

STRUCTURE OF DISPLAY FLIGHTS IN THE LEAST SANDPIPER

EDWARD H. MILLER

ABSTRACT.—Display Flights (DFs) of the Least Sandpiper (*Calidris minutilla*) are described. DFs were prolonged flights (averaging 1.2 min in Manitoba and 3.4 min in Nova Scotia), about 10–30 m in altitude, by unmated males over their future nesting areas. Displaying males alternated brief glides and bouts of rapid shallow wingbeats (Flutters) throughout DFs; the two phases averaged 0.84 and 0.72 s, respectively. Flutters averaged 26 (Yukon) to 37 per min (Nova Scotia). DFs ended in several kinds of descents, from slow parachuting to rapid stooping. Three main call types were associated with DFs. The main Display Flight Vocalization (DFV) was simple and stereotyped, and was emitted rhythmically throughout DFs. DFVs of 22 males averaged 390 ms long with intervals between them of 106 ms. DFVs thus occurred at a rate of about two per second, so were not synchronized with Flutters.

Some features of DFs, such as their monotonous, repeated calls, are shared with many other open-country species with aerial displays (e.g., plovers, pipits). Nevertheless, DFVs are probably plesiomorphous within the Calidridinae. The adaptive significance and ancestral/derived status of these and other features of DFs are discussed.

The Calidridinae (Scolopacidae) consists of 24 closely related species of sandpipers that nest in open habitat in the arctic and subarctic (Pitelka et al. 1974). Their ecological similarities and close affinities make them ideal for study of adaptive radiation and homologies of displays in a non-passerine group. A good candidate for such study is aerial display, which is well developed in open-country species in general, and occurs in numerous charadriiform species, including Calidridinae (Armstrong 1963, Pitelka et al. 1974). In this paper I provide a detailed description of aerial displays in a representative calidridine, the Least Sandpiper (*Calidris minutilla*). This will establish a baseline for future comparative studies, thereby permitting assessment of the relationship of the display's structural features to the different species' spacing and mating systems, and allowing the species' affinities to be considered.

C. minutilla is a subarctic species whose nesting range extends from the Alaska Peninsula to Newfoundland, with some birds breeding as far south as Massachusetts and Nova Scotia (Anderson 1980, Johnsgard 1981). Males of this monogamous species occupy the nesting grounds each spring in advance of females and establish ephemeral territories over which they give Display Flights (DF; see Appendix for a list of abbreviations). Males stop displaying when they acquire a mate, although they nest in the area over which they displayed. Both sexes incubate and care for the brood,

but adults and chicks generally feed in undefended areas distant from the nesting grounds. Males assume an increasing role in incubation as it proceeds, and are mainly responsible for raising the brood (Miller 1977, 1979a). The aerial displays of unpaired males in this species are very restricted in occurrence and function: a male may engage in display flights for only a few days each spring, and these apparently serve solely to attract a female to a suitable nesting area, while simultaneously repelling competing unpaired males.

STUDY AREAS AND METHODS

I studied Least Sandpipers at three locations: Sable Island, Nova Scotia (43°57'N, 59°55'W) from 17 May to 23 July 1975, and 14 May to 3 August 1976; near Churchill, Manitoba (58°24'N, 94°24'W) from 24 May to 6 July 1978; and in the Blackstone River Valley, Ogilvie Mountains, Yukon Territory (64°39'N, 138°27'W) from 30 May to 2 June 1979. Many birds were individually color-banded in the Nova Scotia study (see Miller 1977, 1979a).

Display flights were timed with a stopwatch and were filmed with a super 8-mm movie camera at 24 frames per second. Data on wind velocity were obtained from Environment Canada, Atmospheric Environment.

Vocalizations on Sable Island were recorded at 19 cm/s using Scotch tape 176 and a Uher 4200 Report Stereo IC tape recorder, with a Uher M517 dynamic microphone mounted in a Dan Gibson parabolic reflector. All other

recordings were made on Scotch tape 208 matched to a Nagra IS tape recorder, and Sennheiser MKH816 "shotgun" microphone covered with a wind sock.

