

THE NON-SONG VOCAL REPERTOIRE OF THE WHITE-CROWNED SPARROW

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ABSTRACT.— We investigated the non-song vocal repertoire of the White-crowned Sparrow (*Zonotrichia leucophrys*) during the breeding season of 1981. Nine distinct vocalizations were recorded from males. Females used five of these; no calls were recorded exclusively from females. This limited sexual dimorphism in repertoire suggests that both vocal and non-vocal cues may be used in sex recognition. Most calls occurred in a variety of situations and appeared to convey only generalized behavioral messages. The structure of those calls whose information content seemed clear conformed to the predictions of models of selection pressures determining the physical forms of both long- and short-distance animal vocalizations.

Several authors have proposed explanations for the size, information content, and structure of display repertoires of social vertebrates. Smith (1969a) and Moynihan (1970) independently concluded that most species possess relatively small repertoires, usually around 40–45 displays. Smith argued that this limit imposes generality on the information carried by displays, with the result that most are used in a variety of behavioral situations. Vocalizations comprise a major portion of avian display repertoires (Wilson 1975). According to Smith's (1969a) prediction, most of these calls should be used in a variety of situations.

A number of studies support this prediction. The Eastern Phoebe (*Sayornis phoebe*) uses eight calls, three of which are common and used in many contexts (Smith 1969b). Ficken et al. (1978) found that many of the 13 vocalizations of the Black-capped Chickadee (*Parus atricapillus*) are used in a variety of contexts. Most of the 13 non-song vocalizations of the Ovenbird (*Seiurus aurocapillus*) are used in a variety of situations (Lein 1980). Both Ficken et al. (1978) and Lein (1980) found considerable sexual dimorphism in vocal repertoires of the monomorphic passerines they studied. Lein hypothesized that sexually-dimorphic vocalizations may assist in sex recognition in species which are monomorphic in appearance.

Several workers have proposed that the physical structure of vocalizations is not arbitrary. Calls that carry messages to be conveyed long distances are thought to be subject to selection pressures imposed by physical laws of sound transmission (Marler 1959). The information content of some long-distance calls is most efficiently used if the call is localizable. Such calls should have a wide frequency range

with many changes in frequency or repeated interruptions of the sound. Other long-distance calls carry information which is best used if the call is not localizable (e.g., alarm calls). These calls should have a narrow and intermediate frequency and should lack sudden changes in frequency (Marler 1959). In contrast, calls that convey information which is valuable only over short distances should be influenced by a relationship between motivation of the sender and structure of the call (Morton 1977). These motivation-structural rules (M.-S. rules) state that aggressive calls should be harsh, abrupt, and of low frequency. Calls least indicative of hostility should be pure tone-like, and of higher frequency (Morton 1977).

To test the generality of these ideas, we conducted a message-meaning analysis of the vocal repertoire of a monomorphic emberizine, the White-crowned Sparrow (*Zonotrichia leucophrys*). These birds were chosen for the study because a color-banded population was locally available. The specific questions asked were: (1) How large is the vocal repertoire? (2) Are most calls used in a variety of behavioral contexts? (3) Does the repertoire show sexual dimorphism? (4) Are the structures of long- and short-distance vocalizations consistent with those predicted? This lexicon of non-song vocalizations also complements the extensive literature on singing behavior in White-crowned Sparrows (reviews in Baptista 1977, Baptista and King 1980).

METHODS

Field work was conducted from 15 May to 15 July 1981 at Link Creek in the Rocky Mountain foothills, approximately 65 km SW of Cal-

gary, Alberta, Canada. The habitat consisted of grassy meadows with patches of bare ground, shrubs (mostly *Salix* spp. and *Betula pumila*), and conifers (primarily *Picea glauca*), and was crossed by several small streams. These habitat features match those described by DeWolfe and DeWolfe (1962) as universal elements of nesting sites of *Z. l. oriantha* in the western United States.

We recorded the calls of 20 color-banded individuals, using a Gibson P-650 electronic parabolic microphone and a Sony TC-142 cassette recorder. Verbal descriptions of relevant behavior (behavior of vocalizing birds before, during, and after the calls, and behavior of other birds in the immediate vicinity) were recorded simultaneously on the same tape, using a second microphone. Our familiarity with individual birds and the location of their territories allowed us to describe their location with respect to territorial boundaries. Most of the detailed observations were made on a subset of birds (approximately 10) that were either easily accessible for recording, or easily observed, or both. In most cases, it was possible to work within 15–25 m of the birds without causing a noticeable change in their behavior. Although we attempted to watch males and females equally, the data are biased towards males (65% of the recordings came from males).

