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DISPLAY BEHAVIOR OF OVENBIRDS (*SEIURUS AUROCAPILLUS*) I. NON-SONG VOCALIZATIONS

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Although detailed investigations of single displays have furnished insights into their proximate causation and adaptive roles in regulating social behavior (Smith 1977, Sebeok 1977), they contribute relatively little to our understanding of the evolution of animal communication at a somewhat higher level. Smith (1969a) and Moynihan (1970) pioneered consideration of the evolutionary pressures shaping the total display repertoire of a species. However, such studies are hampered by a paucity of information about the size and composition of repertoires of most animals, since detailed inventories are time-consuming and are frequently by-passed by workers studying single displays or small portions of a repertoire. Generalizations are therefore based on a few species whose display behavior is known in sufficient detail, and their validity depends on how well additional studies conform to the patterns found.

During investigations of behavior of wood warblers (Parulidae) I obtained information on the display repertoires of various species. In this paper I describe the non-song vocalizations of breeding Ovenbirds (*Seiurus aurocapillus*) and suggest some of the functional aspects of vocal communication and the evolutionary pressures that possibly have shaped its display repertoire. The songs of males and visual displays will be dealt with in subsequent papers.

The Ovenbird is an excellent subject for behavioral investigation. It is widely distributed and abundant throughout the wooded regions of North America, occupying open woodlands, generally with little underbrush but with an abundance of fallen leaves, logs and rocks (Bent 1953, Griscom and Sprunt 1957). This warbler's vocal nature during the breeding season, its open habitat and its largely terrestrial lifestyle facilitate observation. Although Ovenbirds are drably (and possibly cryptically) colored, they are easily followed on the forest floor. The sexes are monomorphic, but may be distinguished reliably through the use of behavioral characters.

Hann's (1937) extensive life history study of the Ovenbird included observations on behavior. However, descriptions of non-song vocalizations in the literature are limited and little recording and audiospectrographic analysis of such displays have been undertaken. Since wood warblers are numerous in both the tropical and temperate regions of the Americas, the Ovenbird invites behavioral comparisons leading to the elucidation of the evolution of its displays. Also, as a monomorphic species in a family whose temperate zone representatives are predominantly sexually-dimorphic in plumage (Hamilton 1961), its behavior may provide insights into the interaction between the visual and vocal components of the display repertoire.

METHODS

Fieldwork was conducted in the breeding season from 1970–1972 at 2 locations in New England. The main study area was the Pickman Area, Concord Field Station of the Museum of Comparative Zoology of Harvard University, Bedford, Middlesex Co., Massachusetts. The second area was a farm in South Lyndeboro, Hillsboro Co., New Hampshire. The habitat in both locations consisted of open second-growth mixed forest with a sparse understory, regenerated on fields abandoned 50–75 years ago. This forest is dominated by large white pines (*Pinus strobus*) 25–30 m in height. The main deciduous trees are maples (*Acer rubrum* and *A. saccharum*) and oaks (*Quercus* spp.), with some gray and paper birches (*Betula populifolia* and *B. papyrifera*) and other hardwood species.

I made detailed observations on 5 pairs of Ovenbirds in 1970, 3 pairs in 1971 and 7 pairs in 1972. Other pairs were observed more casually. During 1971 and 1972 nine males were individually color-banded; I identified unbanded males by their location and distinctive songs. I followed a known individual or pair for extended periods, making a verbal record of behavior with a cassette recorder. The sex of unbanded birds could usually be determined from distinctive vocalizations or other behaviors (Hann 1937, this study). High-fidelity recordings of vocalizations for audiospectrographic analysis were made whenever possible with a Nagra IIIB tape recorder and a Norelco D-119ES cardioid dynamic microphone. The continuous observation periods were typically at least 30 min long, often lasting up to several hours, enabling me to determine the status of birds in the breeding cycle and to obtain a representative sample of their behavior. I was usually able to work within 15–30 m of the birds. They were visibly disturbed by my presence only when I moved too close to them or to a nest, or during the nestling and fledgling periods. Such disturbance was obvious from their behavior and I have allowed for it in interpretation of the results. Most observations were made during the period of maximum activity (between dawn and 11:00 EDT), but comparative observations were made at all times of the day.

During the continuous observations I noted locations of birds on their territories relative to mates, neighbors and nests—features of critical importance in interpretation of displays. Territorial boundaries were determined by noting song perches and locations of territorial disputes. I transcribed the observation tapes and tabulated all occurrences of each identifiable display, along with pertinent contextual details. Sonograms were made with a Kay Elemetrics 6061B audiospectrograph using the wide-band filter and high-shape setting over a frequency range of 160–16,000 Hz and were used to identify each vocalization. Because of the impossibility of eliminating background noise, I have used tracings of selected records for illustration, rather than the actual sonagrams.

In interpreting the functional significance of Ovenbird vocalizations, I follow the method of Smith (1965, 1977) in determining and classifying the messages encoded by displays. Readers unfamiliar with this terminology should consult these works.

I recorded 7 types of vocalizations (excluding song) from male Ovenbirds, and 6 from females. Since there is only 1 possible homology between the calls of the sexes, I describe them separately. The term recorded means that the vocalization was tape-recorded and identified from sonagrams. The entire sample of recorded vocalizations from birds of known sex and status has been included in the analysis.

