nearer one endpoint than the other. (From Morton, 1977.)

of these moods. The potential combination of sound qualities and frequency changes is enormous.

The bark appears in the center and is characterized by a rise and fall (or fall and rise) in frequency. The rise and fall means that neither endpoint is being approached; therefore, unlike nonchevron sounds that tend toward one of the motivation-structural endpoints, barks symbolize neutral or adaptively indecisive motivation. Barks code arousal and interest but not necessarily motivational tendencies if they have an average frequency intermediate to the low and high endpoints. However, bark structures may also vary in frequency and sound

quality representing motivational tendencies toward either endpoint (e.g., Morton and Shalter, 1977). Barks function in a great diversity of contexts, for example, from precopulation and contact calling to mobbing, territorial defense, and alarm. A vocalizer may either attract or repel others by barking, depending on its species and context.

### C. Motivation-Structural Code and the Functions of Vocalizations

Through evolutionary time, various sound structures from the motivation-structural code may be favored by selection and become characteristic of the vocalizations of species, populations, or individuals. Some species might evolve to use only the aggressive end of the code while others use the entire code and others replace vocalizations with other communication modes. The selection pressures are derived from functional benefits to vocalizer fitness. Functions determine which particular sound structures will be used, what modifications may be adaptive (e.g., to enhance locatability or species distinctiveness), the contexts in which it is beneficial to use them, the amount of structural variation, and the timing of use or disuse during ontogeny. Functions can only be determined by studying living animals, of course, but comparative studies of closely related species can give some insight to the evolutionary time scale in which selection operates (Thielcke, 1976, p. 142).

However, the study of function apart from signal structure, as has been prevalent in the past, may not lead to an understanding of the evolution of vocal expression, for there is little basis for generalization (e.g., the *caw* of a crow and the *chip* of a sparrow would not be identified as barks with motivation-structural code similarity).

Selection may wed the motivation-structure code to function in ways that are subject to misinterpretation if only function and receiver reactions are considered. For example, a vocalization of the Herring Gull (*Larus argentatus*) termed the "food finding" call is reported to function in attracting other gulls to food (Frings *et al.*, 1955). In fact, single gulls remain silent when they locate food; it is only when potentially competing gulls are near that the call is given (J. Hand and E. Morton, unpublished data). Furthermore, a small single food item that can be swallowed immediately does not elicit a call from a gull finding it, while large items which a single gull is unable to swallow quickly do elicit the call. It seems unlikely that the "food finding" call functions to attract others since it is not given simply when food is found but only when other gulls are close enough to compete for the food. The call's structure is tonal and high in frequency, which the motivation-structural code predicts would be given by a frightened gull. The context, with other gulls coming in to chase the sender, seems consistent with the idea that the sender is frightened but this does not explain why

selection has favored the sender giving the call. What benefit does the sender receive? One hypothesis is that the call sometimes causes hesitation in the receivers, they may look for a predator, permitting the sender to grasp the food.

Another example is provided by the Purple Martin (*Progne subis*), a cavity-nesting colonially breeding swallow. Competition, often involving vicious fights, occurs over nest sites in "martin houses" provided by humans. The plumage of first-year males resembles that of females and they arrive at colonies several weeks after adult males have usurped nest sites (Rohwer and Niles, 1979). Young males encounter intense aggression by adult males when the former try to take nest sites (Johnston, 1966). During attempts to land on the martin house, it is common for young males to utter a series of high-frequency barks, identical to those elicited by dangerous predators (E. S. Morton, unpubl. data). This causes members to vacate, leaving time for the young male to enter a nesting cavity. A relatively high frequency bark is given by alarmed martins. In this case again, selection has favored the vocal expression of fear in a context where it is only of benefit to the sender.

What selection has favored in both gull and martin is the *vocal expression of mood*. The gull and martin probably are fearful: they experience aggression in the contexts described. There is no deceit involved on their part; their use of fear sounds in the two contexts may be manipulative in effect, but the sounds appear to truly reflect their motivational states. Selection has favored their vocal expression of this mood since reactions to it are often beneficial to them. In the gull and martin examples, receivers respond to the senders' calls because the average consequences of doing so are also of benefit to them, even if not beneficial in the specific contexts described. If this were not so, selection would favor receivers who ignore these sounds.

The motivation-structural code thus provides a basis to study the significance of sound structures in communicating birds. It provides an explanation of the historical origin of the physical structure of vocalizations that should be useful to researchers studying the functions of vocalizations.

## III. GRADING, DISCRETENESS, AND REDUNDANCY

### A. Distance and the Motivation-Structural Code

Marler (1967) and others have noted that long distance calls of birds tend to form discrete classes more frequently than do those used over short distances. As the distance between sender and receiver increases, small changes in sound structures will increasingly tend to be obscured by sound attenuation to the point that there is no selection pressure favoring the use of graded vocalizations. With sounds used only in long-distance communication, such as many passerine bird

songs, selection may favor the use of sound structures adapted for propagation across long distances that also code for species specificity. Thus selection favoring motivation coding may take a back seat for these distance-adapted sounds. When the sender is usually highly visible to receivers, long-distance calls may also contain the motivation-structural code and exhibit grading. Payne (1979), for example, reported the lowest and harshest songs of the Senegal Indigo-bird (*Vidua chalybeata*), a bird of open habitat, to be correlated with sender aggressiveness.

Vocalizations of the Carolina Wren (*Thryothorus ludovicianus*) show the relationship between variability of sounds within one class and the general distance between sender and receiver(s) (Table I). The sound classes are given onomatopoeic names (except song) with sound quality to the human ear indicated. The physical structures of sounds within each class are more variable in those sound classes used by birds close to recipients. The harsh quality sounds are more variable than sounds with a tonal quality. *Chirts* and *pi-zeets* may grade between classes as may *pees* and *scees*; grading occurs within but not between other classes. The two long-distance sounds, individual male songs and male *cheer*, are discrete, but each male has from 27 to 41 different songs.