Sound spectrograms of the calls were made with a Kay Elemetrics 6061B audiospectrograph using the wide-band filter. Terms used in description of the vocalizations were either taken from Harris and Lemon (1972), or adapted to non-song vocalizations from Borror's (1965) terminology for song description. They include: *Note*—a sound producing a continuous trace on the sonagram, *Phrase*—a group of one or more notes, *Syllable*—a phrase containing a serially-repeated note or combination of notes, *Call*—any phrase normally delivered as a unit and separated from comparable units by an average time interval longer than the intervals between notes and/or phrases within a unit, *Bout*—consecutive calls of a single type given without a change of context.

In this paper, the term "recorded" means that the vocalization was tape-recorded and identified on a sound spectrogram. Calls heard but not tape-recorded, even when a behavioral description accompanied the call, are not included in the tabulated results. A single bout is considered as a single occurrence of the call, regardless of the number of calls within the bout. Because naming of calls by reference to their underlying motivation implies that the display has only one function (Smith 1968), names given to calls were based on their phys-

ical appearance on sonagrams, or were verbal or onomatopoeic descriptions of sound quality. We used Smith's (1965, 1977) method for determining and classifying the messages encoded by the vocal displays.

RESULTS

We distinguished nine vocal displays (exclusive of song) used by some sex and age classes of White-crowned Sparrows.

PINK (FIG. 1A)

This was the most common and conspicuous call of the White-crowned Sparrow. It was brief (<0.1 s) and spanned a frequency range from approximately 3.0 to 7.0 kHz. *Pink* notes were often given in rapid succession, and bouts were sometimes longer than one minute in duration.

We recorded *pinks* on 108 occasions; 70 bouts were by males and 38 were by females. This call was used in a striking variety of situations (Table 1). Males were recorded using *pink* in a wider variety of situations than were females, probably because of the greater conspicuousness of males, their tendency to vocalize from exposed perches, and their higher frequency of using certain behaviors (e.g., fighting).

On 27 occasions, *pink* was associated with locomotion (Table 1). It was given on 35 occasions when an observer approached an active nest. We recorded the call only once during non-copulatory interactions between males and females, and never during copulatory interactions. The absence of the call in most male-female interactions, plus its occurrence after several unrecorded interactions between males (not included in Table 1) suggest the possibility of an agonistic message. The broad range of situations of use indicates a more general message, however, perhaps an indication of high arousal, or a state of indecision regarding subsequent behavioral acts.

Pink resembles the mobbing calls of various passerines (Marler 1958). Although we never saw predators near the sparrows and, hence, never witnessed mobbing behavior, the common occurrence of *pink* when humans approached nests suggests that it is probably used in such situations. DeWolfe (1968) described a scolding note used by White-crowned Sparrows to "protest intrusion by a person or animal," and Petrinovich and Patterson (1981) observed that "short, rapid notes covering a broad frequency band" were used when a disturbance occurred in the territory. Both of these descriptions probably refer to the *pink* note and provide further support for our belief that it is used as a mobbing call.