RESULTS

Male vocalizations.—Seven vocalizations were distinguishable, in addition to "song" and "flight song."

(1) *Soft sip* (Fig. 1A–D).—*Soft sip* is a high-pitched call, virtually inaudible at distances of more than 15–30 m, or when there is wind or background noise. It is an extremely brief note, and may grade into *chep* by the addition of a stronger descending arm (see below).

I recorded *soft sip* on 20 occasions, but heard it frequently. Ten occasions involved a male interacting with his mate; 7 times the male was moving toward the female or was chasing her. Once a male gave a long series of *soft sips* following a copulation.

In 8 recorded cases "flight songs" were prefixed by a series of *soft sips*, and presumably identical vocalizations were heard prefixing other "flight songs." Hann (1937) noted a "few sharp chips" at the beginning of "flight songs."

I recorded *soft sip* only once during male-male encounters, given by a male flying toward a territorial boundary where his opponent was singing. Vocalizations believed to be *soft sip* were often heard during other encounters, but the rapid movements of males prevented recording such low volume sounds.

Soft sip was recorded in 2 other circumstances. Although I believe it was given by males on all occasions, none of these cases involved banded birds. Long sequences of *soft sip* were given twice, presumably by the same bird, in response to a screaming Broad-winged Hawk (*Buteo platypterus*) perched nearby. I recorded *soft sip* from birds scolding me at nests on 3 occasions. Known females never used this vocalization.

Weeden and Falls (1959) described a "sharp high-pitched note" given by males in response to other Ovenbirds or to human disturbance. This may be *soft sip*. Nice (1931) also noted a high-pitched *tchip* used by scolding males and commented that it graded into a lower-pitched *tchuck*, which probably is the same as *chep* (see below).

The common feature of all uses of *soft sip* seems to be a conflict between tendencies to fly and to engage in some other activity. This conflict may be the result of low light intensity (in association with "flight song," which is given primarily at dusk [Eaton 1957]), simultaneous attack and escape tendencies (during territorial encounters), or simultaneous tendencies to flee and to remain in place (in response to "predators" and mates). The display may thus indicate a state of indecision with regard to several behavioral alternatives, 1 or more of which may involve locomotion.

(2) *Chep* (Fig. 1H–L).—Some examples of this call show a slight ascending arm (Fig. 1K) or 1 or more rapid frequency modulations of the descending arm (Fig. 1L). All variations of the call may be used by the

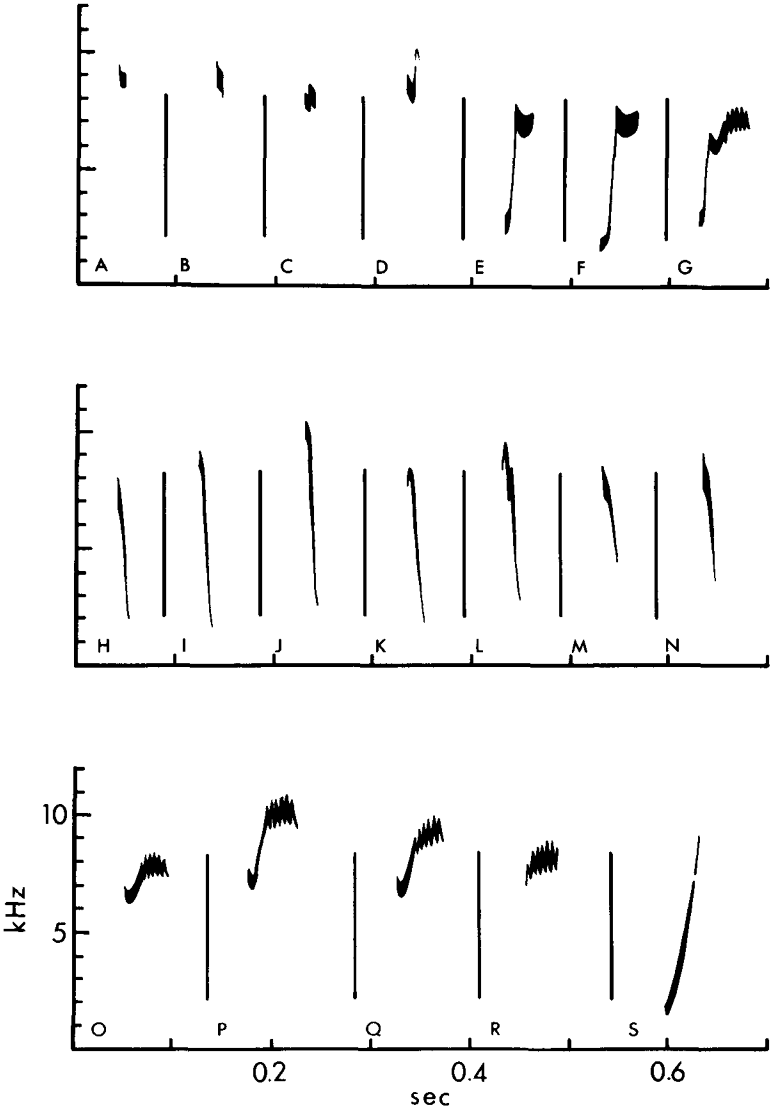

FIG. 1. Vocal displays of male Ovenbirds. A–D: *soft sip* vocalization. E–G: *Pink* vocalization. The example in G appears intermediate between *pink* and *seep*. H–L: *chep* vocaliztion. Different examples show the range of variation observed in this study. M–N: Intermediates between *soft sip* and *chep* vocaliztions. O–R: *seep* vocalization. The extreme variant in R was rarely recorded. S: *whip* vocalization.