## B. Grading and Discreteness

### 1. Grading

More attention is being given to the significance of graded sound structures to vocal expression as equipment to analyze long sequences of vocalizations has become available. Statistical techniques to analyze graded vocalizations are also being developed (see Miller, 1979, and references therein).

The motivation-structural code is followed both within and between vocalization classes. The vocalization classes in Table I show relatively discrete sounds that would have been called displays by earlier ethologists. The *growl*, *pee*, and *dit*, for example, are sound classes whose structures fit the aggressive endpoint, fear endpoint, and chevron-shaped bark, respectively, as shown in Fig. 1. Within-class variation is illustrated in Fig. 2. Here, *scees* (Table I) showing structural variation are being uttered by a male Carolina Wren losing in a fight with another male, who remained silent. During the first 12 sec of the fight (see Fig. 2) the losing male continually attempted to flee but was held by the strong feet of the winning male. The sounds during this time have a rising frequency and harsh quality. The sounds are similar to the structure diagrammed in the lower right block of Fig. 1, and show a high level of both fear and aggressive motivation. At 20 sec, the sounds do not consistently rise in frequency and at 22.5 sec the losing male pecked back. This was accompanied by a change in sound structure: the sound became greater in bandwidth and lower in frequency. The structure of the losing male's vocalizations followed his overt behavior in the ways predicted by

TABLE I

Sounds of the Carolina Wren (*Thryothorus ludovicianus*) Arranged in Order of Decreasing Sender to Receiver Distance

Sound	Distance from sender to receiver	Sound structure	Structural variation within sound class
♂ Song	Long	Tonal	None
♂ Cheer	Long to medium	Tonal	None
♀ Chatter	Medium to short	Harsh	Little
♀ Dit	Medium to short	Tonal	Little
♂ Dit	Medium to short	Tonal	Little
Rasp	Short	Harsh	Great
Chirt	Short	Tonal to harsh	Great
Pi-zeet	Short	Tonal to harsh	Great
Tsuck	Short	Tonal	Little
Nyerk	Short	Harsh	Great
Scee	Short	Tonal to harsh	Great
Pee	Short	Tonal to harsh	Great
Growl	Short	Harsh	Moderate

the motivation-structural code. Morton (1977) and Morton and Shalter (1977) discuss grading in other species and vocalization classes of the Carolina Wren as examples of the motivation-structural code. Miller and Baker (1980) describe graded calls of the Magellanic Oystercatcher (*Haematopus leucopodus*) and suggest that grading provides a "high information content." In the Common Loon (*Gavia immer*) gradation in the tremolo call indicated the probability that the calling bird would attack. Higher frequencies indicated a greater reluctance to attack (Barklow, 1979). Perhaps the most intensely studied avian graded vocalization system is that of the Northern Jacana (*Jacana spinosa*) with five of six vocal classes grading into one another (Jenni *et al.*, 1974). Jenni *et al.* discuss the problems of subjectivity encountered when attempting to categorize such an extensively graded vocal system.

### 2. Discreteness

When classes of vocalizations do not grade they are termed discrete, but this designation is a relative term and should not imply that no variation exists. Often birds are said to have discrete vocalizations relative to mammals (Marler, 1967). This apparent difference between the two groups could be related to differences in vocal tracts: mammals have flexible pharynges with a high potential for resonating sounds; birds have relatively rigid tracheas with little resonating potential (Greenewalt, 1968). Therefore, mammals are able to vary sound structures through resonance changes without changing tension in the vocal membranes.

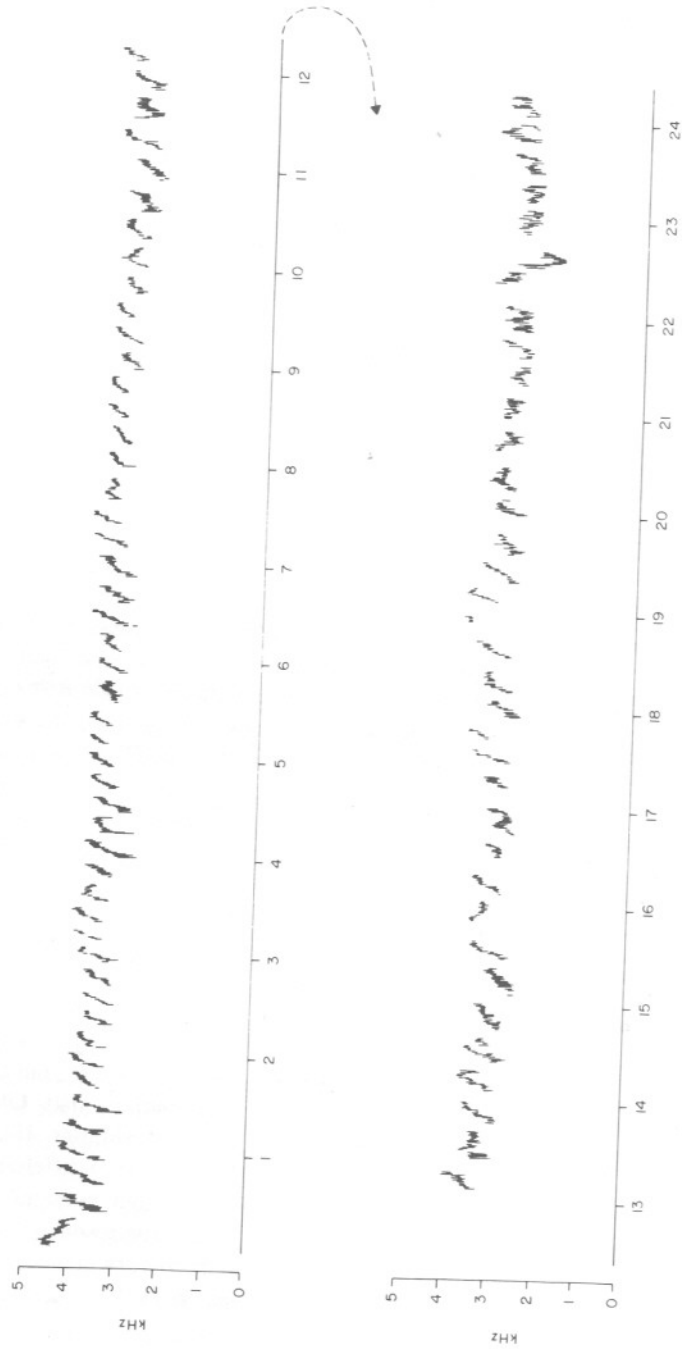


Fig. 2. A graded sound sequence produced by a Carolina Wren being defeated by another in a fight. The sharp drop and then rise in frequency near 22.5 sec occurred when the bird pecked back at his assailant.