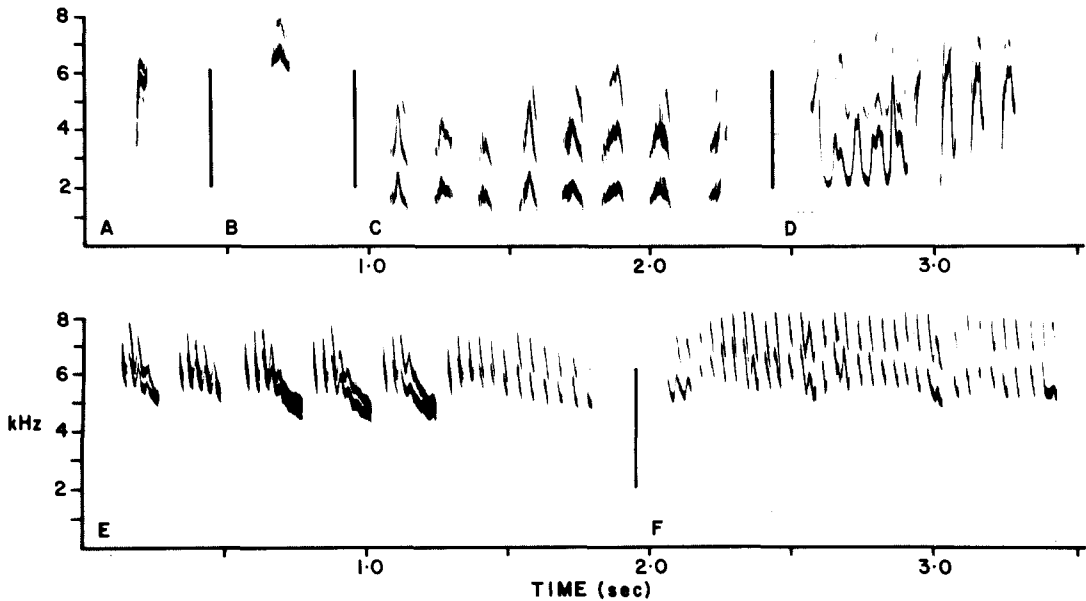


FIGURE 1. Calls shared by both sexes of White-crowned Sparrows: (A) *pink*; (B) *sip*; (C) *whine*; (D) *teez*; (E, F) two examples of *trill* showing typical variation. Vertical lines separate calls that are not continuous in time.

WHINE (FIG. 1C)

This harsh call was much quieter than *pink* and was usually audible to us only within 15 m. It consisted of a fundamental that increased, then decreased, in frequency and at least two harmonics. Figure 1C shows a series of successive notes given by one individual, but typifies the range of variability recorded in the total sample. The fundamental ranged in frequency from approximately 0.6 kHz to 1.5 kHz. *Whines* were invariably given in series with approximately 0.1 s between successive notes. The duration of series varied from about 0.1 s (single notes) to more than 3.0 s.

We recorded *whines* on 62 occasions, 31 times from females and 31 times from males (Table 1). We found no differences between sexes in the usage of the call. Like *pink*, this call was given in a wide variety of situations, but in 36 instances the calls were directly associated with locomotory behavior. The probability of locomotion was low in only four instances (while perched alone) in which *whine* was recorded. All situations of association involved at least some conflict of behavior, and imminent locomotion was a distinct possibility. *Whine* appears to indicate the high probability that the caller is, or will be, undertaking locomotory behavior.

TRILL (FIG. 1E, F)

This call was given by both males and females and was usually accompanied by a horizontal body posture, fluttering of the wings, and raising of the head and tail. *Trill* was audible to

us only within 15 m. It consisted of a series of repeated notes; series varied from 0.1 to 7.0 s in duration. The form of the notes also varied widely, both within and among individuals (Fig. 1E, F).

The observed variability and complexity of *trill* may mask consistent differences between the sexes in the call. All recorded occurrences of *trill*, including consecutive calls given within a single bout, were examined in greater detail. Significant differences were found in four characteristics (Table 2). *Trills* of females were longer, used fewer note types per call, and were lower in frequency than were those of males.

Males and females also differed in their use of *trill*. In 31 of 44 recordings from females, the call was given while in association with another bird, including eight copulatory interactions and 12 non-copulatory male-female interactions. The remaining 11 cases of female *trills*, which occurred in the presence of another bird, were given while associating with an unsexed bird, possibly a male (Table 1). We suggest that the female *trill* carries a narrow behavioral message relating to copulation and that it functions in soliciting a male. Blanchard (1941) observed that females begin to "utter low metallic trills and flutter their wings" at the onset of the breeding season while in the presence of displaying males. This observation undoubtedly refers to *trill*, and is consistent with our interpretation.

Bouts of male *trills* were recorded on 30 occasions, in a variety of contexts (Table 1). In 13 cases, this call was given during interac-

TABLE 1. Contexts of use of calls by male (M) and female (F) White-crowned Sparrows.

