SEASIDE SPARROW DISPLAYS: THEIR FUNCTION IN SOCIAL ORGANIZATION AND HABITAT

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THE behavior of the Seaside Sparrow (*Ammospiza maritima*) is of general interest because of this species' wide range of densities (Post 1974) and variation in patterns of dispersion in its breeding populations (Tomkins 1941, Woolfenden 1956, Post 1974). Woolfenden (1956) and Norris (1968) provided some information on the species' voicings and copulatory behavior, but for the most part its display behavior is unknown. This is perhaps due to the difficulty of watching Seaside Sparrows in the dense marsh vegetation they inhabit and to the low rate of social interaction in the sparse breeding populations that have been studied. The purpose of this paper is to (1) describe the displays of the Seaside Sparrow, (2) provide preliminary information on the displays' functions, and (3) suggest how the species' display behavior is related to its social organization and habitat.

METHODS

We studied free-living *A. m. maritima* at Oak Beach, Tobay, and West Gilgo Beach, New York during the summers of 1968, 1970, and 1971. Three study sites were in unaltered (unditched) salt marshes and three were in ditched salt marshes, described by Post (1970a, 1970b). The mean density of pairs of Seaside Sparrows was 24.8 per ha in the unaltered study sites and 1.0 per ha in the ditched study sites. We watched color-banded birds from elevated (1.5 m high) blinds or from the ground, recording oral descriptions of behavior on magnetic tape. From February through April 1970 we studied captive birds housed on a 14 h light-10 h dark regime.

In the field we measured the amount of time that individual males engaged in certain behaviors during continuous 30-min periods. We divided the daylight period into eight equal length intervals with 1300 as the midpoint. Observation sessions were distributed throughout the day, and the subjects watched during any diurnal interval were chosen in random order. Further details of the method by which we determined time budgets is given by Post (1974).

To mark the study areas we placed stakes every 25 m (sparse populations) or 12.5 m (dense populations). We determined the sizes of activity spaces by plotting the points at which individual birds were seen, connecting the outer points to form a polygon with only positive outer angles, and measuring the polygon with a compensating polar planimeter.

We recorded voicings with a Uher 4000 Report-L tape recorder using a microphone mounted at the focal point of a 24-inch parabola, and at a tape speed of 7.5 ips. Spectrograms were prepared on a Kay Sona-Graph, using the wide-band filter. Most illustrations of sounds used in this paper were traced from the spectrograms. The tracings are exact and not stylized.

Terminology used in verbal descriptions of spectrograms follows Bondesen and Davis (1966). A vocal display represented by a single figure on a spectrogram is

termed a "call." A call containing a narrow, uniform band of frequencies over time is referred to as a "note."

VOCAL DISPLAYS

Primary song.—Fig. 1 shows a representative spectrogram of the primary song. It is about a second in duration and consists of (1) a short vertical figure followed by a brief buzzy trill motif at a lower average frequency, (2) three to four additional short figures arranged in a broken V shape leading into (3) a buzzy terminal motif. To the human ear this song gives the impression of two short, somewhat harsh introductory sounds, the first at a slightly lower pitch than the second, followed by a trill. The last motif is not a true trill as it lacks the organization of sound into repetitive units uttered rapidly. Rather it is characterized by a general absence of temporal organization of sound while it has some frequency structure. Prolonged wavy tracings are stacked one above the other on the frequency scale over the lower frequency range where sound energy is concentrated. The spectrogram of the Seaside song given by Borror (1961) shows three sharp, weak notes preceding by 0.3 sec a second group of notes that correspond to our (first) short vertical figure. Borror's three notes are probably not part of the song; 0.3 sec spacing between groups of sounds in the Seaside song would be unusual. The spectrogram shown by Robbins et al. (1966) shows several very short, sharp low frequency tracings just before the accented trill sequence that is the first group of sounds we depict. Perhaps these are the "short, sharp notes" Borror mentioned.

Interindividual variation in song structure is apparent from field observation, but differences are not large. Some birds have fewer or more introductory sounds or an abbreviated or lengthened buzzy terminal motif. Intraindividual variation may be present to a small extent but cannot be characterized at the present time. Borror (1961) says that individual Seasides may sing four or more different patterns, differing primarily in the nature of the first two parts of the song. This is apparent from an examination of the three spectrograms available. Individual male Seaside Sparrows definitely do not have song repertoires containing several distinct patterns as is known for certain other emberizines, e.g. Rufous-sided Towhee (*Pipilo erythrophthalmus*) (Kroodsma 1971) and the Song Sparrow (*Melospiza melodia*) (Mulligan 1966). The general impression is one of relative uniformity in song form and quality in the populations investigated here.

The male usually sings from an elevated exposed perch within or close to his defended activity space, throwing his head back as he sings. The earliest we heard males singing was 9 April at Oak Beach. Before the

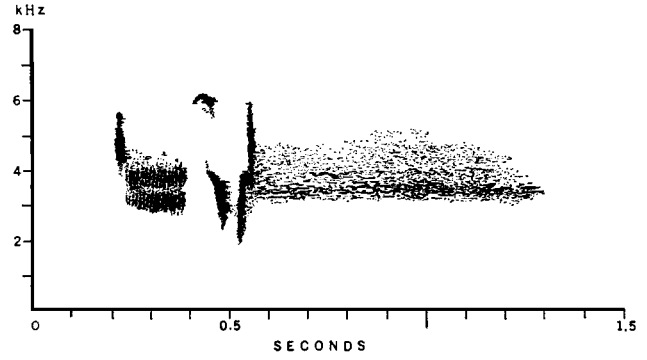

FIG. 1. Spectrogram of a representative primary song depicted at normal speed. See text for details.

females arrived, males spent a great amount of time singing (Table 1). During the period when the males were feeding the young, singing was greatly reduced, to 4.9% (dense populations, unaltered marsh) and 2.7% (sparse populations, ditched marsh) of the daylight period.

Peaks in singing activity occur in the early morning and late afternoon (Table 1). The same diurnal pattern is found for visual display, but males spend 6.2 times as much time engaged in primary song as in visual display (Table 1). Song rate during a song bout was 10.6 songs per min (12 birds were watched for a total of 82 min of singing, and song rate was measured during 56 intervals of longer than 1 min). One bird Woolfenden (1956) timed for 1 h sang 395 times or 6.6 times per min. During the middle of the daylight period, singing birds sometimes assume a resting position by settling on their tarsi. Periods of singing at this time often are alternated with other activities such as foraging or body maintenance. Birds sometimes sing during aggressive encounters, often in connection with wing raise display (see below), and if the opponents are at close quarters the song sometimes is muted. Flying birds sometimes give the primary song, usually just before landing. We heard single songs at night.

In dense breeding populations (24.8 pairs per ha) defended activity spaces (areas defended by visual display or fighting) were 81% the size of the singing activity spaces (areas in which males sang), but 10 out of 19 males did all their singing within their defended activity spaces. Foraging sites extended beyond the sites where visual and vocal display occurred (Table 2). Moreover birds with small activity spaces foraged at undefended localities separated from the activity spaces surrounding their nest sites. Birds in dense populations tended to remain silent when they foraged off their defended activity spaces, probably because they were attacked frequently when they sang.

TABLE 1

PERCENT OF DAYLIGHT PERIOD THAT MALE SEASIDE SPARROWS ENGAGED IN PRIMARY SONG AND VISUAL DISPLAY

Phase of breeding cycle activity	Dense populations (unaltered salt marshes)				Sparse populations (ditched salt marshes)			
	Before female's arrival (n = 88)[1]		After female's arrival and before incubation (n = 101)		Before female's arrival (n = 49)		After female's arrival and before incubation (n = 66)	
	Primary song	Visual display	Primary song	Visual display	Primary song	Visual display	Primary song	Visual display
Diurnal interval								
1	59.6	2.9	17.6	8.1	42.3	0.2	53.1	0.4
2	30.1	11.5	14.1	13.6	47.4	2.8	26.1	5.2
3	25.8	11.8	17.2	12.3	36.3	0	32.7	2.4
4	41.4	4.3	18.3	9.5	16.0	7.3	17.7	2.3
(1300)								
5	15.4	0.2	27.1	0.4	14.9	0	22.9	2.4
6	12.3	14.5	28.2	1.7	25.6	0	19.5	0
7	19.3	2.4	27.0	7.9	32.4	2.3	18.6	3.1
8	43.8	4.4	28.5	15.1	44.2	0	33.3	0.7
Mean for day	32.1	6.5[2]	22.3	8.6[2]	32.4	1.6[2]	30.0	2.1[2]

[1] Number of 30-min observation periods.