In birds there may be, in addition, a relationship between the frequency and quality of vocalizations and discreteness. Low-frequency sounds may acquire a broadband spectrum and hence a harsh quality when tension on the vibrating membrane producing them falls low enough to produce nonharmonically related tones. If this observation were raised to the level of a prediction, a dilemma would arise, since in small birds their lowest frequency sounds are generally low in amplitude and used while senders are close to receivers. Sounds used at close distances tend to be graded apart from their frequency (Section III, A). Carolina Wren sounds show a tendency for harsh vocalizations to be used over short distances and exhibit the most grading (Table I). The question of why selection favors either graded or discrete vocalizations in particular contexts remains open. So far, the only general prediction is related to communication distance.

Discrete vocalizations may be combined to produce structurally complex vocal expressions. The *chickadee* call of the Black-capped Chickadee (*Parus atricapillus*) provides an example (illustrated in Ficken *et al.*, 1978). The call consists of two to four chevron-shaped notes ("chicka") that decrease in frequency followed by still lower frequency and harsh "dee" sounds. These components are also used separately, which is why the call is termed compound (Ficken *et al.*, 1978). Using the motivation-structural code, I would describe the sound as a series of barks followed by low, harsh sounds. The barks indicate that the sender has perceived something of interest, with the decrease in their frequency indicating increasing aggressive tendencies. The last notes are indicative of an aggressive motivation but not at the aggressive endpoint, for this species' repertoire contains lower frequency and harsher sounds used in fighting (the *snarl* described in Ficken *et al.*, 1978). The motivation-structural code suggests that whatever stimulus elicited the call, the sender is interested in it, and it is not something that causes fear in the sender, or movement away from it, as indicated by the broad-band, aggressive, structure/mood relationship. The call is used most frequently by individuals in flocks during the nonbreeding season, apparently in situations of mild alarm (Ficken *et al.*, 1978). In the presence of stimuli that elicit a compound sound with these motivation-structural components it may benefit the sender to attract other chickadees, which, indeed, is the function of the *chickadee* call (Ficken *et al.*, 1978).

Figure 3 illustrates nine discrete calls of three different structures uttered rapidly in 2 sec by a captive 3-day-old Black Crake (*Limnocorax flavirostra*). The use of such differing sound structures in such a short time period would seem difficult to explain. In the wild, or when reared by parents in captivity, 3-day-old crakes are fed by their parents and the chicks compete for parental attention and the food they peck from the parent's beak (E. S. Morton, unpublished data). When this chick was not being fed by us, it uttered only the chevron-shaped barks recorded in Fig. 3; they sound like the *peeps* common to Domestic Fowl (*Gallus domesticus*). The crake uttered the two other sounds described in Fig. 3

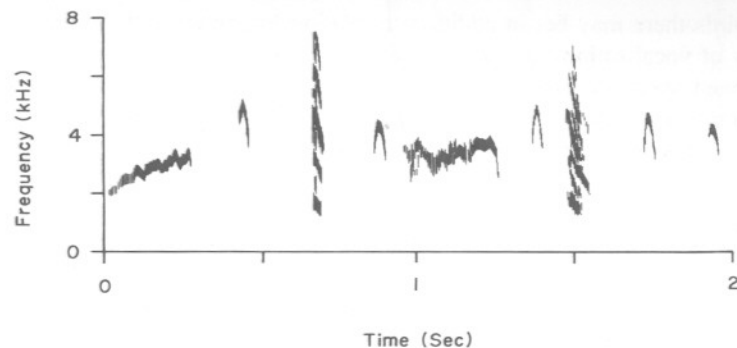


Fig. 3. Three structurally divergent sound types of a captive 3-day-old Black Crane (*Limnocorax flavirostra*) approaching a forceps holding food (see text).

only when we approached it with forceps holding food. From time 0 to 1 sec, the chick used a rising tonal sound when seeing the forceps, then a bark, then a broadband call dropping in frequency. This sequence is repeated again from 1 to 2 sec as indicated in Fig. 3. I believe it is the natural context of parental feeding plus sibling competition that explains this sequence of widely varying components from the motivation-structural code. The rising tone might be due to increasing fear or appeasement directed toward the parent, followed by a bark when the food (item of interest) is approached, followed by an aggressive sound structure just following food taking at both 0.7 and 1.5 sec (Fig. 3). The aggressive sounds might function to ward off siblings competing for the food.

## C. Redundancy in Passerine Songs

### 1. Songs and the Motivation-Structural Code

The mechanisms by which songbirds produce their high-amplitude songs are not well known and are under debate. The debate is over the contribution of syringeal membrane vibration versus an aerodynamic whistle mechanism in song production (A. Gaunt, unpublished data). The whistle mechanism, using aeolian forces to produce sound, is capable of explaining the high source amplitudes songbirds produce in their far-carrying songs. But high source amplitude may be more important to our understanding of the functions and evolution of song than solely as an accouterment to increase sound propagation.

If songbirds use aeolian forces to produce song, then sound amplitude takes on greater importance in symbolizing large size than does sound frequency. For a whistle of a given size, the greater the airflow rate through it, the higher the sound amplitude produced. Also, the frequency of sound produced increases

directly with airflow rate, as anyone who has blown a whistle knows. Therefore, a larger animal might symbolize its size advantage or aggressive motivation by illustrating its ability to produce a call with higher frequency and amplitude than those of another animal if the sound is produced by aeolian forces. Rats (*Rattus norvegicus*), which produce their ultrasonic calls using aeolian whistle mechanisms, use an 80-kHz call when aggressive and about a 20-kHz call when losing a fight (Roberts, 1975). Since the motivation-structural code stresses the relationship between aggressive motivation and low sound frequency, when the sounds are produced by vibrating vocal membranes, I would like to think that the use of high sound frequency by aggressive rats, using an aeolian sound production mechanism, is the exception that "proves the rule."