Sound spectrograms were prepared on a Kay Elemetrics Sona-Graph 7029A. Oscillograms were prepared on a Honeywell Visicorder system 1858. Time scales are based on those displayed by the machine. Power spectra (Fig. 10) were traced from plots obtained from a Princeton Applied Research Model 4513 FFT, and are based on 8 to 10 consecutive calls from each of the three males shown.

RESULTS

CONTEXTS OF OCCURRENCE OF DISPLAY FLIGHTS; DURATIONS; GENERAL DESCRIPTION

Display Flights (DFs) were performed only by males, especially unpaired males, and were longest and most frequent in the morning (Miller 1977, 1979a, b). They began without evident social stimulus, or in response to DFs by other males, often followed aerial chases of females or intruding males, and occurred after fights, or during pauses in lengthy fights.

DFs in Nova Scotia averaged 3.36 min in duration (median = 2.63 min), and had a frequency distribution that was strongly right-skewed ($t_s = 19.1$, $df = \infty$, $P < 0.001$; Fig. 1). One DF lasted 27 min and another only about 5 s. The few very brief DFs were atypical, because the displaying males never reached full altitude and hovered there, but just rose 5 or 10 m then descended. DFs in Manitoba and the Yukon were briefer, with median durations of 1.20 min and 2.15 min, respectively. Dwight (1895) reported that DFs of this species on Sable Island lasted about 10 min, and Saunders (1902:28) noted that the monotonous calling in DFs there lasted "perhaps three or four minutes." A similar estimate of DF duration was given by Moore (1912) for a bird disturbed at its nest on the Magdalen Islands, Quebec.

A bird usually started a Display Flight by flying up from the ground at a steep angle, reducing the speed and angle of ascent as maximal altitude was approached, then levelling off when about 20 m high. He remained at about that height throughout the DF while hovering over a small area ("treading"), then letting the wind carry him over another area, and so on; a single DF crisscrossed an area up to 200 m across in this manner, though most covered less. In the Yukon, where the species nests at lower density, DFs were higher (perhaps 30–40 m) and wider ranging; Townsend's (1927:202) observation that they may attain heights of "50 or more yards," based on his

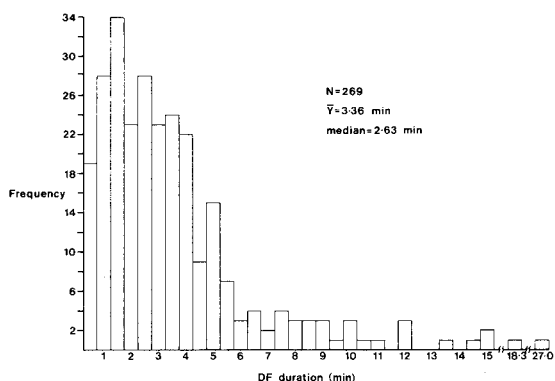


FIGURE 1. Frequency histogram of the durations of Display Flights (DFs) by male Least Sandpipers.

observations in Nova Scotia and Labrador, seems exaggerated. Birds in DFs appeared distinctive because they hung in the air while Fluttering the wings and holding the wings motionless, in alternating rhythm. I call this flying mode *Punctuated Fluttering* (PF). PF began near the end of ascent, and continued through the DF virtually without pause. Birds that began DFs spontaneously usually started emitting monotonous, rhythmically repeated *Display Flight Vocalizations* (DFVs) shortly after takeoff, but sometimes leapt into the air with *Song* or *Chattering* before starting DFVs, in the same context. DFVs were uttered in almost unbroken rhythm throughout a DF, though *Song* and *Chattering* were usual when descent was imminent. DFVs and PF were not in phase with one another (contra Townsend 1927:202).