[2] Males in dense populations spent a greater amount of time engaged in visual display than did males in sparse populations ($P < 0.01$; $F = 23.3$). There was no difference in the amount of time engaged in primary song.

In sparse breeding populations (1.0 pair per ha) visual displays and fighting were largely confined to a nest centered area about 47% the size of the singing activity space (Table 2). Birds often sang as they foraged and, perhaps because they had few neighbors, they could sing almost anywhere they foraged.

Subsong.—The subdued song (Armstrong 1963) or subsong was frequently sung by two young captive males. It is a muted complex warble interspersed with tuck notes and snatches of primary song. We did not hear it in the field. A more advanced subsong (Fig. 2) was given by captive and free-living first-year males. This sequence contains a series of figures that resembles an incomplete primary song phrase with short extra trills and calls, including tuck, interspersed. The primary song pattern in the subsong at this stage differs in detail from the fully developed primary song. The terminal buzzy phrase is abbreviated, although it contains the typical frequency-dependent wavy tracings stacked one above the other with sound energy concentrated in the lower frequencies. The short introductory figures are present also, but vary in overall pattern from one song rendition to the next (compare the top panel with bottom, Fig. 2). The primary song patterns in the subsong differ further from fully developed song phrases in lacking the short trill following the first introductory figure(s) (see Fig. 1). The short extra trills interspersed among the incomplete primary song patterns of the subsong may become incorporated into the introductory phrase of the complete primary song at a later stage.

The subsong sequence depicted in Fig. 2 differs from early subsong in other passerines (Thorpe 1961: 64–70) in the following respects: (1) the main fundamental frequencies of the advanced subsong are higher, resembling those of the fully developed primary song; (2) the extreme frequencies have largely disappeared; and (3) the pattern of sound figures shows an organization that approaches that of the full primary song.

The advanced subsong resembles early subsong in that (1) it is prolonged, more or less continuous, with variable overall duration; (2) it contains extra short figures and trills; (3) it is uttered in relatively subdued tones; and (4) the lengths of the song bursts differ from those of full song—shorter in this case.

Thorpe (1961) pointed out that subsong is most likely to be recognized in species in which the primary song is a "loud and fairly stereotyped utterance in use as a territorial proclamation." In species where song has little territorial function, subsong may be less readily separable as a distinct category of vocalization. For example the Sharp-tailed Sparrow (*Ammospiza caudacuta*) does not appear to have a distinct subsong.

Complex flight vocalization.—Only males give the flight song. Fig. 3

TABLE 2
SIZES OF ACTIVITY SPACES (M^2) OF SEASIDE SPARROWS

	Dense populations (unaltered salt marsh)				Sparse populations (ditched salt marsh)			
	N	Mean	SE ($S\bar{x}$)	Range	N	Mean	SE ($S\bar{x}$)	Range
Total activity space	25	1203	240	160–6190	13	8781	2435	810–17,640
Foraging activity space	21	1039	238	170–5135	11	8121	2448	520–17,510
Singing activity space	21	484	111	88–2590	11	4669	1408	505–9000
Defended activity space	19	393	90	35–1296	5	2183	976	430–3250

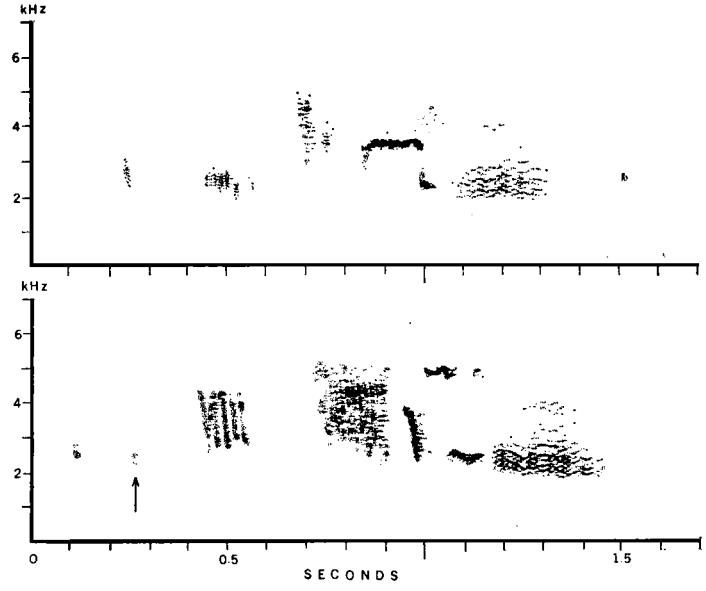

FIG. 2. Sequence of advanced subsong recorded in March from a dominant male Seaside Sparrow held in an outdoor aviary. The arrow in the bottom panel indicates the last figure of the top panel. The sequence illustrated is not a tracing but the original spectrogram. Time sequence is shown separately for each panel. The total length of the song as illustrated is about 2.7 seconds.

shows a representative complex flight vocalization. It consists of four distinct motifs and a terminal song phrase uttered in sequence: (1) a series of high-pitched si notes, fairly steady with a low frequency range; (2) two or more tuck sounds; (3) a series of somewhat variable, short, wide frequency figures (perhaps modified, high intensity tuck or tchi) forming a trill motif; (4) a short series (two in this case) of high-pitched figures descending in frequency; and (5) an abbreviated version of the primary song phrase. Shortening of the song phrase is accomplished by premature cessation of the buzzy terminal motif (compare Fig. 3 with Fig. 1).

The introductory si notes may be given on the ground or during early ascent and are somewhat run together at first, becoming regular just before the tuck figures. The initial irregularity may be associated with commencement of flight. During the ascent phrase, si and tuck notes are given. One or two primary songs may terminate the flight vocalization. The first may be given during ascent or at the apogee of the flight; the second, if present, is given during descent. If the last is initiated just before landing, it may be especially abbreviated. The two primary song

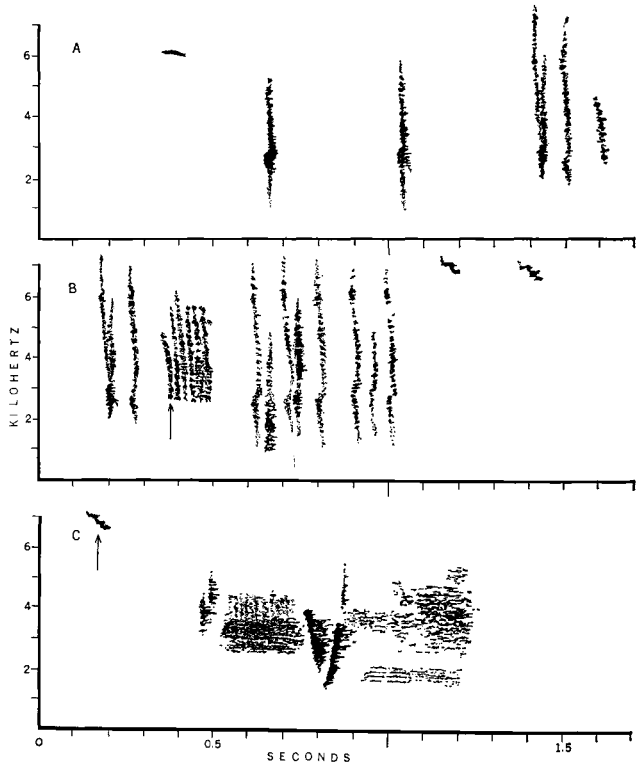

FIG. 3. Complex flight vocalization showing the different types of sounds. Arrows indicate the last figure in the preceding panel. Only the last of seven of the introductory si notes is shown in panel A. The time sequence is given in seconds separately for each panel. The total length of the vocalization as illustrated is about 3.3 sec.

segments are uttered one after the other without the usual pause heard during regular bouts of singing the primary song. Details of the flight display are given later.