Context of caller	Number of bouts of call																	
	<i>Pink</i>		<i>Whine</i>		<i>Flag</i>		<i>Trill</i>		<i>Sip</i>		<i>Chatter</i>		<i>Rasp</i>		<i>Teez</i>		<i>W-call</i>	
	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F
Foraging alone	7	3	3	2	3	—	—	1	7	—	—	—	—	—	—	—	—	—
Conspicuous perch, alone	16	6	3	1	2	—	11	4	14	1	1	—	—	—	—	—	1	—
In flight	8	6	6	11	6	—	1	3	9	6	—	—	—	—	—	—	—	—
Associated with flight	4	5	3	7	3	—	—	—	6	—	—	—	—	—	—	—	—	—
Locomotion (non-flight)	3	1	3	6	4	—	—	1	—	—	—	—	—	—	—	—	—	—
Foraging in a group	1	—	2	1	1	—	—	—	5	—	—	—	—	—	—	—	—	—
Near an unsexed bird	8	—	7	1	1	—	4	11	5	—	—	—	—	—	—	—	—	—
Non-copulatory M-F interaction	1	—	1	2	—	—	—	12	2	—	1	—	—	—	—	—	—	—
Copulatory interaction	—	—	—	—	—	—	—	8	1	—	—	—	—	—	—	—	—	—
Non-fighting M-M interaction	2	—	—	—	—	—	8	—	4	—	3	—	—	—	—	—	—	—
During chase*	—	—	1	—	1	—	—	—	—	—	1	—	4	—	—	—	—	—
During fight*	1	—	2	—	3	—	1	—	—	—	—	—	1	—	—	—	—	—
Human approach to nest	19	16	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Context unknown	—	1	—	—	—	—	5	4	1	—	—	—	—	—	—	—	—	—
Other (see text)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	94	—	—
Subtotal	70	38	31	31	24	0	30	44	54	7	6	0	5	0	94	1	—	—
Total	108		62		24		74		61		6		5		94		1	

* Birds assumed to be males.

tions, but we never recorded it during interactions with a known female. We managed to record male *trills* during only one fight between males, but we heard them often in such situations. Of the eight occurrences during non-fighting interactions between males, four were given during obvious territorial disputes and were accompanied by strong singing. Six of the 11 recordings of *trill* from lone, perched birds (Table 1) involved territorial males who had recently (within 1 min) expelled an intruder from their territory. These observations suggest that the male *trill* is used in territorial defense and encodes information pertaining to attack behavior. We also recorded *trill* on 16 occasions (not included in Table 1) in apparent response to playback of tape-recorded songs, supporting this conclusion. Because the display was also given by (but not recorded from) males intruding on a neighbor's territory on several occasions, it may convey the more generalized message that the caller is undecided about subsequent actions (in this case, attack or escape). Blanchard's (1941) observations of male *trill* occurring after fights, during approach of neighbors, and "without special conditions," conform almost perfectly to this interpretation.

It is possible that the sexual differences in the *trill* are not recognized by the birds. If so, it is likely that the call carries a more general message that indicates only a high probability of interaction. The actual meaning of the call could then be determined by contextual information accompanying it, such as possible

differences between the sexes in the postures given with the display.

FLAG (FIG. 2A)

This call resembled *pink* in form, but frequencies above 6.0 kHz were emphasized in *flag*, while frequencies below 6.0 kHz were most prominent in *pink*. *Flag* usually was given in series of two or three notes separated by intervals of variable duration. *Flag* was frequently preceded by *pink* notes and followed by *whines*, suggesting that it might be an intermediate between these calls. The physical form of *flag*, however, was not intermediate between *pink* and *whine*.

Classification of *flag* as a discrete call is based primarily on its occurrence. All 24 recorded bouts were given by males (Table 1). This call occurred in a variety of situations, but 14 of 24 occurrences were directly associated with locomotion.

The use and, hence, the information content of *flag* appeared to resemble those of both *pink* and *whine*. Thus, *flag* may encode messages of both indecisive behavior (like *pink*) and locomotory behavior (like *whine*). Two lines of evidence, however, indicate that *flag* may carry a narrower, agonistic behavioral message. It was never recorded during male-female interactions, and the only male-male interactions during which *flag* was recorded were clearly agonistic (i.e., chases or fights) (Table 1). We suggest, therefore, that *flag* contains information pertaining to the more specific behavioral messages of attack or escape. Because

TABLE 2. Characteristics of male and female trills.