The importance of sound amplitude to our understanding of song function and evolution will remain little known until sound production mechanisms are better understood. However, Kroodsma (1979) argues convincingly that amplitude was related to dominance and to "leader/follower roles" during song matching in Long-billed Marsh Wrens (*Cistothorus palustris*).

### 2. Redundancy and Song Function in the Carolina Wren

Oscine song behavior is remarkable for its diversity of singing styles and repertoire sizes (Hartshorne, 1973). I want to focus on the singing behavior of the Carolina Wren, a species with a male song repertoire averaging 32 songs within a range of 27–41 for a sample of 15 males (Chu, 1979). What is the selective value and function of this *redundancy*: having more than one song type with seemingly identical functions? Only males sing in this species, the only member of the genus to reach the temperate zone latitudes, but in the 17 tropical species females also sing, often duetting with their mates (E. S. Morton, unpubl. data). Most tropical passerines are permanently pairbonded and their songs function in territorial defense (Morton, 1980). In species with female and male song, songs seem to be directed toward like-sexed territorial intruders (see Chapter 4 by Farabaugh, Volume 2).

Perhaps there has been a temperate zone bias in the determination of song function, when mate attraction is suggested as one main function of song? In the Carolina Wren, males may form pair bonds even when they are too young to sing fully developed songs and then continue singing throughout the year even while they are constantly paired (Morton and Shalter, 1977). Territorial defense is also a permanent feature of this wren's social system. The Carolina Wren ranges from Maine to Florida, west to central Oklahoma, south to southern Tamaulipas, Mexico, with separated populations in Yucatan, Mexico, and portions of Guatemala and Honduras.

The structural features of the song used in species recognition are not well known but, through playbacks, I determined that songs from widely separated populations are responded to by any Carolina Wren as conspecific. Yucatan



wrens responded to songs from Maryland and Florida wrens and vice versa. But at the local population level, 66–75% of the 32 song types in a male's repertoire are held in common with one or more neighboring males. Repertoire sharing results from young males settling near established males and copying their songs (Helgeson, 1980), just as Kroodsma (1974) described for the closely related Bewick's Wren (*Thryomanes bewickii*). The percentage of songs held in common among males decreases directly with distance. Chu (1979) determined that males 100 km apart have only 20–25% of their song types held in common, if the sampled males are connected by continuous wren populations. If the wren distribution is not continuous, for example, if an island population is compared to a mainland population 3 km distant, only 12% of the songs are held in common. Some songs are unique to a single male wren, most songs in an individual's repertoire are held in common with neighbors, as mentioned, but about 3% of the songs have a much wider geographic range for reasons that are not clear. These few song types were found throughout the 140-km linear transect studied by Chu (1979).

With the above information in mind, I now describe how individual males use their songs before offering an hypothesis to explain the function and adaptive significance of redundancy in Carolina Wren singing.

Males repeat the same song type from a few to many times before they switch to another song type. The highest number of repetitions I have observed is the singing of one song type 206 times for a duration of 21 minutes without a break. A repetition of the same song type is called a bout (AAA . . . BBB . . . CCC . . .). Kroodsma (1977) has compared singing styles in North American wrens; the Carolina Wren has a song of low complexity along with the Cactus Wren (*Campylorhynchus brunneicapillus*) and the Rock Wren (*Salpinctes obsoletus*), since each song consists of the repetition of one syllable type. Carolina Wren song bouts are lengthier from awakening to about 1000 hr after which the bouts are shorter with more nonsinging time between each bout (Table II).

It takes an observer about 2 full days to record all of the song types in a male's repertoire, or about 75 bouts of singing (Chu, 1979; E. S. Morton, unpublished data). The important point is that the singing behavior does not seem to maximize the potential diversity of songs a male could sing. Thus, the question of why Carolina Wrens have so many song types does not seem to be answered by the antihabituation hypothesis (e.g., Krebs, 1976), which states that large song repertoires reduce the chance that listening conspecifics will ignore a male's songs through classical habituation. Certainly, that hypothesis does not explain the large size of the wren's repertoire: most commonly studied temperate zone passerines with redundant repertoires have fewer songs, usually about 5–20.

Could some songs differ in information from others, thus suggesting a "need" for a large repertoire? This has been suggested for the small song repertoires in other species, wherein unmated males sing a song type different from that of

TABLE II

Relationship of the Duration of Song Bouts to Time of Day in One Carolina Wren (*Thryothorus ludovicianus*)<sup>a</sup>

	Time of day (hr)		
	0612 <sup>b</sup> –1012	1012–1412	1412–1812
No. of bouts	18	10	16
Mean no. of songs/bout	99* ± 50.9 <sup>c</sup>	41 ± 19.8	25 ± 16.6
Mean duration of bout (sec)	521 ± 277.8	201 ± 109.3	158 ± 87.0
No. of different song types used	18	10	10

<sup>a</sup> Data for 11 March 1976.

<sup>b</sup> Time of first song.

<sup>c</sup> Mean ± standard deviation.

\*Mean significantly higher than other time periods ( $p < 0.005$ ) by  $t$  test.

mated males or males sing some song types while in the center of their territories and others when interacting with another male at a territorial boundary (Morse, 1970; Lein, 1978; Smith *et al.*, 1978). There is no indication of this for Carolina Wrens. Males do not sing one song type preferentially over others in their repertoire, position within the territory is unimportant in predicting which song type they will sing, and time of year is unimportant (E. S. Morton, unpublished data).