Flight songs were more common after females arrived on their males' territories. Before the arrival of females on the males' territories, we did not hear this voicing during 69 h of observation of individual males. In 84 h of observation during the period after females were on territory males spent 0.1% (dense populations) and 0.2% (sparse populations) of the daylight period engaged in flight display. Some males give the flight display much more frequently than others on a given day. Typically the flight song is not repeated immediately; rather the bird waits a varying but usually prolonged interval before its next song flight.

Flight songs are widely distributed among emberizines, but are more typical of species living in open, relatively simple habitats. Other species such as the Rufous-sided Towhee lack a specialized flight song. In the Song Sparrow the ordinary primary song may be given in flight but the characteristic flight song consists of a "tit-tit-tit" twitter followed by the regular song or a jumble of variable, short sounds (Nice 1943). It thus resembles that of the Seaside Sparrow in containing the twitter (fear notes of Nice) as an introduction and the primary song as a terminal flourish.

Female songlike vocalization.—This sounds to the human ear as a "tijeeep" or "beeert," buzzy and with the same tone as the trill of the primary song. This sound was heard from only three females, just before or immediately after copulation. It is given with the wing raise, either from the ground or an elevated perch. The female songlike vocalization attracts males, and it may serve a function similar to the whinny. The sound is called songlike because of its resemblance to the primary song, and because it appears to serve a more narrow function than the whinny, that of attracting a mate to the female's vicinity.

Female song has been reported in a few other emberizines. In the Song Sparrow, Nice (1943) described it as short, simple, and unmusical. It usually occurs before nest building and is associated with a generally higher level of aggression than is often seen in females on territory.

Whinny vocalization.—The whinny (Fig. 4A), a nasal, whining vocalization with a distinct quaver, varies in length and intensity. The sound figures are all below four kHz and are typified by a distinct downward slur, forming a reverse J figure. The first harmonic is shorter, more U-shaped, and is followed by a downward slurred segment. The vocalization may be transcribed as "whiu whiur wheeurr wheeurr." It sometimes is immediately preceded by the tchi vocalization (see later).

Only females give the whinny, and it appears to function primarily to attract the mate. Birds give the whinny repeatedly during solicitation (copulatory display), and also after copulation, particularly when the female is gathering nest material. The female often used it (14 of 19 cases) in the presence of the male; and if he is absent, he is attracted to the vicinity of his mate when she gives the call.

We observed the following associated postures in one case: low oblique to nearly horizontal body stance, crouch, neck moderately extended, wings raised and outspread (bilateral but asymmetrical) about 45° above the horizontal and waved, with moderate fluffing of the body feathers. In one case, a whinny from a female immediately followed the utterance of primary song by a male. At variable intervals the male gave primary songs 0.5 to 1.0 m from the female. She then interrupted apparent forag-

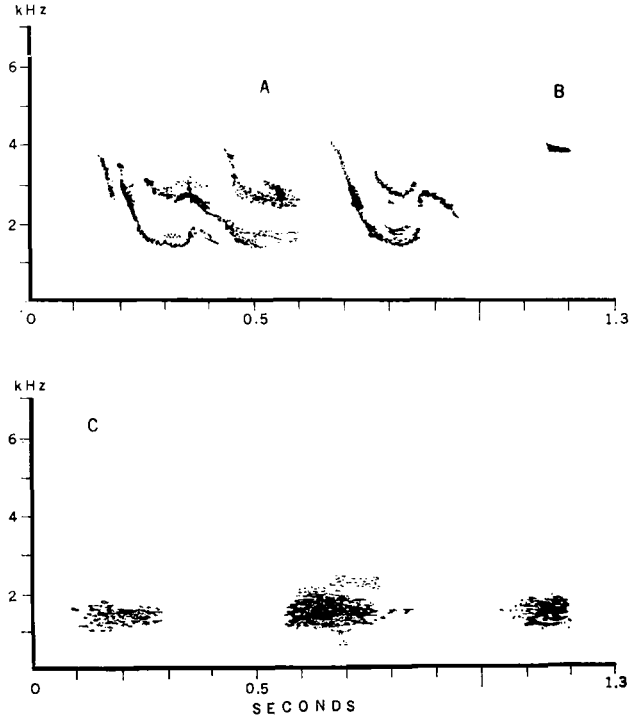

FIG. 4. Seaside Sparrow spectrograms. A, a complete (short) whinny; B, tsip call; C, three chew calls in sequence. See text for details.

ing and gave the whinny with associated postures. The male was erect, watchful, but did not approach. The primary songs of the male seemed slightly subdued in tone and came at irregular intervals.

Vocalizations used by the female in sexual solicitation contexts (mate or other male attracted during period when displaying female is sexually receptive) have been described for all emberizines whose behaviors have been closely studied (Tinbergen 1939, Nice 1943, Andrew 1957b, Moynihan 1963, Nethersole-Thompson 1966). In some emberizines, e.g. *Emberiza* spp. and Rufous-sided Towhee (Greenlaw MS), the solicitation vocalization is relatively high-pitched and repeated in series as a chatter. The call is usually given before and sometimes during copulation, but in the Rufous-sided Towhee (Greenlaw MS) and Seaside Sparrow, the female may utter it in the presence of a male-male interaction involving her mate. In the Seaside Sparrow and Green-backed Sparrow (*Arremonops conirostris*) (Moynihan 1963) the elements of the solicitation call are strongly slurred downwards (plaintive quality). In other emberizines

this vocalization of the female is relatively harsh, perhaps indicating a strong agonistic message (chatter in the Song Sparrow and skirr in the Snow Bunting, *Plectrophenax nivalis* (Nice 1943, Nethersole-Thompson 1966)). This vocalization is typically associated with a bill-up-tail-up, concave posture, and wing quivering.

Tsip call.—This call, described by Woolfenden (1956), is a single note, moderately high-pitched, sibilant, and relatively short (Fig. 4B). It is given by both sexes during aggressive interactions involving either sex. After the primary song the tsip call is the most common vocalization heard in the breeding season. In 12 of 19 cases it was given during an aggressive encounter and less often (7 of 19 cases) on the approach of a predator.

The tsip seems to be associated with mobbing behavior, where its message signifies strong conflict between a tendency to leave and one to remain. Perch changes are frequent but localized, and exposed birds maintain their distance from the observer. When a nearby observer moved suddenly, the bird uttered a si twitter (see later), which changed to single, spaced tsips and then to tucks interspersed with occasional tsip calls. In a disturbed pair one bird may tuck call and the other, at a greater distance from the disturbance, and perhaps more prone to change perches, gives the tsip call.

We heard Sharp-tailed Sparrows give a vocalization similar to the tsip call.

Si twitter.—This is a series of rapidly repeated notes, "si-si-si-si-si." The si note may be a high intensity tsip call differing only in the probability modifier of its message content (see Smith 1969). Yet the si series is distinctive enough (repeated rapidly and higher pitched than tsip) so that it is advisable to retain the separation between the two. As indicated above, the si twitter, like the tsip call and tuck call, seems to be part of mobbing behavior. We often heard it at the same time that neighboring Red-winged Blackbirds (*Agelaius phoeniceus*) gave their hawk alarm call (Orians and Christman 1968). On several occasions captive Seasides gave the si twitter when they were mounted by either a Sharp-tail or another Seaside. In these cases the call was probably associated with a strong fear (tendency to flee) rather than a sexual tendency.

Both the si twitter and tsip call are associated with a sleeked crown, moderate crouch accompanied by bobbing (see later), tail cocked about 30° above the horizontal, and wing-tail flicking with each sudden movement of the bird. The si twitter is sometimes given during flight, and also it is apparently the same twitter that makes up the first part of the complex flight vocalization.

In the presence of predators or in similar contexts in which a bird shows

a strong tendency to flee, freeze, or hide (fear), calls are high-pitched and often somewhat prolonged (Thorpe 1961). In the Seaside Sparrow the si note is short but repeated as a chatter. The Song Sparrow utters a series of high-pitched tik notes (Nice 1943) in contexts that may induce rapid fleeing. Other emberizines (*Emberiza* spp.) may only give a single, more prolonged call in the presence of predators (Andrew 1957b).

Chew call.—Repeated, as "chew-chew-chew," this call is given only by females, either directed to predators (in five instances in the presence of an observer) or in the presence of a Seaside Sparrow who is not their mate. It is given with the wing raise, usually from an exposed perch.

The chew call is depicted in Fig. 4C. The three calls shown were uttered in sequence and differ in intensity of utterance. The chew call lacks the higher frequencies characteristic of the zuck call.