Characteristic	Male (n = 82) $\bar{x} \pm SD$	Female (n = 68) $\bar{x} \pm SD$
Duration (s)*	1.54 \pm 0.92	1.90 \pm 0.80
No. of notes per call	22.68 \pm 15.30	26.54 \pm 13.79
Notes per second	14.38 \pm 5.47	14.12 \pm 4.97
No. of different syllables	1.74 \pm 0.89	1.80 \pm 0.69
No. of different note types*	4.15 \pm 1.50	3.28 \pm 1.24
Maximum frequency (kHz)*	7.61 \pm 0.51	7.35 \pm 0.61
Minimum frequency (kHz)*	3.97 \pm 0.58	3.75 \pm 0.50
Frequency range (kHz)	3.64 \pm 0.69	3.60 \pm 0.73

* Significant male-female differences ($P < 0.05$, two-tailed t -test).

we do not know whether the calling bird was attacking or being attacked, we cannot determine which of these latter messages is carried by *flag*.

SIP (FIG. 1B)

Sip was one of the quietest calls given by these sparrows and was usually inaudible to us at distances greater than 5 m. It was typically a high-frequency (approximately 7.5 kHz) note which showed only slight frequency modulation. Many instances of *sip* showed less modulation than the example provided.

Fifty-four of 61 recorded bouts of *sip* were given by males, in a wide variety of contexts (Table 1). Twenty-one bouts of male *sip* were given by lone, mated birds, and 17 were given during non-agonistic encounters (Table 1). Females used *sip* almost exclusively during flight

(Table 1). Such flights were invariably by incubating females returning to the nest. Indeed, we were able to use this vocalization as an aid in finding nests. Perhaps most notable is that *sip* was never recorded during fights, chases, or other agonistic encounters. In light of this absence in agonistic encounters, the message of *sip* is probably best described by Smith's (1969a) category of non-agonistic behavior.

CHATTER (FIG. 2D-P)

Chatter was a complex vocalization comprised of a number of phrases. Unlike the multi-phrased song of this species, which is characterized by only slight variation within individuals (Baptista 1977), *chatters* from a single individual varied greatly. Phrases of this male-only call were always composed of a single note type with 1 to 4 (mode = 2) notes per phrase.

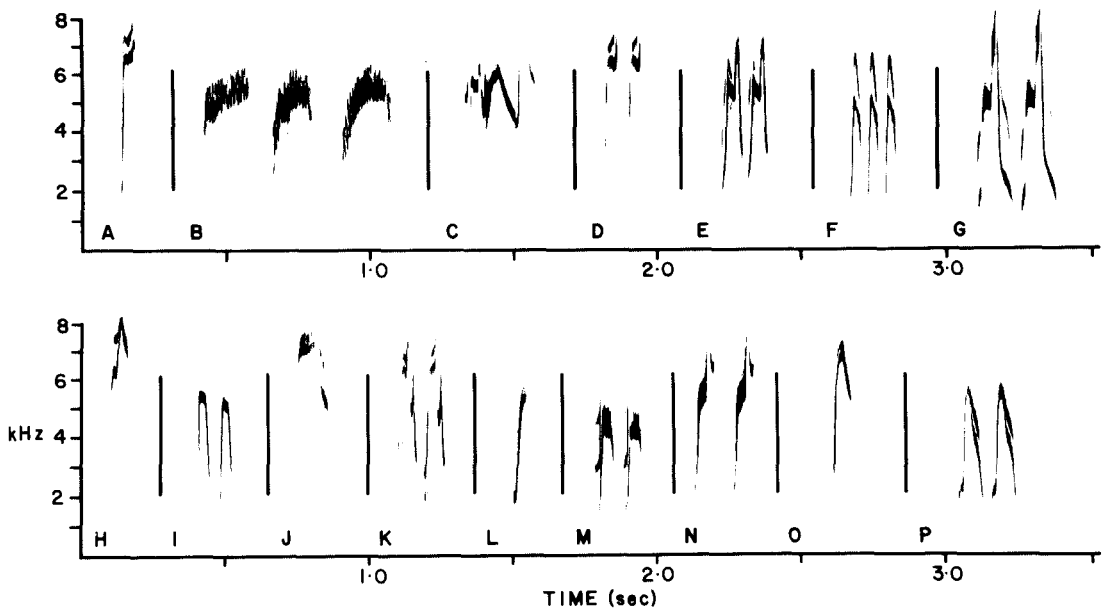


FIGURE 2. Calls recorded only from male White-crowned Sparrows: (A) *flag*; (B) three examples of *rasp*; (C) *W*-call; (D-P) note types used in the *chatter* call (multiple notes shown in D-G, I, K, M, N, P). Vertical lines separate calls or notes that are not continuous in time.