same bird, or by different birds, in the situations described below. *Chep* is much louder than *soft sip* and may be heard at greater distances. *Soft sip* grades into *chep* through intermediates with short descending arms (Fig. 1M, N) that are higher-pitched and may be described as *chip* rather than *chep*. They are rarely used and thus are not described as a separate display.

Chep was recorded in 3 different circumstances. It was most common during territorial encounters and was given prior to, or during male-male chases; in several instances it seemed to be given in direct response to song of an opponent. It was used frequently during male-female interactions as well. Males gave it while perched near their mates or moving with them, and it was recorded on 4 occasions during chases of females by males. Its use in this situation resembles that of *soft sip*, but *soft sip* was given when the birds were in closer proximity. *Chep* was also used in response to my presence near a nest or fledged young; it was recorded 9 times and heard more frequently.

Various workers have described calls that are probably equivalent to *chep*. Weeden and Falls (1959) report a low-pitched *chuck* used at the end of male-male encounters. Stanwood (1911), Nice (1931) and Hann (1937) describe the calls of scolding males as "*cheh–cheh–cheh*," "*tchuck*" and "*chirp*," respectively.

Its frequent use during chasing indicates that *chep* may represent a message concerning the tendency to behave aggressively. The differences between the uses of *chep* and *soft sip* suggest that *chep* indicates a higher probability of aggressive behavior than that shown by *soft sip*. Otherwise, the messages of the 2 calls seem quite similar.

(3) *Pink* (Fig. 1E,F).—This is a sharp, explosive-sounding vocalization which ends with a characteristic "flag" produced by a short period of rapid frequency modulation.

Pink was recorded on 15 occasions during both male-male and male-female interactions. It was heard more frequently, but its similarity to *whink* (see below) prevents positive identification without the aid of sonagrams. Of the 5 recordings made during male-male encounters, 4 were prior to, or during chases. It was twice observed to occur in apparent response to a song by a nearby male. Once a male uttered *pink* as he moved toward an intruding male.

Pink was more common during male-female interactions. I recorded it in 9 such cases and heard it much more often. On 4 occasions the male was simply near the female; no interaction occurred. Twice, however, it was given by males chasing their mates. On 4 other occasions males gave *pink* as they approached their mates; twice the male was flying to copulate with his mate.

Pink was associated with both overt aggressive and sexual activity. It may be uttered just before a male flies to chase another male, or during hesitant flight as a male flies in to copulate with his mate, strongly suggesting that it indicates indecision regarding locomotion and in addition, provides a general message concerning the tendency to interact with the recipient. The cause of indecision appears to depend on the precise circumstances surrounding production of the display. The message may specify, as well, a conflict between escape tendencies and some alternate class of behavior (sexual or aggressive).

(4) *Seep* (Fig. 1O–R).—This is a brief vocalization characterized by its "jagged" terminal portion. Some variation is present in the different examples. In several cases the initial portion of the note was much reduced (Fig. 1R). One male gave several notes which appear to be intermediate between *seep* and *pink* (Fig. 1G), but no other intermediates were recorded.

Seep was recorded on 25 occasions; 20 of these involved male-female interactions. I recorded *seep* during 3 male-male encounters; on each occasion females were present and interacted with the males prior to, or during the encounters. The male giving *seep* in these latter cases had invaded another territory, apparently in response to on-going courtship activities of the residents. Once a male gave *seep* in the absence of a female during a break between bouts of male-female interaction. The only other recording of *seep* in the absence of a female was obtained when I inadvertently flushed a male who gave the call as he flew away.

This display is used primarily in male-female communication. In 14 of 20 such cases it was associated with movement toward the female; the remaining cases involved its use in close proximity to the female. It was often used in conjunction with *ple-bleep* and incomplete songs (see below). Several times it may have been given in response to female *high tsip* or *tsip series* (see below).

Seep is clearly connected with male-female interactions and the message probably specifies that the communicator will engage in a pair bond-limited subset of activities. It might appear that the display is indicative of a strong sexual tendency, but the call was never recorded in connection with copulation attempts. Therefore, the message probably does not specify sexual behavior, but may designate the likelihood of "association" behavior. *Seep* was often associated with flight and may thus also signal probable locomotion.

(5) *Whink* (Fig. 2A–C).—This call has a buzzy or nasal-sounding quality that is produced by repeated large frequency modulations occurring during the note. Some examples (Fig. 2B,C) vary slightly from the typical form (Fig. 2A). One recording (Fig. 2C) has an initial portion resembling that of

pink. Perhaps there is a relationship between these 2 calls although true intergradation was not recorded. *Whink* is usually given as a series of calls at a rate of about 5 vocalizations per sec.