Neighbor recognition via song, wherein a male might not expend much energy reacting to a song it recognized as a neighbor's, does not explain the large repertoire size, although it could explain why neighboring males hold many songs in common (Falls, 1979). However, a male's neighbors are the greatest threat to his territory for 8 months of the year; territorial establishment by the young persists for only about 4 months in my Maryland study site (August through November; E. S. Morton, unpubl. data). In years of high wren density, about four to ten border clashes per day take place between an individual male and his neighbors. If a male is experimentally removed, neighbors take over the territory within 1 day (Morton and Shalter, 1977). Thus, there is no reason to think that neighbors are responded to differently than strangers such as has been reported in some species that are territorial for only the breeding season.

There is one situation where males sing song types chosen nonrandomly from their repertoire. When one male sings other males are apparently stimulated to sing. If the first singer happens to be near the territorial boundary shared with a neighbor, this neighboring male may begin singing the identical song type. This song matching occurs only about 10% of the time one male's singing stimulated others to sing. When song matching occurs, the neighbor male faces the first singer and often moves in his direction if the first singer keeps on singing (E. S.

Morton, unpubl. data). There is little doubt that song matching indicates that singing is being directed toward a specific individual.

The large repertoire and singing style of the Carolina Wren are not adequately explained by current hypotheses offered to explain redundancy in singing (e.g., Krebs, 1977; Payne, 1979). Mate attraction does not appear to be a function of song in this wren, for males who lose mates do not increase singing rates, young males incapable of singing fully developed songs may pair, and most of the time singing occurs with the male paired (E. S. Morton, unpublished data). The Carolina Wren singing behavior suggests to me a new hypothesis that, although not contradicting the others mentioned, explains or incorporates many heretofore isolated facts about passerine bird song. The hypothesis is termed the "ranging hypothesis." I present it to explain singing behavior in the Carolina Wren, then suggest predictions from this hypothesis for other species.

### 3. The Ranging Hypothesis

The hypothesis attempts to explain: (1) the functions of song; (2) the sources of selection favoring large repertoires in the Carolina Wren; and (3) the preferential learning of neighbors' songs by young males.

A major assumption of the hypothesis is that natural selection operates differently on what I term singers and listeners, although obviously individual males are both. Another way of stating this is that the goals of singers and listeners differ; there is no selection favoring sharing of information, and singers and listeners are usually at odds with one another. The ranging hypothesis suggests that the two goals of singing are to disturb neighboring males, in particular to disrupt their foraging behavior, and/or to threaten individual males.

Listeners are under selection pressure not to be disturbed or threatened by the songs of singers. Selection on listeners favors their ability to determine, as accurately as possible, if singers are truly encroaching upon the listener's territory. Singers are selected to produce songs whose physical structures are adapted to propagate with the least possible degradation of source characteristics (source characteristics are the frequency and amplitude characteristics of the song as it emanates from the singer's mouth). By producing songs with this attribute, singers more often accomplish their goal to sound to the listener that they are sufficiently close to constitute a threat to the listener's territory, thereby disturbing him. The ranging hypothesis suggests that *if the listener has learned to sing his neighbors' songs, he can match this undegraded song stored in his brain to the song he hears*. Therefore, if the listener has learned neighbors' songs, he is able to determine more accurately his distance from the singer and therefore challenge the singer if it is near and ignore the singer if it is far away, i.e., respond to the song in a manner of benefit to the listener.

Since selection is suggested to fashion listener responses in the way just described, selection on singers would be expected to favor mechanisms to de-

crease listener ability to accurately determine singer distance. The ranging hypothesis suggests that over evolutionary time individual singers have done this by *increasing the number of different song types in their repertoire*. If a singer has some song types not also learned by a listener, the listener will not be able to determine accurately the singer's distance and the song will disturb the listener. Since male Carolina Wrens are apparently able to learn about 32 song types, a listener will not be able to learn all of the song types of all of its immediate neighbors. I envision the large repertoire size of the Carolina Wren to be the result of an "evolutionary arms race" between the adaptations of listeners to thwart the disturbing effects of songs and the adaptations of singers to continue disturbing listeners (Dawkins and Krebs, 1978, p. 309).

I have used terms such as "disturb" and "degraded song" in the formulation of the ranging hypothesis; I will now define these and provide supporting evidence for the hypothesis. How do Carolina Wrens, and other songsters, judge the distance from themselves to a singing conspecific? Songs decrease in amplitude as they propagate from their source due to spherical divergence (Morton, 1975). But amplitude is not a particularly precise method for judging distance for several reasons:

1. The singer may increase or decrease loudness by facing away from or toward the listener.
2. Amplitude can be distorted by wind and temperature gradients and hence not be a reliable indicator of distance.
3. With a high source amplitude (100–110 dB measured at 1 m, E. S. Morton, unpubl. data.) Carolina Wren songs may be expected to arrive at the listener through direct and indirect sound propagation pathways (e.g., reflections off the ground, vegetation), making loudness fluctuate.

An additional and reliable indication of the singer's distance is signal degradation due to differential attenuation of frequencies, reverberation, deflection, and scattering of the sound (Wiley and Richards, 1978). Richards (1978) found that the amount of degradation, but not song amplitude, was an important predictor of the response given to artificial song playbacks by male Carolina Wrens. He determined that undegraded songs evoked search behavior while a degraded version of the same song evoked only a mild singing response. The difference in energy expenditure responding to song playbacks must be substantial. Wrens responding to song playback by searching spend from 2 to 15 min actively flying and hopping from one bush or tree to another, after which they remain stationary and sing for a relatively short time (E. S. Morton, unpublished data). Wrens responding to a playback of song by singing do not move about, and soon return to foraging. Carolina Wren males respond differently to degraded and undegraded songs and these responses are in the direction predicted by the ranging hypothesis: more energy-consuming behaviors are elicited by undegraded songs.

Since song degradation increases directly with distance from the singer, we may assume that the response differences reflect the listener's adaptive response to the threat of territorial intrusion.