Tchi vocalization.—This may be transcribed as "si si tchi-tchi-tchi-jyuu jyuuu jyuuu." It is somewhat variable in different renditions: si notes may or may not be present and it may have from two to five tchi elements. It is probably the same vocalization described by Norris (1968) as "jee-jee-jee-jee-jee-jeeéu-jeeéu."

The last part of a tchi vocalization given in flight is depicted in Fig. 5A. The shorter, nearly vertical figures, transliterated as "tchi" are followed by a series of prolonged, downward slurred figures, transliterated as "jyuuu." Each slurred figure overlaps temporally with the next one in the series. The lower frequency segments of some of the slurred sounds resemble segments in the whiu whinny vocalization (see Fig. 4A).

The tchi is the fourth most common vocalization heard during the breeding season. Females gave it 42% of the time and males 58% of the time (82 cases). In 43 of 82 cases the tchi was used in flight. On the ground it is often given when a bird is about to fly or has just landed. Both sexes may utter the tchi on leaving the nest, and the male often uses the call on returning from a distant feeding trip off his territory. In 63 of 82 cases the tchi was used during an aggressive encounter with either a Seaside or a Sharp-tail. It accompanies other displays such as wing raise. The female gave the tchi in the presence of her mate in 9 of 32 cases. It was heard twice directed to a predator (man), and was heard once uttered by a bird on release from captivity, this being the only case of the call being heard in the winter. In the fall, we heard it given by several birds that were being held together in a gathering bag.

During aggressive interactions the tchi is sometimes associated with the zuck call. It is often associated with the whinny vocalization, when a female is interacting with her mate. In some cases recorded on tape, a tchi transposed into a whinny, e.g. "si si si tchi tchi tchi jyu jyuu whiuuu whiuuuu."

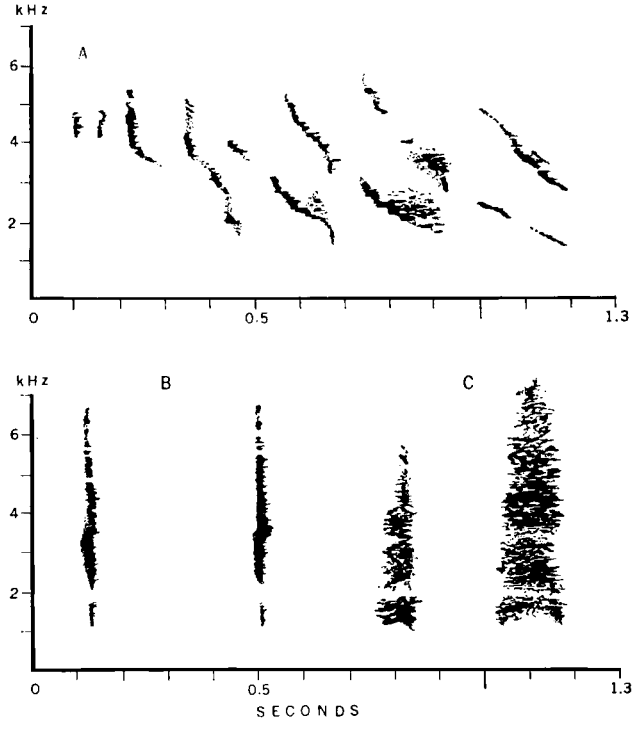

FIG. 5. Seaside Sparrow spectrograms. A, last part of a tchi vocalization showing two types of sound elements, tchi and slurred jyuuu; B, two tuck calls in sequence; C, two zuck calls in sequence. See text for details.

The brown towhees (*Pipilo fuscus* and *P. aberti*) also have a special complex vocalization associated with flight or locomotion in the presence of the mate or an intruder. The messages may be similar and apparently include an element of hostility (Marshall 1960). Green-backed Sparrows give a vocal series, termed medium hoarse notes by Moynihan (1963), in similar contexts, and it perhaps contains similar messages. Moynihan mentions that the vocalization indicates a locomotory tendency and functions as a greeting. These displays may fall in the category of locomotory hesitance vocalizations reported in *Tyrannus* (Smith 1966). Other emberizines lack these complex, locomotory displays, e.g. Song Sparrow (Nice 1943) and Rufous-sided Towhee (Greenlaw MS).

Tuck call.—The tuck is a short abrupt call with a wide range of frequencies (Fig. 5B). A close inspection of the original spectrograms suggests that the call is composed of two separate elements that overlap slightly in time and frequency. One element contains frequencies at about 1 to 3.5 kHz and the other at about 3.2 to 6.5 kHz. The call is often

repeated in series. The rate of cadence is sometimes regular, other times irregular. Samples of cadence are 35/min, 101/min, 102/min, 118/min, 131/min, and 165/min.

The tuck is the third most common vocalization. Both males and females give the call. In 37 of 48 cases it was uttered during aggressive interactions between Seasides. In 5 of 48 cases it was given when a predator (including observer) was nearby. In 3 of 48 cases it was used by a Seaside chasing a Sharp-tail and in 2 of 48 cases it was uttered by a male approaching a female. Tuck is given by parent birds when an observer approaches a nest with young and by birds in the hand or in mist nets. It is heard in the nonbreeding season (fall).

The tsip call and zuck call are often associated with tuck. A tuck-calling bird often is associated with a tsip-calling bird, usually its mate. One bird responded to sudden movement by a nearby observer by uttering the si twitter, which became single, spaced tsips and then as the observer remained still changed to tuck calling with tsip interspersed. The tuck calls switched to si twitter when the observer again moved.

There is little or no wing-tail flicking with tuck calling; there may be some low crest ruffling. Tuck-calling birds seem to have a lower tendency to change perches than those uttering tsip calls.

Female Sharp-tails give a similar call, chuck, when flying to and from nests that contain young. This may be the same call that Woolfenden (1956) refers to as the tsuck alarm call.

Zuck call.—The zuck call is shown in Fig. 5C. The two calls were given in sequence and differ in intensity of utterance. The difference in intensity appears on the spectrogram as differences in overall frequency and timing.

Fighting males give zucks, and they are used in connection with the various visual displays such as wing raise. Zucks are characteristic of intense fights: two opposing males rise in the air, clawing at each other or pulling at each other's breasts with their beaks. One bird sometimes grips the other and holds him down, both birds giving zucks. On one occasion two birds fell in the water locked together, and remained submerged for several seconds, then flew out in a prolonged chase, during which more zucks were given.

Harsh, low-pitched growling calls, either single or repeated, seem typical of strong agonistic situations. The cherr of the Snow Bunting (Tinbergen 1939), the zhee of the Song Sparrow (Nice 1943), the harsh hoarse notes of the Green-backed Sparrow (Moynihan 1963) and the chaa in *Emperiza* spp. (Andrew 1957b) may be homologous to the hoarse zuck of the Seaside Sparrow.

Seeep note.—It is usually uttered by a bird being pursued in flight,

either by a fleeing male or by a female during sexual chasing. It is also given by females immediately prior to and during copulation. It probably functions to convey a weak fear message.

We heard this sound or a very similar one during the nonbreeding season, and it is likely the same note that Woolfenden (1956) referred to as the social call, given commonly by migrant Seasides. The note is heard often in the fall when groups of Seasides gather in tall *Spartina alterniflora* and feed on the seed heads. Sharp-tails utter a similar note during the nonbreeding season, and at that time they often occur in loose feeding groups with Seasides.

Chup call.—Nestlings or fledglings repeat this alarm call rapidly. Young that are almost ready to leave the nest (older than 8 or 9 days) utter the chup call when handled or when they jump out of the nest as they are disturbed. The call attracts adults to the nest.

Scree call.—When they are being handled, adult and immature birds may give this harsh call. It is given most often by a bird immobilized in a mist net.

Visual Displays

Wing raise.—The wings are held up together, usually more than 30° above the horizontal, and as much as 45° (Fig. 6B), or one wing is extended upward higher than the other (Fig. 6A). The wings are vibrated slightly in their extended positions, and often are held out for several minutes. The tail feathers are spread. The body feathers are fluffed or ruffled. Bilateral wing raising is most often seen when interacting males are within 0.2 m of each other, while unilateral wing raises are used during what appear to be less intensive aggressive encounters. With the wing raise the male gives the tchi vocalization and occasionally the primary song.