Whink was used only by males, and in the absence of conspecifics only as a part of the introductory segment of "flight song" (Lein 1973). It was often associated with *ple-bleep* and "song" during both male-male and male-female interactions, but was equally frequent as an isolated display. I heard it more frequently during male-female interactions, but these, in turn, were more numerous than encounters between males.

Six of 9 recordings made during male-male encounters were obtained while active chasing or fighting was occurring. *Whink* was frequently heard during other kinds of chases. It also was recorded during male-female chases, twice involving apparently aggressive contact by the male with his mate. *Whink* was used in the introduction of "flight songs" given by males as they copulated with their mates on 2 occasions. *Whink* resembles *ple-bleep* in motivation and message and is discussed with the latter call.

(6) *Ple-bleep* (Fig. 2D–F).—This is a 2-note vocalization. The notes differ slightly in form; they resemble *whink* but are lower in frequency and different in sound.

Ple-bleep is individually distinctive. Fig. 2D–F shows typical calls of 3 males. No indication of significant intra-individual variation was seen; all examples for each male match that illustrated. Incomplete *ple-bleeps,* consisting of only the first note, were recorded rarely.

Ple-bleep is a regular part of the introduction of "flight song," along with *whink.* It was very common during male-male encounters; of 15 recordings made in such circumstances, 10 were during active chasing or fighting. On several occasions it was definitely the bird initiating a chase that gave the display. *Ple-bleep* was equally common during male-female interactions, and was heard during male-female chases. It was given more commonly by males very near to, or following their mates. It also was recorded during apparent copulation attempts, often along with incomplete "flight song."

Whink and *ple-bleep* were both recorded during intense male-male and male-female interactions. Their occurrence together in these situations and in "flight song," suggests that their motivation and messages are very similar. Were it not for their use in "flight song" and during successful copulations, it would be easy to conclude that these displays indicate an aggressive motivation and an attack message. Both *whink* and *ple-bleep* seemingly reflect ambivalence regarding locomotion. This indecision is especially apparent when the call is used during "flight song" and when the male approaches the female in an obviously hesitant manner. The

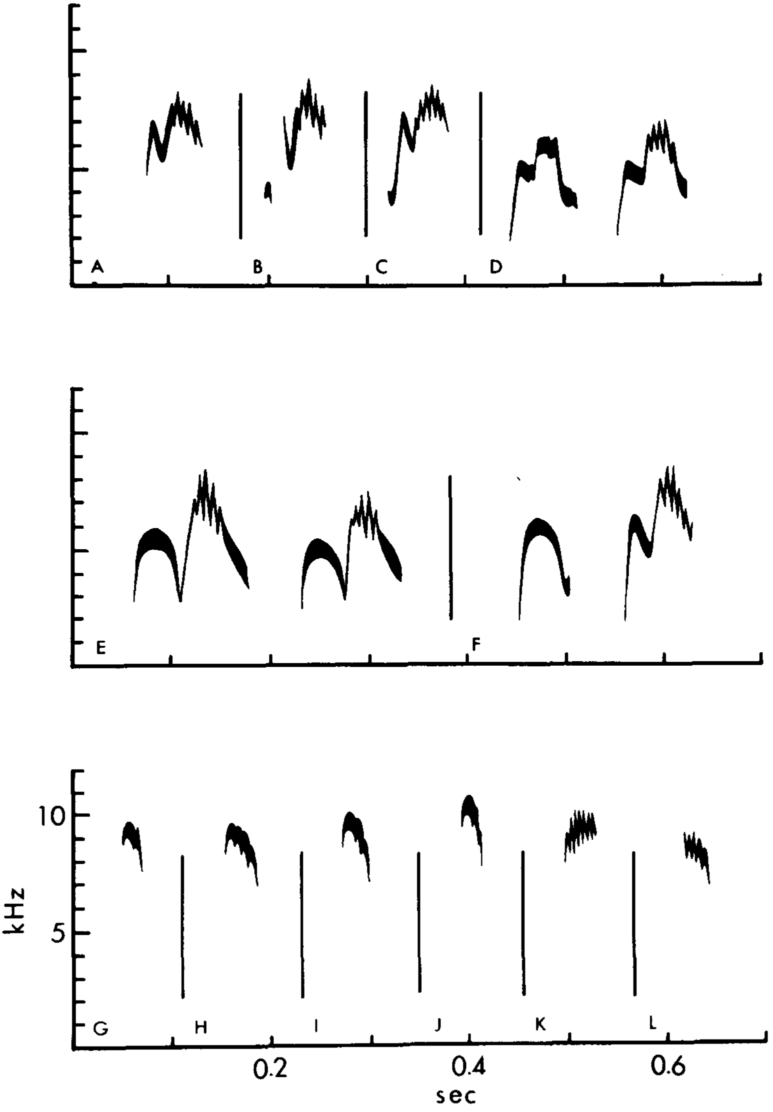

FIG. 2. Vocal displays of Ovenbirds. A–C: *whink* vocalization of males. D–F: *ple-bleep* vocalization of males. The 3 examples show the stereotyped differences that characterize the displays of individual males. G–J: Typical *high tsip* vocalization of females. K–L: *high tsip* variants with high frequency modulation rates.

displays would thus seem to encode messages of locomotory and indecisive behavior, both at high probability and intensity. The reason for the indecision should be available to the recipient from contextual information. There would also appear to be a message relating to a high probability of interaction involving contact.