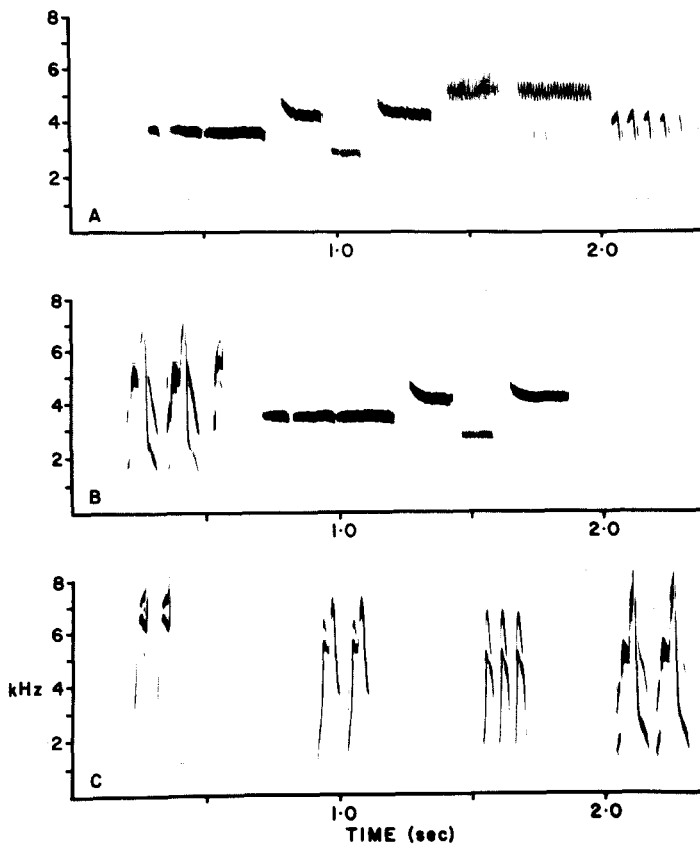


FIGURE 3. Complex vocalizations of male White-crowned Sparrows: (A) typical song of the local population; (B) aberrant song of one individual which incorporates a note type commonly found in the *chatter* call (see text); (C) version of *chatter* delivered most commonly, composed of note types shown in Figure 2D, E, F, and G.

Thirteen different note types were recorded (Fig. 2D–P). All but two (Fig. 2H, J) of these were repeated within a phrase. The interval between successive phrases was usually about 0.5 s, although this varied from approximately 0.1 to 0.9 s. The number of phrases per call ranged from 1 to 11 (mode = 4). Despite this variability, a single group of phrases composed of four note types (Fig. 2D–G), in the sequence DD-EE-FFF-GG (Fig. 3C) was by far the most common. Although the number of repetitions within each phrase of this pattern varied slightly, and occasionally the call was delivered without elements D or G, the sequence of notes just described never varied.

Only six bouts of *chatter* (from five individuals) were recorded, in four different situations (Table 1). All bouts of *chatter* were given by males within their territories. The bout given by a lone, perched bird was accompanied by several *pink* notes, indicating a highly-aroused bird in a state of indecision about subsequent behavior. During two of the three male-male interactions, there were four cases of *trill* be-

fore, and five cases of *trill* immediately after, utterances of *chatter*. In addition, on two occasions, *chatter* graded into a *trill*. On one occasion, alternating sequences of *chatter* and *trill* changed to pure *trill* when the intruding male gave a *whine* call. The bout of *chatter* during a male-female interaction was given while the female, who was not the mate of the caller, was feeding a fledgling that had intruded on the territory of the caller. One of the calls during this bout graded into the introductory whistle of a song. The final *chatter* bout was given as a male chased an intruder from its territory. Unfortunately, we did not know if the caller was chasing or being chased.