How significant is the disturbing effect of song on listeners? During the northern winters, unusually deep snow lasting for several days will lead to 80–90% mortality in Carolina Wrens (Wetmore, 1923; E. S. Morton, unpublished data). This mortality occurs perhaps once or twice per decade in eastern Maryland; between these die-offs, wren densities are high and territories are compressed to about two acres per pair. Therefore, survivors of crashes are essentially founders, hence rapid changes in gene frequencies are possible. A territory which includes fallen limbs, stream edges, or other structures that keep snow from covering the ground leaf litter where wrens forage is best for surviving such crashes. Carolina Wrens that are able to sing when they are satiated thereby may be able to interrupt their neighbors' foraging. The ranging hypothesis suggests that singing could increase neighbor mortality by reducing their foraging time, particularly in winter stress periods. Thus loud and persistent singing, large song repertoires, and the learning of neighbors' songs by newcomers become integrated with relative territorial quality and, in turn, to relative genetic fitness.

This suggests two predictions: (1) the amount of singing should decline with decreasing latitude since winter-induced food stress periods should be increasingly rare to nonexistent in tropical Carolina Wren populations; and (2) males on food-rich territories should sing more than males occupying relatively food-poor territories during winter stress conditions. Table III presents data on the first prediction. The number of songs sung by Maryland wrens during the early morning was much greater than the song output by Florida wrens. Wrens from the tropical Yucatan region did not sing at all. Males in the warmer climates responded to song playbacks with fewer songs than Maryland males (Table III). Thus two measures of the incidence of song use show decreasing song use with decreasing latitude.

The second prediction was tested in Maryland from January 4 to 15, 1981. During this period the ground was snow covered and temperatures were far below normal, ranging from 0°–30°F for night-time lows (mean 10°F) to 18°–41°F for daytime highs (mean 29°F). Normal mean high and low temperatures for this area are 43° and 28°F (National Weather Service records). Four pairs of Carolina Wrens occupied territories at the study site in Severna Park, Maryland. The territories were separated by unoccupied water or salt marsh but all four males could hear each other and earlier it was noticed that singing by one often stimulated the other males to respond. One pair was provisioned with mealworms (larvae of *Tenebrio* sp.), thus artificially increasing food availability, on alternate days during the January period. On days he was provisioned, the male sang persistently whereas no song was heard from the other three males

TABLE III

Latitudinal Variation in the Use of Song Outside the Breeding Season in Carolina Wrens (*Thryothorus ludovicianus*)

	Mean no. spontaneous songs per male, daybreak to 1 hr past	No. males	No. songs following playback $\pm$ SD <sup>a</sup>	No. males
Maryland (Nov.) (Arnold)	357 <sup>b</sup>	11	32* $\pm$ 25.2882	15
Florida (Dec.) (Myakka St. Pk.)	53	6	13 $\pm$ 21.4738	8
Yucatan, Mexico (Sept. 17–21) (near Chichen Itza)	0	4 <sup>c</sup>	8 $\pm$ 11.5866	4

<sup>a</sup> Six song playbacks made within male's territory were used as a stimulus; counts of songs refer only to that male, and do not include neighboring males. Counting continued until singing ceased.

<sup>b</sup> No. calculated from tape recordings of song output from several males simultaneously, therefore no standard deviations are calculated.

<sup>c</sup> Number of males determined through song playbacks after data on spontaneous songs were collected.

\* $p < 0.05$  that Maryland birds sing fewer songs following playback than Florida birds (*t* test).

while I listened from 0730 to 0830 hr. On days he was not provisioned, no songs were heard from any of the males. The songs of the provisioned males elicited *cheer* calls from one male on one occasion (Table I). The results of this qualitative experiment show that wrens will sing when food is provisioned even though temperatures are abnormally low and that singing by neighbors is not necessary to stimulate singing by a provisioned, food-satiated male. It is likely, therefore, that under natural conditions males on territories with relatively high food availability will sing often and potentially increase their relative fitness by increasing mortality in neighbors on poorer territories.

If wrens do die during the winter, the remaining birds expand their territories. Wrens continually attempt to expand their territories, I suggest, because there is no optimum territory size. A territory of a size capable of supporting a pair for the winter may suddenly become unsuitable when the unpredictable abnormally deep and long lasting snows occur. Selection pressures arise from these rare snows that favor territorial expansion: the winners in the game wrens play are those that continue to push for larger winter territories for they attain a higher probability of surviving than wrens less genetically prone to do so. Verner's

superterritory concept is important to mention here (Verner, 1977). Verner suggested that territories are larger than needed to provide sufficient resources because by inhibiting reproduction by others, the holder of a superterritory increases its relative fitness. Rothstein (1979) defined *inhibition* as traits that "reduce the absolute performance of other individuals and may or may not improve the absolute performance of the inhibitor." Rothstein pointed out that it is unlikely inhibitory traits that only reduce another individual's fitness will evolve. One function of song in Carolina Wrens, to disturb other males, should be viewed as a trait that indeed is selected to inhibit others, but that also aids the trait holder. As Rothstein further points out, "once a feature that both aids the trait holder and inhibits others becomes common, the inhibition may contribute enough to fitness to itself become a significant evolutionary factor in maintaining the trait" (Rothstein, 1979, p. 330).

For selection pressures to be adequately predicted by the ranging hypothesis, Carolina Wren singers should use songs that disturb listeners. Thus songs should be selected for that listeners might take as emanating from a disturbingly close singer. This implies more than that the song simply propagates well or is detectable as conspecific to a listener; it implies that songs should maintain their source characteristics, or remain undegraded, for as long as distance as possible. An alternative hypothesis suggests that a singer should use songs that degrade predictably with distance so that listeners can judge the singer's distance and avoid the singer "without risking an interaction" (Wiley and Richards, 1978, p. 91).