Whink is given by itself more often than is *ple-bleep.* The latter display is usually preceded by several *whink* calls. This suggests the 2 displays encode different probability or intensity statements about the degree of locomotory indecisiveness, with *ple-bleep* perhaps specifying a higher probability of flight. The fact that the *ple-bleep* displays of different males are stereotyped in their detailed form implies that individual identification may be an important function of these calls.

(7) *Whip* (Fig. 1S).—*Whip* is a very low volume call which was recorded only once, although it may have been heard on several other occasions. The recorded calls were from a male moving and giving *soft sip* very near his mate. He gave *whip* twice after being chased by his mate. On another occasion a call that was probably identical was heard during a male-male chase. The number of observations is too few to determine the motivation or significance of this display.

Female vocalizations.—Six female vocalizations were distinguished.

(1) *High tsip* (Fig. 2G–J).—*High tsip* typically contains 3 or 4 frequency modulations producing a "saw-tooth" pattern on a sonagram. Infrequently I recorded notes with a more rapid modulation rate and an increase in frequency during their utterance (Fig. 2K). These notes were used in the same circumstances as the typical form and intergraded with it (Fig. 2L). *High tsip* also grades into *chep*; this transition is discussed with the latter display.

High tsip is the most common display of female Ovenbirds during male-female interactions. During the pre-incubation stages of the breeding cycle female Ovenbirds can be located with ease because of their persistent use of this vocalization. *High tsip* occurs most frequently as a response to the mate's songs when the birds are 15 m or more apart. It is also given irregularly as the pair moves together across the forest floor, sometimes in response to the mate's approach or in response to other male vocalizations such as *seep* or *whink.*

High tsip cannot be connected with any particular set of situations or motivational tendencies. It may encode a message specifying the female's readiness to associate with the male since it is used almost exclusively during the courtship period, or during other male-female interactions. There does not appear to be a more specific behavioral message encoded in the signal. One of the most important functions of this display may be the identification of the displaying bird as a female. The calls vary within individuals and are so similar among different birds that it is doubtful if individual identity is encoded.

(2) *Tsip series* (Fig. 4A,B).—This vocalization consists of a series of *high tsip* notes and is classified as a separate display because of its stereotyped form and distinguishable usage. It typically consits of 6–10 *high tsip* notes, but as many as 25 repetitions were recorded. A number of irregularly spaced *high tsips* usually follow it. The notes occur at intervals of about 0.1 sec at the start of the series; the rate of delivery and frequency of the notes decreases (Fig. 4B), giving the display a characteristic fading-out effect. Many examples of *tsip series* are preceded by a single *chep*.

Tsip series was used in situations similar to those of *high tsip* but with some noteworthy distinctions. All records of *tsip series* were obtained from females moving in close association with mates or responding to the actions of mates. As with *high tsip*, *tsip series* was used most conspicuously as a response to the mate's song. However, females used *tsip series* rather than *high tsip* when the male sang very near to them (within 15 m). It was also given frequently in response to a flight by the male toward the female, or in cases where the male was very near (within 3 m). Females also gave *tsip series* as they took off on short flights near a male.

The similarity of uses of this display and *high tsip* suggests that they encode similar messages. *Tsip series* encodes a message specifying association. The frequent conjunction of *tsip series* and flight, situations in which flight might be expected (as when a male suddenly flies toward the female), suggests an additional message of locomotory behavior. By vocalizing as she moves, or when her mate sings, a female can keep the male aware of her location and movements, thus maintaining contact. In addition, the display identifies the communicator as a female and may serve as a form of appeasement display that inhibits male aggression. Alternatively, it may allow the avoidance of misdirected attack from an aggressive male who suddenly encounters another Ovenbird and who may not immediately identify the conspecific as a female.

(3) *Chep* (Fig. 3A–K).—The female *chep* vocalization resembles that of males, but is distinguishable on sonagrams by the presence of a strong harmonic, which is usually reduced or absent in the male vocalization (see Fig. 1H). *High tsip* grades into *chep* by an increase in the descending terminal arm of the *high tsip* and a loss of the initial modulation (Fig. 3D–F). These notes are intermediate in pitch and the series may be represented by the verbal descriptions *tsip*, *chip* and *chep*. Intermediates are uncommon and are not described as a separate display.

Another variant of *chep* (Fig. 3G–K) begins at a lower frequency than the typical *chep* and shows a strong harmonic structure. Some examples (Fig. 3I, J) show an ascending arm, giving the note a chevron shape. These