One additional observation seems relevant in determining the message content of *chatter*: one color-banded male changed his song in mid-summer from the type typical of the local population (Fig. 3A) to an aberrant type (Fig. 3B). The aberrant song consisted of a few repetitions of the *chatter* note type shown in Fig. 2G, followed by a *pink* note (G-G-*pink*), and by the first four phrases of normal song. This

male sang this aberrant song for the remainder of the breeding season.

The message conveyed by *chatter* seems similar to that of *trills* of males. Its combination with *pink* implies that the caller is highly aroused. Its use in association with *trill*, and less commonly with song, suggests that the three vocalizations carry similar messages. It seems likely that the message pertains to indecision regarding attack or escape. One likely way in which the messages of these three vocalizations differ is in the specification of probability of behavior. The progression from song, to *chatter*, to *trill* is probably accompanied by an increasing likelihood that the bird will perform overt aggressive behavior.

RASP (FIG. 2B)

Rasp was a distinctive, harsh call with a duration of approximately 0.2 s, and rapid frequency modulation between 3.0 and 6.0 kHz. The call was given as single notes as well as in series.

Rasp was recorded only from males, and only during chases and fights (Table 1). Despite our limited number of observations, the use of *rasp* suggests that it contains behavioral messages pertaining to attack and escape. Unfortunately, we do not know whether the caller was the attacking or escaping bird. *Rasp* may also indicate that the probability of attack or escape is higher than when *flag* is used.

TEEZ (FIG. 1D)

Teez was a call given by nestlings and fledglings, presumably of both sexes. It was a "noisy" call covering a wide frequency band (from approximately 2 to 8 kHz), and was characterized by rapid frequency modulation and several harmonics. *Teez* varied in duration from <0.1 s to >1.0 s.

Bouts of *teez* were recorded 94 times from fledglings of unknown sex. Seventy-seven of these bouts were recorded while an adult approached a fledgling and fed it. In addition, the call was recorded 17 times while the caller was perched alone but with an adult nearby.

Teez appears to encode information regarding seeking behavior. The caller is attempting to gain the opportunity to perform some other behavioral selection (in this case, feeding). Blanchard's (1941) observations of fledglings uttering a call when the "parents bring them food or come near them in foraging" probably refers to *teez* and supports this interpretation.

W-CALL (FIG. 2C)

Only two examples of this call were recorded during a single bout given by a perched, solitary male (Table 1). The call spanned a fre-

quency range from approximately 4.0 to 6.0 kHz and lasted about 0.2 s. *W*-call might be a variant of another call (e.g., *chatter*), but its distinctive sound quality and appearance on the audiospectrogram lead us to believe that it is a discrete call. The rarity of its use leaves the meaning of this (possibly) male-only call unclear.

DISCUSSION

The vocal repertoire of the White-crowned Sparrow includes at least nine distinct calls (ten, if sexual differences in the form of *trill* are recognized), plus the song of the male. Although the number of visual displays was not determined, it seems that the suggestion that the vocal channel is a major component of avian communication systems (Wilson 1975) applies to the White-crowned Sparrow. Three aspects of the results merit further discussion.

First, all of the five calls most commonly recorded from adults (*pink*, *whine*, *trill*, *flag*, and *sip*) were given in a variety of situations. The situations in which each call was used share some features, but only very imprecise information appears to be contained in each. This conforms to Smith's (1969a, 1977) conclusion that most vertebrate displays carry general, rather than specific, information regarding behavioral choices. Also, the messages conveyed in the calls are well-described by Smith's (1969a, 1977) categories of messages.

Second, sexual dimorphism in vocalizations is not as pronounced in the White-crowned Sparrow as it is in some other monomorphic passerines. Males used nine different calls (Table 1), while females used four of these regularly and one (*sip*) only rarely. In addition, one call (*trill*) possesses sexual differences in structure which are potentially recognizable by the birds. Three of the four calls recorded only from males were rare, and it is possible that females also gave these calls. *Flag* is the only call which was recorded frequently that was given only by males. We believe, however, that *rasp* is another exclusively male call. It was invariably associated with very aggressive interactions between males, encounters in which females were never involved.

If our interpretation is correct, the vocal repertoire of the White-crowned Sparrow consists of four calls shared by the sexes (*pink*, *whine*, *sip*, *teez*), two calls recorded only from males but possibly shared by females (*W*-call, *chatter*), one call showing sexual differences in form (*trill*), and two calls used exclusively by males (*flag*, *rasp*).