Although the wing raise is used most often during border disputes, both sexes wing raise prior to copulation, often while uttering the tchi vocalization. The female wing raises while giving the whinny, and also in response to the presence of an intruding male. Male and female Seasides wing raise in the presence of Sharp-tailed Sparrows.

On one occasion the bilateral wing raise was combined with a peculiar pirouetting movement, in which the male described a 200° arc, repeating the movement several times, and singing at the same time. This dance was performed in the open with another male nearby, for whose benefit it was presumably given.

Raising the wings reveals the yellow carpal feathers that are hidden when the wings are closed. Several other emberizines that have yellow carpal feathers also give raised wing displays, such as Baird's Sparrow (*Ammodramus bairdii*) (Cartwright et al. 1937), Grasshopper Sparrow

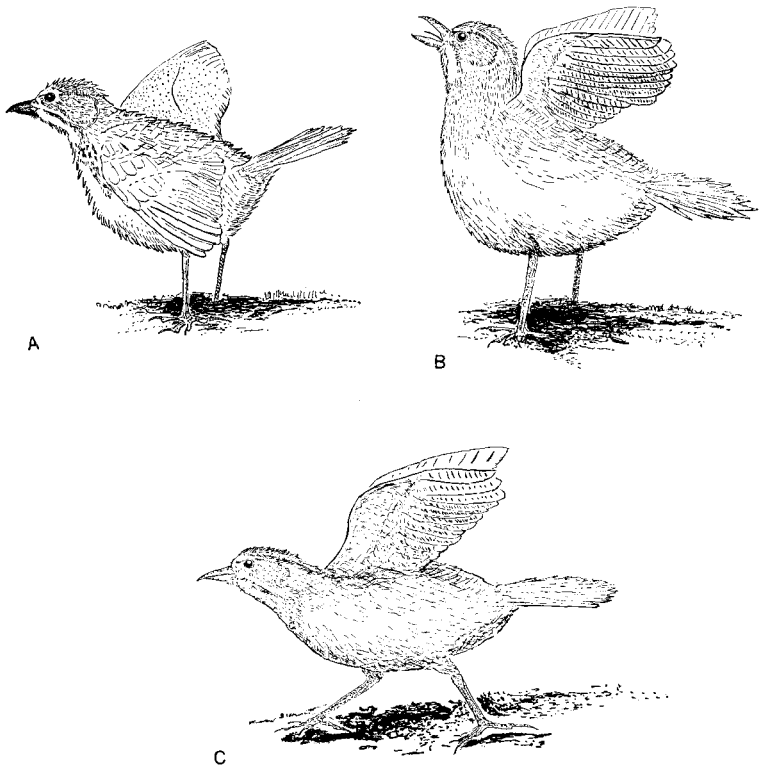

FIG. 6. Visual displays of the Seaside Sparrow. A, wing raise (unilateral); B, wing raise (bilateral); C, distraction display.

(*Ammodramus savannarum*) (Smith 1959), and Green-backed Sparrow (Moynihan 1963). Other North American emberizines that have a wing raise display include the Song Sparrow (bilateral and unilateral (Nice 1943); the Swamp Sparrow (*Melospiza georgiana*) (unilateral) (Greenlaw MS) and the Rufous-sided Towhee (unilateral usually) (Greenlaw MS).

In many aggressive situations the body feathers are raised without elevating the wings. Opponents move together or briefly stand opposed. The wings may be drooped. The degree of body feather raising varies, apparently directly with the intensity of the interaction. Males and females that engage in close quarter interactions with intruders often raise their body feathers to such an extent that they resemble balls of feathers. The combined extreme body feather raise and wing raise resembles the puff-sing-wave display of the Song Sparrow illustrated in Nice (1943: 156).

Bobbing.—When two males face each other in disputes at the edges of their territories, they raise and lower the foreparts of their bodies: erect, with head up, then breast and head lowered (erect, watchful tendency alternating with preflight tendency). Opponents hold their heads at a downward angle or horizontally, often gaping their beaks and fluffing their plumage, with wings slightly lowered. Sometimes opponents parry and thrust at each other with their beaks, as though they were trying to gain an advantageous position to deliver a peck. Tsip, tuck, and zuck often accompany bobbing.

Bobbing or head lowering is seen in near rivals, and perhaps in other contexts, in several *Emberiza* spp. (Andrew 1957a), the Song Sparrow (Nice 1943), and the Snow Bunting (Tinbergen 1939). In several of these species the bill also may be lowered (bill lowering of Andrew 1957a).

Head forward threat.—We saw captive birds give what seemed to be the typical passerine head forward threat posture (Andrew 1957a). The bird lowers and extends its head horizontally and points its beak at an opponent; the beak is often gaped. The plumage is relaxed or sleeked. The display is usually given when birds are disputing perches, particularly at roost time. Often captive Seasides give the head forward threat with the wings raised to the horizontal. The head feathers may be raised and the legs flexed. The head forward threat is given with tuck calls. Captive Sharp-tails commonly give this display and, like Seasides, often continue the head forward threat into an active attack, pulling the tail or body plumage of an opponent. Both species use the display against each other.

In the field the head forward threat appears in boundary disputes, often in combination with several other components: fluffing of the body feathers, raising the wings, and lowering and extending the head. Lowering the head and raising the back and rump feathers give the bird a hunched over appearance. The bird may or may not raise its wings, either to or above the horizontal. When the wings are raised, this posture resembles the ballooning posture of the Song Sparrow ("threat posture, puffing" (Nice 1943: 156)).

In one instance the head forward threat was used in combination with bobbing (transcribed from field notes): "Three males were facing each other in the open. One circled around the other with his back feathers raised, head down with beak pointed horizontally and wings extended outward to the horizontal. The wings were curved, so that the tips pointed downward, and the wing feathers were partially or fully spread. The rump feathers were extremely raised. His head feathers were in the normal position, but breast feathers were raised slightly. He kept flexing his legs at the heels so that his whole body bobbed up and down."

Head forward threat displays in agonistic encounters with conspecifics have been reported for other emberizines by Andrew (1957a), Nice (1943), Tinbergen (1939), Nethersole-Thompson (1966), and others.

Distraction display.—This display was given by females disturbed from a nest that contained eggs or young. The back and crown feathers are raised, the tail spread, and wings raised (Fig. 6C). The bird makes short flights, runs on the ground, and utters tsip and tuck calls. This display is elicited only when the female is actually flushed from the nest; if she is away when the nest is approached, her response is to return and give tsip and tuck calls from a distance. Woolfenden (1956) saw a male and female Seaside give distraction displays in response to his handling their young.

We did not see the distraction display in unaltered (unditched) salt marshes, although we visited 186 nests an average of three times each. Of 19 nests visited in the ditched marshes, three females gave distraction displays repeatedly during one year (one of these did so in 1970 and in 1971). The absence of the display in the unaltered salt marsh populations can probably be explained by the wetness of these marshes, and the resulting scarcity of ground predators. Foxes and weasels are present in the ditched marshes. Orians and Christman (1968) point to the absence of distraction displays in marsh-dwelling blackbirds. In addition, visibility could be a factor (Armstrong 1954), as there would be no advantage in displaying to predators in dense vegetation such as found in unditched salt marshes.

The distraction display, sometimes called injury feigning, is known in several emberizines, including the Song Sparrow (Nice 1943), Snow Bunting (Nethersole-Thompson 1966), Reed Bunting (*Emperiza schoeniclus*) (Andrew 1956a), and Rufous-sided Towhee (Greenlaw MS).

Carrying material.—Often during border disputes a male pulls at the vegetation or wrack debris, sometimes picking up a piece of grass or wrack (in one case, 10 cm long) that he carries in his beak for several minutes while in the presence of his opponent. Birds carrying material usually wing raise or fluff or ruffle their plumage. The material is not carried away from the display site. After copulation males may also pick up material, but they do not engage in nest building. Females carry material immediately after copulation, but they usually transport it to a nest site.

Carrying material by the male in the presence of his mate is known for a number of emberizines and may be widespread. It is seen in the Green-backed Sparrow (Moynihan 1963), Song Sparrow (Nice 1943), several *Emberiza* spp. (Andrew 1957a), Snow Bunting (Nethersole-Thompson 1966), and Rufous-sided Towhee (Greenlaw MS). As in the Seaside Sparrow the Rufous-sided Towhee carries debris in the presence

of a rival male. Female Brown Towhees (*Pipilo fuscus*) sometimes carry material in sexual contexts (Marshall 1960) as does the female Seaside Sparrow.