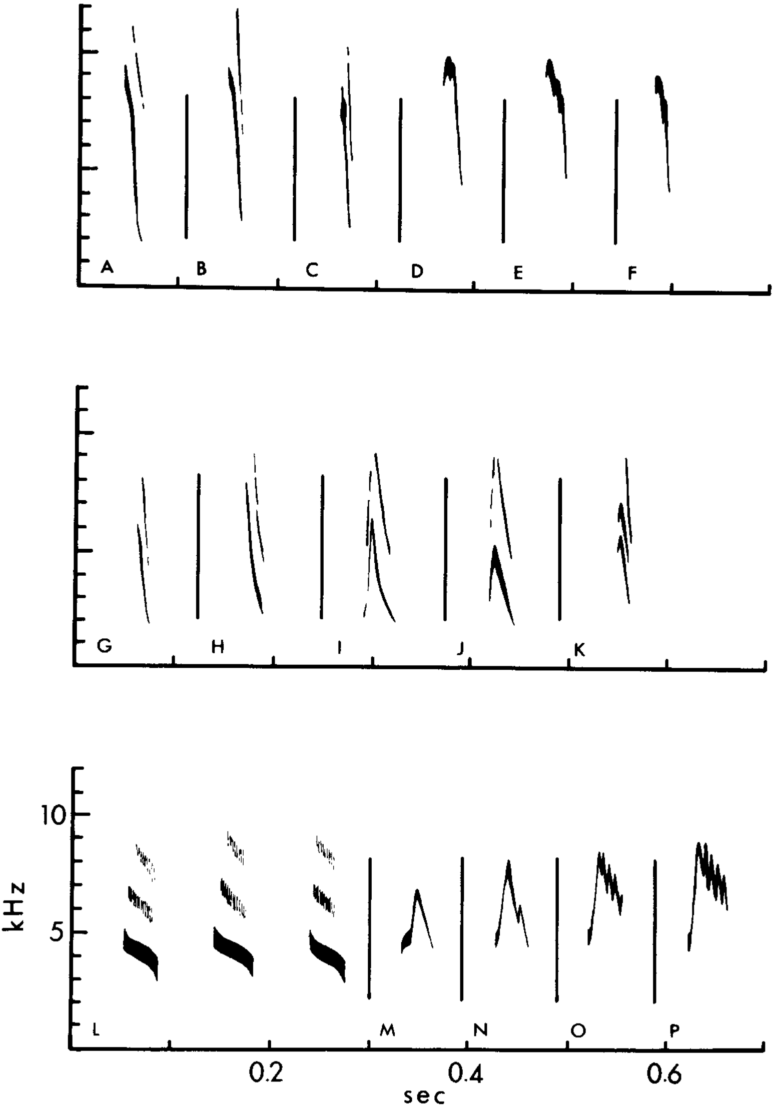

FIG. 3. Vocal displays of female Ovenbirds. A–C: *chep* vocalization. D–F: intermediates between *chep* and *high tsip* vocalizations. G–K: low frequency *chep* variants. L: "whimper" vocalization. Only 3 notes from a long series are illustrated. M–P: *seet* vocalization.

variants sound harsher than typical *chep* and may be described as *chup* or *chuck*. Full intergradation is demonstrated in the recordings of these variants. Hann (1937) commented that the *chirp* of female Ovenbirds when scolding was lower-pitched than that of males.

Females gave *chep* while moving with mates; transitions from *high tsip* to *chep* also occurred in this situation. Females used *chep* in response to a mate's song; *tsip series* given in similar circumstances was frequently prefixed by a single *chep*. *Chep* was given by females several times when they supplanted or chased their mates. In the only known female-female encounter during this study, vigorous chasing was accompanied by repeated *chep* vocalizations.

The other common use of *chep* was as part of the alarm reaction of female Ovenbirds to my approach to nests or fledglings. In these cases *chep* was given very vigorously and was continued until I moved away. This is the only situation in which the low frequency variants were recorded, although both types of *chep* were uttered by the same females on the same occasions.

Chep appears to encode messages relating to the relative probabilities of escape or attack behavior or, possibly, a more general message regarding the probability of locomotion without specifying the nature of the locomotory act.

(4) *Chitter* (Fig. 4C,D).—This display is a series of similar notes distinguishable from *tsip series* by the more rapid rate of delivery of the notes, and by the steady, rather than declining, rate of delivery. These 2 features produce a totally different sound impression, that of a continuous twitter rather than a series of distinct notes. The rarity with which this display was recorded leads to some ambiguity in its description. I recorded 2 distinct types of notes with the above patterning. Some examples (Fig. 4C) had *chip* notes with a long descending arm and little modulation of the fundamental frequency. Others (Fig. 4D) had highly modulated notes resembling *high tsip* notes in form but of a lower frequency. Once a bird switched from *chip* to *tsip* in the middle of a *chitter*. For this reason, plus the fact that the limited sample allows no separation by usage, the 2 types have been combined here.

On 5 occasions *chitter* was recorded from females giving a precopulatory display. At least twice it was followed by an apparently complete copulation. Females interacting with mates gave similar calls on other occasions, but ground vegetation prevented observation of the birds' postures or possible copulation attempts. Hann (1937) described the "mating call" of female Ovenbirds as a "series of chirps given in close succession." This description may include both *chitter* and *tsip series*.