Sheri Lynn Gish and I recently performed a study to differentiate the efficacy of the ranging hypothesis and the "degrade predictably to inform" hypothesis (Gish and Morton, 1981). A test tape containing 50 Carolina Wren songs from two locations was rerecorded 50 m from a loudspeaker playback at sites where the songs were foreign, native, or neutral. The songs did not differ in their frequency ranges or average frequency. We calculated changes in each song's source characteristics by using changes in the proportional distribution of sound amplitude (in dB) within a song between its source and 50 m to arrive at a "change index." A change index of 0 equaled no change in source characteristics over the 50 m. By using proportional (fractional) representation of sound amplitude, we eliminated attenuation due to spherical divergence from the calculations and obtained a measure of the summed degradation effects due to reverberation, differential attenuation of frequencies, reflection, and refraction. We found that Carolina Wren songs native to a test site had lower change indices than songs foreign to the site; sites where none of the playback songs were native showed no trend favoring either song sample. Thus, wren songs are adapted for maximum transmission of source characteristics, as predicted by the ranging hypothesis but not the "degrade predictably" hypothesis. Singers, therefore, preferentially use songs that are difficult for listeners to ignore because these songs mask information from degradation about the singer's distance as much as possible.

The discerning reader might note that the ranging hypothesis now has produced two potential reasons why young male wrens preferentially learn neighbors' songs. As listeners, young males might learn neighbor's songs so that an undegraded version is available to facilitate ranging or estimating the distance of singers, as previously mentioned. It is also possible that young males learn only those neighbors' songs that propagate source characteristics well in the particular site in which they are establishing territories. In other words, young males are being choosy in selecting songs in order to become more effective as singers. In effect, selection should favor the learning of particularly "good" songs both because these will be the most effective when used by neighbors to disturb him (he will be a fit listener) and because these songs are well adapted to propagate in the specific site (he will be a fit singer). Hansen (1979) discusses one of these alternative hypotheses, suggesting that young males learn neighbors' songs to attain songs best adapted for sound propagation in their particular territorial sites.

The ranging hypothesis does predict an important function of song matching during countersinging between two males. In addition to the function of disturbing neighbors, the second major function of song repertoires suggested was to threaten a singing neighbor (male 1) that was determined by the listener (male 2) to be close to their common territorial boundary. When male 1 sings close to the boundary and male 2 is near that border, male 2 responds either by singing the same song type used by male 1 or by using the *cheer* call, a call note held in common with all males (E. S. Morton, unpublished data). The *cheer* (Table I) is used by males in many intra- and interspecific alarm contexts. *Cheer* is replaced by *ti-dink* in male Carolina Wrens living in peninsular Florida north to southeast Georgia (E. S. Morton, unpublished data). The ranging hypothesis suggests the reason male 2 uses either the song type held in common with male 1 or the call note is to *provide precise ranging information to male 1*. In this single context, males near one another, male 2 is selected to provide male 1 with accurate information concerning his distance from male 1. If male 2 responded to male 1 with a random song choice, the ranging hypothesis predicts that, if male 1 did not "know" that song type, he would not receive accurate cues to male 2's distance. Male 2, by providing male 1 with an accurate cue to his proximity, is using song matching as a threat. The song-matching male 2 will often escalate this threat by moving closer to the territorial boundary (E. S. Morton, unpublished data). Boundary defense is the single context where it is in male 2's selfish interest to provide honest information in his song.

#### 4. Predictions of the Ranging Hypothesis for Other Species

Many of the known facts and generally held impressions about passerine song are viewed in isolation. Some that I speculate on include song learning and loss of learning, singing outside of the breeding season in permanent residents and migratory species, repertoire size and individual song complexity, the stability of neighbor-neighbor relations as a selective force on song function, and the wide-

spread use of song in relatively small birds with high metabolic rates. The ranging hypothesis provides an opportunity to bring such diverse aspects of song into a single conceptual framework. Hopefully, the ideas will stimulate others to think about birdsong in new ways. As with the motivation-structural code model, the ranging hypothesis is offered to suggest testable hypotheses about communication based on evolutionary theory.

*a. Song as a Mechanism to Increase Relative Fitness.* Many species begin singing regularly several months before breeding begins, when the cold temperatures and short days of winter still produce food stress conditions. For example, in North America the Song Sparrow (*Zonotrichia melodia*), Cardinal (*Cardinalis cardinalis*), Tufted Titmouse (*Parus bicolor*), and White-breasted Nuthatch (*Sitta carolinensis*) begin singing in mid-January in Washington, D.C., 3 months before breeding (E. S. Morton, unpublished data). Higgins (1979) studied the duration of morning song in the Song Thrush (*Turdus philomelos*), another winter songster. He was surprised that singing duration was longest during the four coldest mornings, but with warmer temperatures (5°–13°C) singing duration was positively correlated with temperature. The ranging hypothesis provides an explanation: song functions to disturb neighbors, thus song should be used when disturbance will provide the greatest fitness benefits to the singer. Climatically induced stress conditions provide the singer an opportunity to increase its relative fitness.

Singing during migration is also frequent for many species of New World warblers (Parulidae) and other tropical migrants returning north to breed. I speculate that this singing, as well, functions to disrupt the foraging of other males. If other males can thus be weakened, singing males might complete the long flight to breeding habitat ahead of others. This suggestion presumes that a high proportion of migrating conspecifics within hearing distance of the songs are heading toward the same breeding neighborhood.

*b. Species Specificity in Song, Song Complexity, and the Ranging Hypothesis.* The ranging hypothesis suggests that selection should favor songs that are difficult to learn. If a singer's songs are not copied correctly by learning males, this singer will not be accurately ranged by listeners and his songs will be relatively more disturbing. However, singers are constrained from continually producing new, different, or more complex songs because songs that are not easily recognized as conspecific will have little disturbing or threatening effects on listeners. I suggest that this constraint has resulted in species-distinctive properties in birdsongs. The ranging hypothesis predicts that species distinctiveness is a "bind" singers face, not a result of evolution to avoid dysgenic hybridization or time-wasting errors (Marler and Hamilton, 1966, p. 444). The ranging hypothesis places selection favoring species distinctiveness in song at the level of the individual male interacting with conspecifics, or conspecifics plus

ecological competitors (Cody, 1973), rather than as a reproductive isolating mechanism operating at the species level (Marler, 1977, p. 57).