DETAILED DESCRIPTIONS OF MOTOR PATTERNS

Qualitative description. A male's ascent seemed to be simple fast rising flight, though he was conspicuous because of the rapidly repeated exposure of the bright white undersides of his wings as he rose. This "twinkling" appearance was particularly conspicuous in early morning or evening, when the sun was low, and by itself occasionally evoked *Song*, *Chattering*, or *Display Flights* from other males. A male's flight pattern changed near the end of ascent, when he began *Punctuated Fluttering*. Males sometimes continued to rise in altitude slightly after PF began, but typically stopped rising when about 10 to 30 m high, then engaged in PF throughout most of the display. The onset of each Flutter began with a very slight quivering of the wing tips, as determined by movie analysis (Fig. 2a, frame 3). This was less obvious in birds viewed from below, but in them the beginning of each Flutter was signalled by slight flexing of the wings, then backward movement

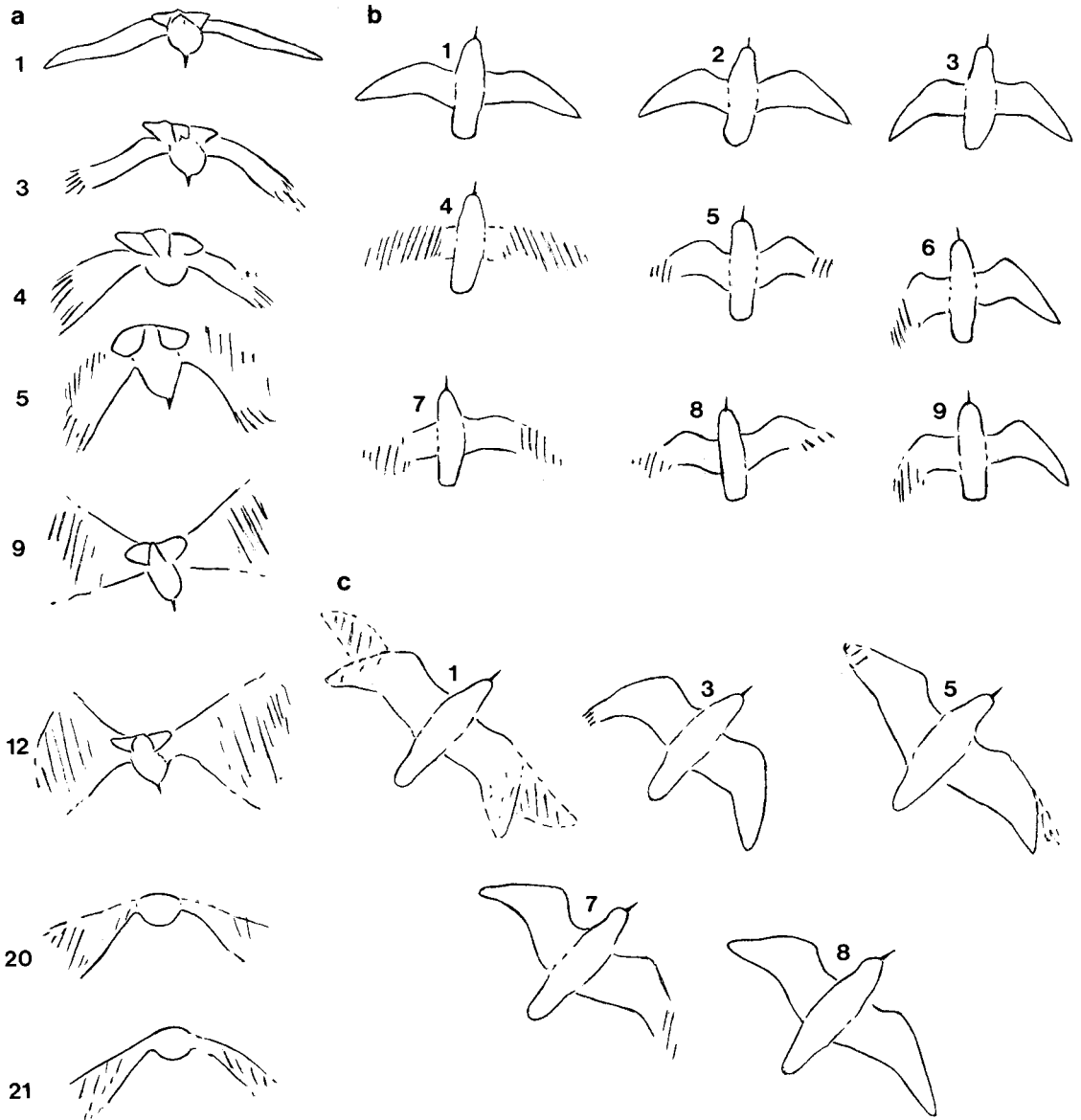


FIGURE 2. Postures of male Least Sandpipers during Punctuated Fluttering (PF) in Display Flights; numerals represent frame numbers on the movie film from which the sketches were made. a—PF as viewed from behind and slightly below. b, c—PF by two different males as viewed from below.

of the wings as part of the first Fluttering actions (Fig. 2b, frames 1 to 3).

The arc of the beating wings was predominantly below the horizontal early in a Flutter (Fig. 2a, frame 5), then they beat rapidly in an arc from just below to about 40° above the horizontal (frame 9). This was followed by the penultimate phase in which the arc was maximal, from nearly 45° above to $45\text{--}50^\circ$ below the horizontal (frame 12). Wingbeats showed decreasing amplitude below the horizontal thereafter (frames 20 and 21), and came to rest (frame 1). It was hard to identify corresponding phases in DFs seen from below (Fig. 2b,

c). Wings moved between positions of extension and flexion, and from front to back throughout PF (Fig. 2b, frames 5 to 9; Fig. 2c, frames 3 and 5). At the end of a Flutter the wings were held flexed briefly, then they were extended and held motionless for the duration of the period between Flutters (the *Inter-Flutter Interval* or IFI). During Fluttering and IFIs many slight adjustments of one or both wings could occur, especially in high winds, so this description should be considered normative only.

Males in Display Flights held the head slightly erect (Fig. 3a, b), distended the throat