Sham feeding.—Two or more males move together, usually parallel to each other, pecking at the substrate, but rarely capturing prey. The rate of movement and rate of pecking appear to be slower than in ordinary foraging. The birds are usually 0.2 to 0.3 m apart. The body feathers are in the relaxed position or fluffed. The birds sometimes wing-tail flick and utter tsip notes. The interacting birds appear to be acting independently of each other, although their movements are parallel in space.

Sham feeding also occurs in the Song Sparrow (Nice 1943), Snow Bunting (Nethersole-Thompson 1966), Rufous-sided Towhee (Greenlaw MS), and other emberizines. It is sometimes called displacement feeding and occurs widely among birds. In the towhee, as in the Seaside Sparrow, food may be captured and eaten, so such feeding cannot always be characterized as incomplete.

Wing-tail flicking.—The wings are moved rapidly over the back, then down and out from the body; simultaneously, the tail is moved up and then down. The tail feathers are not spread. The plumage is sometimes slightly fluffed. The tsip note is usually given. Wing-tail flicking is common during interactions between males and between males and females. Sharp-tailed Sparrows have a similar display.

Wing and tail flicking occurs widely among emberizines and may be universal. Moynihan (1963) described the displays in the Green-backed Sparrow as "ritualized intention movements of flight." Aside from species already mentioned in comparisons of behavior above, wing-tail flicking is known for the Dark-eyed Junco (*Junco hyemalis*), White-throated Sparrow (*Zonotrichia albicollis*) and Chipping Sparrow (*Spizella passerina*). The form and frequency of flicking displays may differ from species to species. In the Rufous-sided Towhee wing flicking is uncommon, while tail flicking involves a sudden opening-closing of the outermost rectrices (Greenlaw MS).

Hunch down.—The head is pulled into the body, the crown feathers are raised, body feathers ruffled, and the tail is held up (Fig. 7A). A subordinate bird, if approached too closely by an opponent, assumes this posture, often crouching down on its legs. The subordinate sometimes bill wipes. Among captive birds the hunch down is common, as birds have no way of escaping from dominants. But free-living birds that intrude on the territory of another and are challenged either escape or hide under the vegetation, and in the latter case often raise the crown feathers. This display resembles the female copulatory display, and may function as an appeasement. Sharp-tails give a similar display.

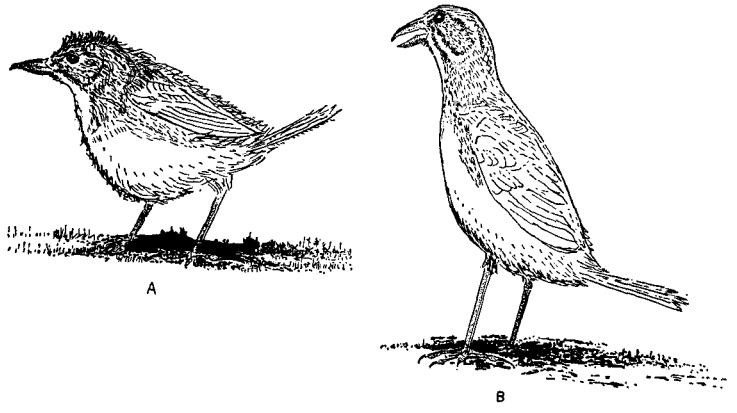

FIG. 7. Visual displays of the Seaside Sparrow. A, hunch down; B, erect posture.

Erect posture.—This was seen in captive birds (Fig. 7B) but not in the field. This posture is assumed by a dominant bird approaching a subordinate, particularly at a food dish. It is often accompanied by wing-tail flicking and gaping. The feathers of the head and neck are sleeked. Captive Sharp-tails also assume the erect posture, often with gaping.

Wing trailing.—We did not see this display in the field. The tail is maintained at a downward angle, the remiges are spread, and the wings are extended slightly downward, but in to the body. As with the erect posture birds give this display when approaching their subordinates. The display is most often given in interactions at the food dish.

Gaping.—This display was noted often in captive birds, but infrequently in the wild. A threatening bird opens its beak and points it in the direction of its opponent. Birds that have assumed the erect posture (Fig. 7B), the head forward threat, and wing trailing often gape. Captive Sharp-tails also gape during aggressive encounters. Subordinate birds, both Sharp-tails and Seasides, often gape in defense when they are challenged by a superior of either species.

Bill wiping.—Captive birds commonly wipe their beaks by moving one side of the beak and then the other over the perch. Subordinates waiting for a superior to leave the feeding dish give these movements frequently, as do birds that are supplanted or have been chased. In these cases bill wiping is being used in an irrelevant context, as it usually serves to clean the beak after feeding or preening. Bill wiping occurs during reproductive fighting of several species of *Emberiza* (Andrew 1956b).

Flight display.—Males usually fly up from an elevated perch, but occasionally from the ground, ascending to a height of 5 to 15 m. The angle of ascent varies from nearly level flight to as much as 50° or 60°

above horizontal. During the ascent the bird gives the introductory segment and may give the first primary song segment of the complex flight song, as described above. At the apogee the bird may momentarily hold stiffened wings outstretched and above the body horizontal, with the beak oriented upward. The first primary song segment may be given at this point rather than during ascent. The bird then descends with a reduced rate of wingbeat and during the descent phase often utters a second primary song. The angle of descent is usually 20° to 40° below the horizontal, and on approaching the ground, birds often continue the flight display into level flight, landing as far as 50 m from the original perch. Woolfenden (1956) also described the Seaside flight display.

The form of the flight display of the Seaside Sparrow, consisting of ascent, a horizontal component in which the bird modifies body orientation and wingbeat pattern, and then a gliding descent, resembles that described for the Snow Bunting (Nethersole-Thompson 1966). In contrast, the flight display of the Song Sparrow involves a simple ascent and descent (Nice 1943). Murray (1969) described the flight displays of the Sharp-tailed Sparrow and Le Conte's Sparrow (*Ammospiza lecontei*).

Copulatory display.—In this display females fluff their body feathers and bring their wings up to the horizontal, extending them outward, and quiver them, while raising and spreading the tail and pointing the beak upward. The female frequently whinnies, and as the male approaches more closely, or jumps on her back, she utters seeep notes. Copulation may be repeated up to three times within 5 min. After coition, the female sometimes gives the female songlike vocalization, and begins gathering nest material, while uttering the whinny.

The male does not assume any special posture, although he usually gives wing raises. Coition lasts 2–3 sec, with the male standing on the back of the female, sometimes gripping her nape with his beak, with his wings extended horizontally and fluttered slightly. After coition males often gather material in their beaks. The male mandibulates the material, usually dead grass, wrack, or feathers, carries it a short distance, and drops it. As noted above, males also carry material in boundary disputes with other males.

The form of the copulatory display seems generally similar to that of all emberizines in which it has been described. Andrew (1957a) calls it the soliciting posture and Moynihan (1963) bill-up tail-up. It is widespread and probably universal among emberizines.

Message Content of the Displays

Variability exists even in stereotyped displays, although it must be limited if the displays are to serve as a means of communication. Some

TABLE 3
SUMMARY OF VOCAL DISPLAYS OF THE SEASIDE SPARROW

Display	Accompanying visual displays	Contexts in which elicited[1]	Observed response of recipient[2]	Probable messages[3]
Primary song	Wing raise, bobbing	Male: 1, 2, 3, 5	Attracts or neutral: b Neutral or repels: c, d, f Repels: e	I, III
Complex flight vocalization	Flight display	Male: 5		II–IV
Female songlike vocalization	Wing raise	Female: 2	Attracts: a, c-f	VII, VIII
Whinny vocalization	Wing raise, copulatory display	Female: 1, 2	Attracts: a, c, f Attracts or neutral: d Neutral: f	VII
Tsip call	Bobbing, head forward threat, distraction display, carrying material, sham feeding, wing-tail flicking, erect posture, wing trailing	Male: 1, 2, 4, 5 Female: 1–5	Attracts: a, b	I–VI
Si twitter	Distraction display, wing-tail flicking	Male: 4, 5 Female: 4	Hide: a-f	III, IV
Chew call	Wing raise	Female: 1–4	Attracts: a Repels: e	III, IV

[1] Contexts in which elicited: 1, in presence of intruder or neighbor; 2, in presence of mate; 3, in presence of Sharp-tailed Sparrow; 4, in presence of predator; 5, in flight.
[2] Recipients of displays: a, male on his activity space; b, female on activity space of her mate; c, neighboring male on his activity space; d, neighboring female on activity space of her mate; e, male intruder; f, female intruder.
[3] Probable message: I, general set; II, locomotion; III, attack; IV, escape; V, nonagonistic subset; VI, association; VII, bond-limited subset; VIII, copulation; IX, frustration.