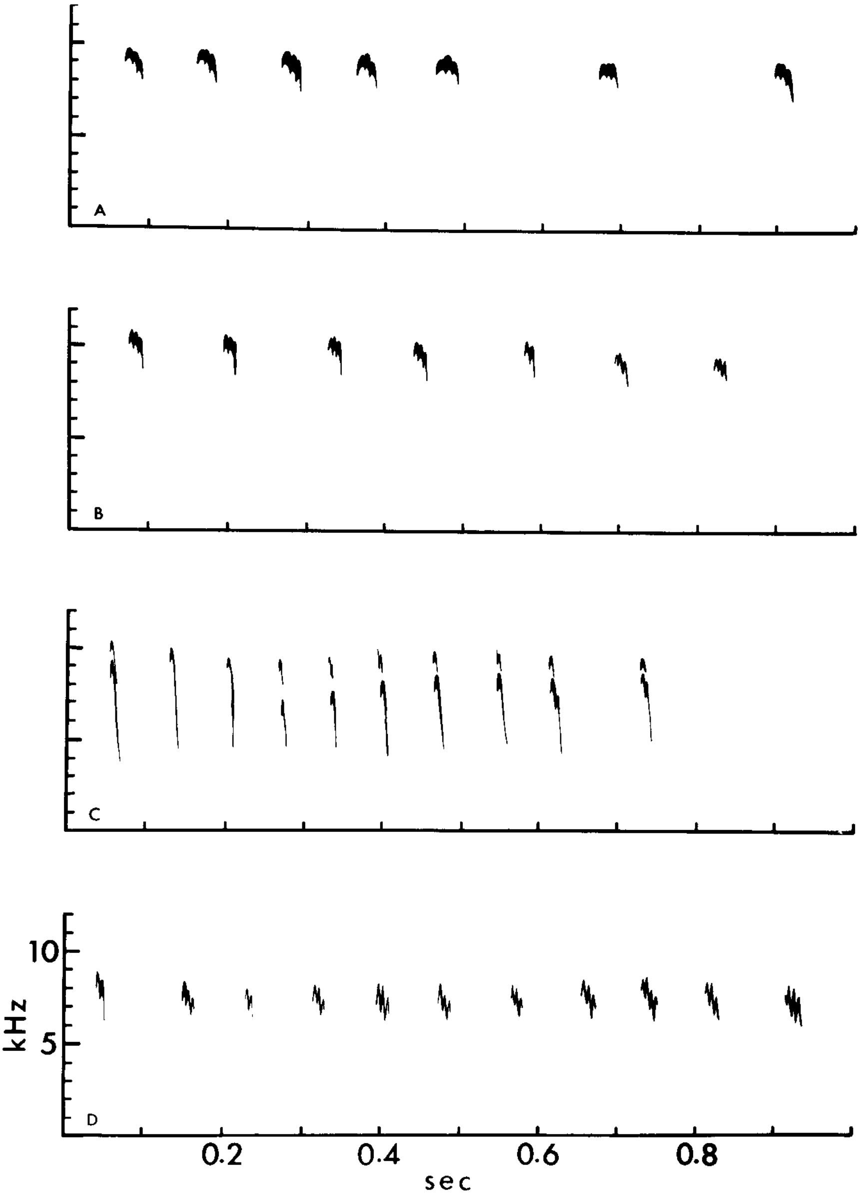

FIG. 4. Vocal displays of female Ovenbirds. A–B: *tsip series* vocalization. Note the gradual decline in rate and frequency of the notes during the series. C–D: "*chitter*" vocalization. Note that the rate of calling is higher than for *tsip series,* and that the notes in the example in D are of lower frequency than those of *tsip series.*

Chitter seems to be associated with a strong tendency on the part of the female to engage in sexual behavior. The message may be as specific as this would imply, but the use of this vocalization with the precopulatory display suggests a message concerning inhibited locomotor tendencies as well.

(5) "Whimper" (Fig. 3L).—This is a very soft vocalization, audible only within 5–10 m. The individual notes consist of a fundamental plus at least 2 weaker harmonics, and are repeated in long series lasting up to several seconds. "Whimper" was heard only once. A female gave it repeatedly during a strong distraction display as I banded the young in her nest. The significance of this vocalization is uncertain.

(6) *Seet* (Fig. 3M–P).—*Seets* are chevron-shaped notes that vary in the amount of modulation of the descending arm. The highly modulated notes have the highest peak frequency. Those notes lacking modulation (Fig. 3M) may be described as *chip.* All the notes illustrated were recorded in a single series lasting less than 2.0 sec, given by a female during an intense distraction display.

DISCUSSION

The Ovenbird is a remarkably vocal species, with regard to both the variety and frequency of vocal displays. I have described 13 different vocalizations in the present paper. Two distinct types of songs can also be recognized (Hann 1937, Lein 1973), giving a total of at least 15 vocal displays used by breeding birds. There are also several vocalizations used by nestlings and fledglings in begging or alarm situations (Nice 1931, Hann 1937). Various postures and other visual displays are also used (Hann 1937, Freeman 1950, Lein 1973), suggesting a total display repertoire as large as that of many social vertebrates (Smith 1969a, Moynihan 1970). It is clear that vocal communication is a major component of behavioral interaction among Ovenbirds. It thus warrants careful attention in any consideration of the evolutionary forces shaping the behavior of the species.

Table 1 summarizes the non-song vocalizations of adult Ovenbirds and the situations in which they are used, as determined by this investigation. Three points are worthy of special attention. First, there is almost no overlap between the vocal repertoires of the sexes. Only *chep* may be homologous in the 2 sexes and even it shows what appear to be sex-specific differences.