The ranging hypothesis predicts that song complexity should arise for the same reasons that favor increased repertoire size. Singers' evolutionary responses to song learning by listeners may be manifested either by increasing the number of differing song elements (i.e., increase complexity) or by increasing the number of song types. The path a species follows depends on the innate species-specific properties in its song(s). For example, the Carolina, Rock, and Marsh wrens have simple songs composed primarily of one repeated element (Kroodtsma, 1977). They have evolved along the increased song repertoire route, with 27 to 100+ songs. The Bewick's Wren, in contrast, has fewer but more internally complex songs. Bewick's Wrens in Colorado average 10 songs per male while males from Arizona average 17.5 songs. However, the number of elements sung is the same in both populations: Colorado birds have longer songs than Arizona birds and the former have more elements per song (Kroodtsma, 1973). The Bewick's Wren has taken the path toward increasing song complexity. In both cases, the ranging hypothesis suggests that the evolutionary reason is to increase singer effectiveness against a selective background of listener counteradaptations.

In addition, singers may improve their songs' disturbing effects by changing the amplitude of song during delivery while still maintaining song structure within species-specific constraints. The Ovenbird (*Seiurus aurocapillus*) changes the amplitude of its song during delivery (Falls, 1963). I suggest that singers thereby make it more difficult for listeners to judge their range.

*c. To Learn or Not to Learn Songs?* Learning songs through an interaction with experience and an innate template is not the rule among all passerine birds. Song learning does not seem to occur among the more primitive passerines such as the New World Dendrocolaptidae, Furnariidae, Formicariidae, and Tyrannidae, but to my knowledge no controlled learning experiments have been performed on these (see Chapter 1 on ontogeny, by Kroodtsma, Volume 2). The suggestion that songs are innate comes from the observation that songs in species from the above families do not vary geographically and where variation is found it is suspected that speciation has occurred (E. Eisenmann, unpublished data). One such instance of suspected speciation was confirmed for an *Empidonax* flycatcher (Stein, 1963). The ranging hypothesis suggests a reason why selection has not favored song learning: song functions only to threaten other males, not to disturb them; song has only the song matching, honest distance-cue-providing function. Song learning is selected for when the disturbing function of song may lead to relative fitness advantages. Most of the passerine species purported not to learn songs are endemic to tropical climates where, as discussed above, disturbing neighbors may not function to increase relative fitness.

In species that do learn songs, it is often mentioned that this learning ability

disappears after songs have crystallized (Konishi and Nottebohm, 1969). Kroodsma (1980) suggests that social interactions may play a crucial role in determining "exactly where, when, and from whom songs are learned." The ranging hypothesis suggests that the end to song learning occurs when it is advantageous for a singer to become a song model for newcomers. An older male has the advantage of prior territorial occupancy that may be maintained against newcomers that are not effective in disturbing him through their songs if he is copied: he "knows" the song. If newcomers do not copy his songs exactly they may thwart this advantage. "Copying errors" or "drift" (Lemon, 1976) may thus be an adaptive trait in newcomers rather than inevitable developmental errors. Selection favoring when and from whom songs are learned or no longer learned may also be derived from demographic characteristics of the local population that I term neighborhood stability.

*d. Song Redundancy and Neighborhood Stability.* Small, often one-song repertoires, and high among-individual song variability are predicted to be adaptive in populations where neighbor changeover is high between breeding seasons or there are many newcomers seeking territories. The ranging hypothesis suggests that this is due to a lack of selection pressure favoring newcomers that learn the songs of neighbors with whom they interact for a short time. Instead, selection favors the development of individually distinctive songs to afford listeners only inaccurate distance cues. Examples are found in the Field Sparrow (*Spizella pusilla*) (Goldman, 1973) and White-throated Sparrow (*Zonotrichia albicollis*) (Falls, 1969). Neighbor recognition, wherein the playback of a neighbor's song elicits a reaction milder than that of the playback of a stranger's song, has been reported in species with high neighbor changeover (e.g., Falls, 1969). These studies are describing the adaptive response of the birds only as listeners; there is no information to suggest individually distinctive songs function to promote neighbor recognition. Perhaps the critical time for singers is during territorial establishment before neighbors have learned to respond adaptively and are more easily disturbed by songs new to them that they cannot effectively range.

Where neighborhood stability is high, selection may favor either increased repertoire size, as in the Carolina Wren, or single-song repertoires, depending upon the climate during the singing season. If the climate is harsh and unpredictable or territories vary greatly in quality, large repertoires should be favored because the disturbing function of song will favor them. If the climate is mild and stable, selection is predicted to favor low repertoire size. Now threat may be the important function of song. Song matching overbalances selection favoring disturbing in stable situations where the territorial boundaries are established between the same neighbors for long time periods. Dialects arise in this situation: young birds learn older males' songs, selection is against making copying errors, and songs are used to threaten neighbors over established territory borders.

Dialect species should respond more vigorously to native relative to foreign songs in contrast to species having distinctive individual songs. In the former, foreign songs are predicted to produce milder responses because no accurate distance cues are perceived and the bird responds as though the sound is degraded and of little threat. Milligan and Verner (1971) believe that White-crowned Sparrows (*Zonotrichia leucophrys*) respond less to foreign dialect songs.

#### IV. SUMMARY REMARKS

The evolutionary context in which I have placed singing behavior has yielded the prediction that songs function to disrupt conspecific males by providing poor distance assessments and/or to threaten them by providing accurate distance assessments. The information in song is predicted to be simple; species distinctiveness is important since this property is essential to the effectiveness of the behavior. Species distinctiveness is part of a feedback system constantly balancing, in some species, increased repertoire size and/or internal song complexity against its effects on conspecific recognition; it cannot function without recognition. The ranging hypothesis, and thus the discussion in this section, is concerned only with intrasexual selection. Selection of males through female mate choice is undoubtedly an important source of selection on male song, but reproductive isolation per se is probably of lesser importance than previously thought.

An overall review of the kinds of birds that use song supports the functions attributed to song by the ranging hypothesis. Attempts to increase relative fitness by disrupting neighbors, and described above, are largely found in small-sized species with relatively high metabolism and low energy storage capacity relative to the daily energy budget (Faaborg, 1977). A single hypothesis that encompasses such diverse aspects of what is known about passerine songs should, at least, challenge our assumptions.

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