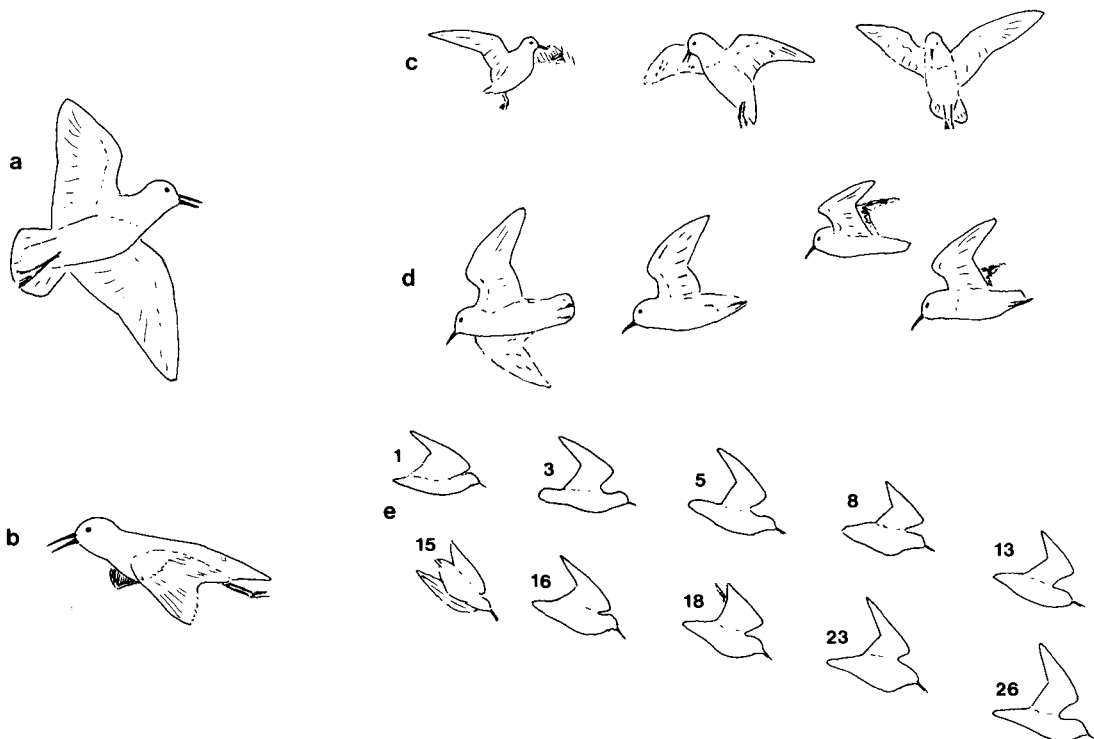


FIGURE 3. Postures of male Least Sandpipers in Display Flights (DFs). **a, b**—Male in DF as viewed obliquely from below and slightly behind (**a**), and from the side (**b**). **c**—Three sketches of Parachuting during descent from DFs. **d**—Early phases of descent from a DF; the third sketch from the left suggests a Butterfly posture. **e**—Rapid descent from a DF; numerals represent frame numbers on the movie film from which the sketches were made. The film was exposed at 24 frames per second, so the sequence shown lasted just over a second.

(Fig. 3b), and opened and closed the bill rhythmically as they emitted DFVs. The tail was used much in aerodynamic adjustment, and was sometimes fanned completely or only on one side, briefly or for lengthy periods. Seen from below, the fanned tail was strikingly white with a dark central stripe (due to the dark central rectrices and the legs). The pale “window” on the wings was similarly conspicuous when backlit and seen from below, but was less so when viewed from above (I observed some DFs from atop a 20-m tower and from the top of some tall dunes).

Punctuated Fluttering continued in a DF until it was nearly over, but included short periods when the male started to sing, fanned and depressed the tail slightly while the body assumed a more vertical position, with the wings in a *Parachuting* posture (named after a similar display of male White-rumped Sandpipers, *Calidris fuscicollis*; see Fig. 5 of Drury 1961). He slowly descended thus for one or a few meters until the Song ended (Fig. 3c). This was generally followed by a brief period of silence, then DFVs, and PF resumed and altitude was regained. Such periods of embedded *Parachuting Song* (PS) sometimes occurred

spontaneously, but more often occurred in response to the sound or sight of another displaying male. When neighboring males were simultaneously in DF, they sometimes engaged in unsteretyped brief chases back and forth at high altitude, during which Chattering, Song and the *Butterfly Song*, or BS display occurred (named after a display of the Baird’s Sandpiper, *Calidris bairdii*; see Fig. 6 of Drury 1961; see also his Fig. 5 for “song to intruder” by White-rumped Sandpipers). In BS the wings were held stiffly and slightly flexed about 45° above the horizontal, as the displaying male sang continuously while gliding at a gentle angle downward (Fig. 3d, last two sketches). The display was most pronounced when two neighboring males glided downward slowly in mutual BS along the common boundary between their territories (more accurately, this was generally an area of some overlap between the areas over which they gave DFs), until they were near the ground. They remained side by side throughout such formal descent. High altitude BS and mutual, descending BS between tenured males apparently functioned to affirm boundaries between their adjacent DF areas. Males also used BS when they were close to

females whom they were chasing; they then glided beneath and often slightly ahead of the female while singing repeatedly. This displayed the upper wing surface and the pale wing stripes to the female. It was my impression that established males (i.e., those that held DF areas) attempted to give BS display beneath intruding males while chasing them out, at least sometimes (see next paragraph). I did not discern this in mutual BSs between neighboring established males, but it sometimes occurred during breaks in fights involving an established male and an untenured male who was trying to establish himself.