TABLE 3—*Continued*

Display	Accompanying visual displays	Contexts in which elicited[1]	Observed response of recipient[2]	Probable messages[3]
Tchi vocalization	Wing raise, bobbing	Male: 1–5 Female: 1–5	Attracts: a-d Repels: e, f	III–IV, VI
Tuck call	Wing raise, bobbing, head forward threat, distraction display, carrying material, sham feeding, erect posture, wing trailing	Male: 1–5 Female: 1–4	Attracts: a-c Repels: e	II–IV
Zuck call	Wing raise, bobbing, head forward threat, carrying material, sham feeding	Male: 1, 5	Attracts: a-d	II–IV
Seeep note	Copulatory display	Male: 1, 5 Female: 1, 2, 5	Neutral: a-d	II, IV
Chup call		(given by young only)	Attracts: a-d	IX
Scree call		Male: 4 Female: 4	Attracts: a-d	IX

postural or vocal components are contained in several displays, or may be found in different combinations under different conditions. In categorizing the displays of the Seaside Sparrow, we have necessarily been arbitrary. Some of the primarily agonistic displays such as bobbing, wing raise, and head forward threat have common postural elements, are given in the same situations, and may be similarly motivated. We feel that the displays as we have described them are sufficiently distinct and occurred alone frequently enough so that they serve different functions. For example, although bobbing shared postural features in common with wing raise, the characteristic motor patterns (raising and lowering of the body by flexure of the legs, beak jabbing) are so complex and distinct that they alone imply a different signal function.

A display must be judged on the basis of inferred communicative significance. The function of the displays may be deduced from the situations where they are given and the responses of recipients (Tables 3, 4). The basic function of any display is the transfer of information between individuals, this information being the messages of the display. Each display carries one or more messages plus two modifiers (identification and probability), and the recipient may interpret a display by the particular combination of messages it contains, and by the context in which it is given (Smith 1969).

The probable functions of the displays of the Seaside Sparrow may be examined in terms of nine message categories. These are discussed in detail by Smith (1969). He lists 12 message categories, but two of these, identification and probability, are contained in all displays. For one other category, play, we have no data for the Seaside Sparrow. The message categories used here are:

(1) General set: displays used in association with many different activities. The message may specify that a change in the activity is likely.

(2) Locomotion: displays used during locomotion or at the start and finish of locomotion, including motor patterns that may indicate a tendency to fly, such as wing and tail flicking.

(3) Attack: displays used in attack or when communicator is making an intention movement that is followed by attack.

(4) Escape: displays used during escape or gradual withdrawal; displays that indicate locomotory hesitancy may carry escape messages.

(5) Nonagonistic subset: a subset within the general set of behavior—displays given under a number of conditions—when communicator may flee, associate, forage, or preen, but not attack.

(6) Association: an individual may use displays in approaching another individual without gaining contact, and at the same time avoid contact, or passively permit approach.

TABLE 4

SUMMARY OF VISUAL DISPLAYS OF THE SEASIDE SPARROW

Display	Accompanying vocal displays	Contexts in which elicited[1]	Observed response of recipient[2]	Probable messages[3]
Wing raise	Primary song, female songlike vocalization, whinny vocalization, chew call, tchi vocalization, tuck call, zuck call	Male: 1, 2, 3 Female: 1, 2, 3, 4	Neutral: a, b Neutral or repels: c, d Repels: e, f	II, III, IV
Bobbing	Primary song, tsip call, tchi vocalization, tuck call, zuck call	Male: 1	Repels: e	II, III, IV
Head forward threat	Tsip call, tuck call, zuck call	Male: 1, 3 Female: 3	Repels: a-f	II, III, IV
Distraction display	Tsip call, si twitter, tuck call	Female: 4	Attracts: a	II, III, IV
Carrying material	Tsip call, tuck call, zuck call	Male: 1, 2 Female: 2	Neutral or repels: c Neutral or attracts: b	II, III, IV, IX
Sham feeding	Tsip call, tuck call, zuck call	Male: 1, 2	Neutral or repels: c	II, III, IV, IX
Wing-tail flicking	Tsip call, si twitter	Male: 1, 2, 4 Female: 1, 2, 4	Neutral: a, b Neutral or repels: c, d Repels: e, f	II, III, IV
Hunch down	Tsip call	Male: 1	Neutral or repels: c	II, III, IV
Erect posture	Tsip call, tuck call	Male: 3 Female: 3	Seen only in captives	II, III, IV
Wing trailing	Tsip call, tuck call	Male: 3 Female: 3	Neutral: c, d Neutral or repels: a, b Repels: e, f	II, III, IV
Gaping	None heard	Male: 1, 3 Female: 3	Repels: e, f	III
Bill wiping	None heard	Male: 1, 2, 3, 4 Female: 1, 2, 3, 4	Neutral: a, b, e, f	V, IX
Flight display	Complex aerial vocalization	Male: 5		II, III, IV
Copulatory display	Whinny vocalization, seeep note	Female: 2	Attracts: a, c, e	VII, VIII

[1, 2, 3] Footnotes explained under Table 3.

(7) Bond limited subset: behavioral acts occurring between mates or between parents and young.

(8) Copulation: displays used only before or during copulation.

(9) Frustration: displays used only when a particular behavior would occur if the opportunity were available, or when the opportunity is no longer available.

Of the 14 visual displays we have described, 11 appear to contain both attack and escape messages. On the basis of an evaluation of the situations in which they were given and of the observed responses of recipients (Table 4) we can tentatively grade this series (not including flight display) according to the relative strength of these two messages. The probability of correlation with attack increases and the probability of correlation with escape decreases in the following series: hunch down, wing trailing, erect posture, wing-tail flicking, sham feeding, carrying material, distraction display, head forward threat, bobbing, and wing raise. The following six vocal displays may be graded in a similar manner: si twitter, tsip call, tuck call, tchi vocalization, chew call, and zuck call.

Certain vocalizations seemed to contain the locomotion message: tchi call, seeep note, tuck call, and complex flight vocalization (Table 3). The scree call, hunch down, and perhaps sham feeding and carrying material may encode a frustration message. Only the female Seaside appears to possess displays incorporating the copulation message: female songlike vocalization and copulatory display. Association messages are apparently carried in the tchi vocalization, seeep note, tuck call, and female songlike vocalization. Bond-limited messages are transmitted by the whinny vocalization and the chup call.

The male song functions primarily as an identification message, but it may act as an aversive stimulus (attack message) to other males and also as an attractant to females (association message or bond-limited message). These ideas are based on the following circumstantial evidence: (1) unmated males continue in persistent song while during the same period mated birds greatly reduce the amount of time devoted to singing. (2) Song is reduced when the female arrives on the territory (Table 1). (3) In sparse breeding populations the space in which singing takes place is larger than the space defended by visual display, but in dense populations, the singing ground is often smaller than the defended territory (in 10 of 19 cases). Peek's (1972) experimental study of the visual and vocal displays of the Red-winged Blackbird indicate that visual displays are more effective repelling stimuli than is advertising (primary) song. Our data on the size of the places in which visual and vocal display take place confirm Peek's model that vocal display constitutes the first defense

perimeter, and visual display the second line of defense of the nesting territory. (4) That song is an important identifier of sex is revealed by the observation that in the early spring, when territories were being established, males followed each other around and displayed (wing raise, sham feeding, head forward threat) for extended periods of up to 22 min, but fighting only occurred when one of the birds gave the primary song. Thus, song may provide an important modifying message for other displays such as wing raise, which is given by both sexes.