In the Black-capped Chickadee (Ficken et al. 1978) and the Ovenbird (Lein 1980), large proportions of the vocal repertoire are limited

to one sex or the other. This limitation appears to assist sex recognition in both of these monomorphic species. The situation in the White-crowned Sparrow is ambiguous. If, as suggested, two of the rarely-recorded calls of males are shared by females, then only two (or four, if the *trills* of males and females are distinctive) calls could serve to distinguish the sexes. All of these vocalizations are used rarely, or in highly specific situations. Therefore, sex recognition in most circumstances must rely on differences in visual displays or other behavior. The related ability of these sparrows to distinguish individuals in dominance hierarchies (Parsons and Baptista 1980) lends support to this suggestion.

Third, the physical form of calls does not appear to be arbitrary. Once the message content of a vocal display has been determined, it is possible to classify the call as subject to long- or short-distance selection pressures. Ficken et al. (1978) and Hope (1980) both stated that selection pressures on short-distance calls would differ from those on long-distance calls. In examining the vocalizations of the Black-capped Chickadee, however, Ficken et al. (1978) considered primarily selection pressures governing long-distance calls in their explanation of the physical form of the calls. The approach met with only limited success. Hope's (1980) broader approach also considered selection pressures relevant to short-distance calls to help explain the form of the calls of the Steller's Jay (*Cyanocitta stelleri*). Using this approach, she was better able to explain the physical form of most vocalizations.

Because the absolute auditory sensitivity of oscines is only slightly less than that of humans (Dooling 1982), we assume that calls that we could hear over a long distance would be similarly heard over a long distance by the sparrows. *Pink* was the only call audible to us over a long distance. Also, on the basis of its information content and the usual proximity of a recipient, *pink* appears to be the only call of the White-crowned Sparrow that conveys information over long distances. Its probable use as a mobbing call suggests that it should have features promoting localizability. Its wide frequency range, abruptness (Fig. 1), and repetitive delivery appear to conform to the selective requirements suggested for such vocalizations.

The remainder of the calls of the White-crowned Sparrow appear to be used in short-distance communication. The messages conveyed by some of these calls are difficult to dichotomize as either aggressive or non-aggressive. Some of the better-understood calls, however, approach the end points of this motivational continuum. *Sip* carries the message

of non-agonistic behavior. The M.-S. rules (Morton 1977) predict that it should be a high frequency call with only slight frequency modulation. Its physical form (Fig. 1B) agrees with this prediction.

Rasp is used only in highly aggressive situations, although we were not able to determine whether it was used by attacking or fleeing birds. Its harshness and emphasis of low frequencies appear to fit the M.-S. rules for aggressive signals. On the basis of these rules, we suggest that it is the aggressor who gives *rasp* in such encounters.

Like *rasp*, *flag* seems to convey specific information regarding agonistic behavior, but we were unable to clearly associate the call with either attack or escape. Analysis of *flag* in terms of M.-S. rules is ambiguous. Its abruptness suggests an aggressive use, but its emphasis on high frequencies suggests a non-aggressive motivation. Perhaps both messages are being encoded at once; a single broader message of either attack or escape may be encoded in this display.

Trill, *chatter*, *teez*, and *whine* are vocalizations whose uses fall between the end points of the continuum between aggressive and non-aggressive behavior. Two of the M.-S. rules appear relevant. First, calls whose frequency rises and falls more or less equally are believed to indicate that a stimulus of interest has been received by the caller (Morton 1977). *Trill*, *chatter*, and *teez* are calls characterized by rising and falling of frequency. Their messages of either attack or escape behavior (*trill*, *chatter*), or of seeking behavior (*teez*), fit this category of reception of a stimulus of interest.

The second relevant guideline is the widespread use of chevron-shaped calls by animals intending to move toward or away from a stimulus (Morton 1977). *Whine* consists of repeated chevron-shaped calls. Its use in situations involving locomotion seems to support the generality of Morton's ideas.

The existing theories governing avian vocal repertoire size, information content, and structure adequately predict and describe the non-song vocalizations of the White-crowned Sparrow. The proposed relationship between visual sexual monomorphism and vocal dimorphism appears less general in applicability. Further research on other monomorphic birds and mammals may reveal other factors which act in modifying the relationship between visual and vocal dimorphism.

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