I suggest that this non-overlap of repertoires assists in sex recognition in a species which is monomorphic in appearance. Hamilton (1961) has argued that sexual dimorphism in plumage in migratory, temperate-zone parulids is an adaptation insuring unambiguous sex recognition, resulting

TABLE 1
SUMMARY OF THE VOCALIZATIONS OF BREEDING OVENBIRDS AND THE SITUATIONS IN WHICH THEY ARE USED

		Situation					
Vocalization	Sex	Male-female association	Copulation	Male-female chases	Male-female interactions	Alarm reactions	"Flight song"
Soft sip	M	++[a]	+	++	+	+	+
Chep	M	+		++	++	++	
Pink	M	++	+	+	+		
Seep	M	+++			+	+(?)	
Whink	M	++	+	+	++		+
Ple-bleep	M	++	+	+	++		+
Whip	M	+					
High tsip	F	+++					
Tsip series	F	++		+			
Chep	F	+		+		++	
Chitter	F	++	+				
"Whimper"	F					+	
Seet	F					+	

[a] The number of plus (+) symbols indicates the relative frequency of uses for that vocalization only, and do not refer to comparisons between vocalizations.

in a simplified and shorter courtship in species which face a breeding season of restricted duration. I believe that Ovenbird vocalization represents an alternate solution to this problem. Ovenbirds provide information regarding the sex of an individual through sexually-dimorphic vocalizations rather than through distinctive male and female plumages. My comparative investigations of other warblers support this suggestion. The Chestnut-sided Warbler (*Dendroica pennsylvanica*), a sexually-dimorphic species, has at least 6 vocalizations used in male-female interactions, of which 3 are identical in both sexes (Lein 1973). This compares with 1 shared vocal display out of 11 recorded in such encounters in the Ovenbird (Table 1). A similar explanation has been proposed for sexually-dimorphic vocalizations in the monomorphic Black-capped Chickadee (*Parus atricapillus*) (Ficken et al. 1978).

This reliance on vocal labels of sex identity may be related to the terrestrial habits of the Ovenbird. Sexual dimorphism in wood warblers generally involves a rather brightly-colored or conspicuous male plumage. If the olive-brown coloration of Ovenbirds indeed serves as camouflage, such an evolutionary option might be precluded. Vocalizations, unlike plumage patterns, can be turned off or on at will. However, this means that sexually-monomorphic birds may have to vocalize more frequently in order to provide relatively continuous information on their sexual identity, especially during close encounters. This suggestion is supported by my observation that female Ovenbirds are much more vocal during the pre-incubation period than are females of the sexually-dimorphic warblers I have studied (Lein 1973).

Table 1 also demonstrates the second point, that most vocalizations are used in a variety of situations. As intensive studies of complete display repertoires accumulate it is becoming evident that this is a general phenomenon (Smith 1977) and that the concept of each display possessing a single, precise meaning (e.g., "threat" display) is unlikely to be true in most cases. It appears that evolutionary pressures related to the misinterpretation of extremely similar displays and problems associated with very rare displays may restrict the total size of display repertoires (Smith 1969a, Moynihan 1970). Therefore, selection may favor displays that encode rather general messages which can be interpreted in various ways, depending on the recipient and on contextual information (Smith 1977:189). My findings on Ovenbirds are clearly in accord with this suggestion. Most displays were recorded in such a variety of situations that it is difficult to extract features that are common to all their usages. The messages that I suggest are thus very broad, the most common being one relating to the probability of locomotion. This message seems to be particularly common in the repertoires of other species as well (Smith 1969b).

The results of the generalized messages encoded by Ovenbird displays is that the effectiveness of communication must depend very heavily on contextual information available to recipients. Although detailed information on the responses of different classes of recipients to the same display is not available for the Ovenbird (or for most other species), the fact that identical vocalizations are given by male Ovenbirds in situations as different as territorial fights and copulation attempts suggests that contextual information must be critical for efficient communication. Important contextual variables are likely to include spatial features such as the location of the interaction in relation to territory boundaries, nests or mates, and temporal features such as immediately preceding events or the history of interactions between the individuals. Detailed studies of response of different recipients to the same display is a critical next step in increasing our understanding of the communication process.

The third point is the large proportion of vocal displays that are used in male-female interactions. Eleven of 13 vocalizations are used in such situations, a higher proportion than in other warblers I have studied (Lein 1973). This suggests that the pre-incubation period, which is when most male-female interactions occur, may involve rather difficult behavioral adjustments between the members of the pair and that, therefore, a major portion of the space in the limited total repertoire has been "allotted" by natural selection to this important behavioral task. This idea is supported by the high proportion of their time that the members of Ovenbird pairs spend in association and interaction during this phase of the breeding cycle (83.4% of 452 min of observation on birds whose exact breeding status was known) in comparison to the dimorphic Chestnut-sided Warbler (16.4% of 373 min).

SUMMARY

During a 3-year study of the behavior of Ovenbirds in New England, 13 non-song vocalizations were recorded from breeding adults. Most of these vocal displays are used in a broad range of situations, suggesting that they encode very general messages and that specificity in communication depends largely on the nature of the recipient and on contextual information. Most of the vocalizations are restricted to a single sex, possibly to assist in sex recognition in a species that is monomorphic in appearance. The use of 11 of the 13 vocalizations in male-female interactions suggests that pair-formation and courtship in this species involve complex behavioral adjustments.

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