Display Repertoire in Relation to Social Organization and Habitat

Seaside Sparrows were found nesting in a wide range of densities, as low as 0.6 pair per ha in altered salt marshes and as high as 30.0 pairs per ha in unaltered habitat. Birds that nested in sparse populations (ditched salt marshes) defended large activity spaces (Table 2) and fed in areas adjoining their nests. In contrast, birds breeding in the dense populations defended small activity spaces and often fed communally in places at some distance from the activity spaces surrounding their nests.

The Seaside Sparrow is monogamous. Males arrive on their territories 5 to 14 days before their females. The male's role is at first confined to defense and advertisement of the activity space surrounding the nest. The female alone builds and attends the nest. The male begins to feed the young when they are 3 to 5 days old, and then he supplies food as often as the female. Both sexes feed the fledglings.

An apparent consequence of the different densities and dispersion patterns of the populations was the significantly greater amount of time that males in the dense populations (unaltered habitat) spent engaged in visual display (Table 1). No differences existed in the amount of time spent in primary song.

We have described 27 displays (13 vocal and 14 visual, not including the male subsong). This display repertoire size falls well within the range of 15 to 45 known for vertebrate species in general (Smith 1969). The display repertoire is evenly divided between vocal and visual displays (Table 5). This may be adaptive in the Seaside Sparrow as it occupies such a wide range of territory sizes. Visual displays are effective in close quarter interactions, which are common in dense populations. Vocal display would not be as useful in densely populated breeding grounds because of the noise. In such populations selection may favor a smaller vocal repertoire and less elaborate songs. In sparsely populated areas vocalizations are more effective than visual displays as they carry over long distances.

As in marsh-dwelling icterids (Orians and Christman 1968) the territories of the Seaside Sparrow are relatively small, perhaps resulting in

TABLE 5
CONTEXTS IN WHICH DISPLAYS WERE GIVEN BY FREE-LIVING SEASIDE SPARROWS

	Territorial defense[1]	In presence of predator	In presence of mate	Total displays for each sex
Male: Visual	10	2	5	11
Vocal	6	5	4	9
Female: Visual	6	4	5	9
Vocal	6	6	6	9
Total displays for both sexes	18	10	11	27

[1] Display given in presence of Sharp-tailed Sparrows and Seaside Sparrows.

reduced selection for individuals with complex song. The structure of the primary song with its introductory notes and buzzy terminal trill is similar to the songs of colonial icterids (Orians and Christman 1968) and the colonial ploceids (Collias 1963). The short, unmusical song of the Seaside Sparrow probably evolved from aggressive notes. The introductory notes of the Seaside primary song resemble the tuck call (compare Fig. 1 and Fig. 5B).

The male has a well-developed set of displays associated with territorial defense (Table 5). The female uses fewer displays in territorial defense, but she fulfills an important function in warning the male of the arrival of intruding Seasides, both male and female, by giving tchi calls, tuck calls, and wing raising. Females also actively challenge and chase Sharp-tailed Sparrows from the territory. Nice (1943: 165) reported that female Song Sparrows helped their mates drive off intruders, and also drove them off alone, but generally female territoriality is unusual or rarely reported.

In the presence of predators females give more displays than do males. This is to be expected, as only females attend nests until the young are 3 to 5 days old. Females are also more closely tied to the territory than males during the incubation and nestling phases, and males spend proportionally more time feeding on distant feeding grounds.

Males and females have the same number of visual displays associated with mating and pair bond (Table 5). This equality may be related to the monogamus mating system of the Seaside. In polygamous species such as the Red-winged Blackbird the male has a larger set of displays than the female (Orians and Christman 1968), which presumably facilitates his breeding with more females.

Although the male and female Seasides use the same total number of vocal displays (Table 5), the female has several specialized vocalizations concerned with mating. This may be due to their importance as locational

(identification) messages in the dense vegetation, but also they are presumably bond-limited messages, and as such act to strengthen the pair bond.

The Seaside Sparrow lives in a structurally simple habitat where selection for cryptic coloration and secretive behavior probably has been important. The plumage has only two bright spots, the yellow of the lores and of the carpal feathers. The latter apparently has a signal function during wing raise displays. In aggressive encounters, males display at close range, and the wings and body feathers are used as display signals. In close quarter interactions bright colors may be superfluous.

The Seaside's flight song is well-developed. Armstrong (1963) noted that flight song is more common in birds living in open country, perhaps because of a scarcity of song perches, and because flying birds are conspicuous over low, uniform vegetation. Mengel (1951) pointed to scarcity of song perches as a possible factor in the evolution of flight display. Although the presence or absence of song perches may have influenced the evolution of flight display, our data do not indicate that number of song perches acts as a proximate factor in determining the frequency of flight display. We could find no difference in the number of flight displays given by males between the two habitat types we studied, despite the abundance of elevated perches in the altered salt marches and general vegetative uniformity of the unaltered salt marshes. Flight display is rather infrequent, and in both habitats an individual male usually gave no more than two flight displays per hour.

The distraction display is given by females nesting in the drier (ditched) salt marshes. The absence of the display in the wet (unaltered) salt marshes is probably related to the absence of ground predators. A similar explanation is offered for the lack of a distraction display in marsh-nesting icterids (Orians and Christman 1968).

Structural simplicity of habitat is thought to be a contributing factor to the high incidence of interspecific aggression among grassland birds (Verner and Willson 1966). Seaside Sparrows nesting in dense populations show a persistent aggressiveness towards Sharp-tailed Sparrows. Both male and female Seasides chase Sharp-tails. Of the 19 displays that carry an attack message, 10 were used in the presence of Sharp-tails. A Sharp-tail landing in a Seaside's territory is immediately approached by the male, followed on the ground, sometimes displayed to, and usually chased. Sharp-tails invariably flee from challenging Seasides. Information on the foraging behavior (Cody 1968) and nesting behavior (Post MS) of the two species suggests that they are not competing for food or nest sites. Thus the fact that Seaside Sparrows show aggression toward Sharp-

tails supports Murray's (1971) hypothesis that interspecific territoriality is misdirected intraspecific territoriality, i.e. male Seasides react to Sharp-tails as other Seasides and therefore as potential competitors for female Seasides or for space. The two species are very similar in plumage. Captive male Sharp-tails attempted to copulate with Seasides on 15 occasions, while Seasides mounted Sharp-tails on six occasions. Montagna (1942) saw a male Sharp-tail mount a female Seaside in the field.

The Sharp-tailed Sparrow has fewer displays than the Seaside: our studies and those of previous workers indicate that the Sharp-tail has only about five vocal displays (tsip call, seeep note, chuck call—tsuck of Woolfenden 1956, primary song, aerial vocalization) and seven visual displays (wing-tail flicking, erect posture, gaping, bill wiping, head forward threat, hunch down, and flight display). Most of the Sharp-tail displays appear to incorporate locomotion and/or attack and escape messages; the species does not appear to have displays transmitting bond-limited or copulation messages. The Sharp-tail is promiscuous: both sexes mate indiscriminately with the other sex (Woolfenden 1956). Males do not defend an activity space, and females alone care for the young. Lack of complexity in the Sharp-tail social system is correlated with the small size of the species' display repertoire.

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SUMMARY

The Seaside Sparrow has 27 displays (14 visual and 13 vocal, not including the male subsong). The displays are described and discussed in terms of the contexts in which they are given. Comparisons are made with other emberizines. The probable functions of the displays are examined in terms of nine message categories.

Seaside Sparrows nesting in dense populations (24.8 pairs per ha) spent a significantly greater amount of time engaged in visual display than did birds in sparse populations (1.0 pair per ha), but the amount of time that males spent singing did not differ between the two population densities. In the sparse populations the space in which singing took place was always larger than the defended territory where visual display and

fighting took place, but in dense populations, the singing ground was often smaller than the defended area.

Females nesting in ditched marshes gave a distraction display not given by females nesting in unaltered marshes, probably because of the scarcity of ground predators in the latter habitat.

The Seaside Sparrow display repertoire is moderate in size compared with those of other vertebrates. In comparison to females, males have more displays concerned with territorial defense, while females have more displays concerned with pair bond and defense against predators. The size and nature of the display repertoire is related to the Seaside's social organization and habitat.

The Seaside Sparrow uses 10 displays in the presence of the Sharp-tailed Sparrow. Interspecific aggression is felt to reflect competition for mates or space rather than for some other resource. In contrast to Seaside Sparrows, Sharp-tails have few displays, which reflect the latter's (apparently) simpler social organization.

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