Males that encroached upon an established male's Display Flight area were generally chased out in fast flight with Song, Chattering, or other calls, and such chases could take a defending male well out of his DF area. When the chasing male was close to the chased male, Butterfly Song could occur below him, as mentioned. Males also chased females well beyond the limits of their DF areas. Such chases often attracted several other males and could take place at very high altitudes, when territorial limits seemed to be ignored. Chases of females by unmated males occurred regardless of whether they were paired and being attended by their mates.

The end of a DF typically started with a slight loss of altitude, cessation of Fluttering, and a change from Display Flight Vocalizations to silence, or an acceleration in the delivery of DFVs (which also became briefer), then Song. Descent took various forms. It could start with a slow, stepwise loss in altitude, coincident with changes in flight pattern and calls just noted. There was a gradual transition to a Parachuting posture, a transition that could include Butterfly-like postures (Fig. 3d), with or without Song, then the male parachuted slowly to the ground singing lustily (Fig. 3c). Males could stall in the Parachuting posture for several seconds, and rock the body back and forth while maneuvering the fanned tail and wings, seemingly to make their descent as slow as possible. Most often, however, a male followed his incipient loss of altitude with a steep, very rapid stoop (Fig. 3e, frame 15). Most rapid descents began with assumption of a posture with the wings partly flexed and held above the back, suggestive of a harrier (Fig. 3e). From there the wings were flicked rapidly in some manner (it was unclear how, even in movies), and the bird descended swiftly. Wing movement during such descents was difficult to detect by direct observation, but was apparent in movies. Song overlapped the initial drop in altitude and the beginning of rapid descents, but the terminal (fastest) part of such

descents was generally silent. The male pulled out of his stoop at low altitude, decelerated just above ground level then landed gently. He sometimes showed a suggestion of Butterfly or Parachuting very briefly just before touching down, or glided low over the ground for some distance. Landing was sometimes accompanied by a stereotyped posture in which one or both wings were held extended above the back, and this was usual when a male landed beside his mate. Ground courtship could follow. However, most males that gave DFs were not mated, and their landings were performed without flourish. A male sometimes fluffed or started feeding, or ran into concealing vegetation immediately after landing.

Males remained approximately stationary over one or several small areas during DFs. PF broke down when males moved between areas; they sometimes increased the lengths of their Flutters or simply glided, assisted by the wind. Thus DFs were characterized by PF while treading over one small area, rapid irregular movement with a breakdown in PF until over another area, a resumption of PF and treading there, and so on. Many minor adjustments occurred, of course. Males commonly responded to an intruding person, dog, or vehicle by shifting the location of the DF so that they were above the intruder, often at lower altitude than normal.

QUANTITATIVE DESCRIPTION; EFFECT OF WIND VELOCITY; INDIVIDUALITY

Punctuated Fluttering by a male that was fairly stationary in the air seemed very rhythmic. Combined data on durations of Flutters and Inter-Flutter Intervals are summarized in Figure 4. Means of Flutter and IFI durations summed to about 1.6 s. Distributions of both were strongly right-skewed (for Flutters, $t_s = 74.2$, $df = \infty$, and for IFIs, $t_s = 56.9$, $df = \infty$; for each, $P < 0.001$). Frequency histograms based upon all raw data (equivalent to using weighted mean figures for different males; shaded histogram), and upon the unweighted means for males are distinguished in Figure 4. These differed little, although the unweighted means provided slightly greater estimates of the mean and median of Flutter duration. The descriptive statistics refer to the raw data.

Different samples of Flutter and IFI durations varied considerably; some extreme samples are summarized in the lower half of Figure 4. Such differences may have arisen from differences among males, or from effects of wind velocity, or both. I performed median tests on the lumped data for 12 males whose DFs were sampled in high and low wind (low wind = 9 to 23 km per h; high wind = 25 to 37 km per

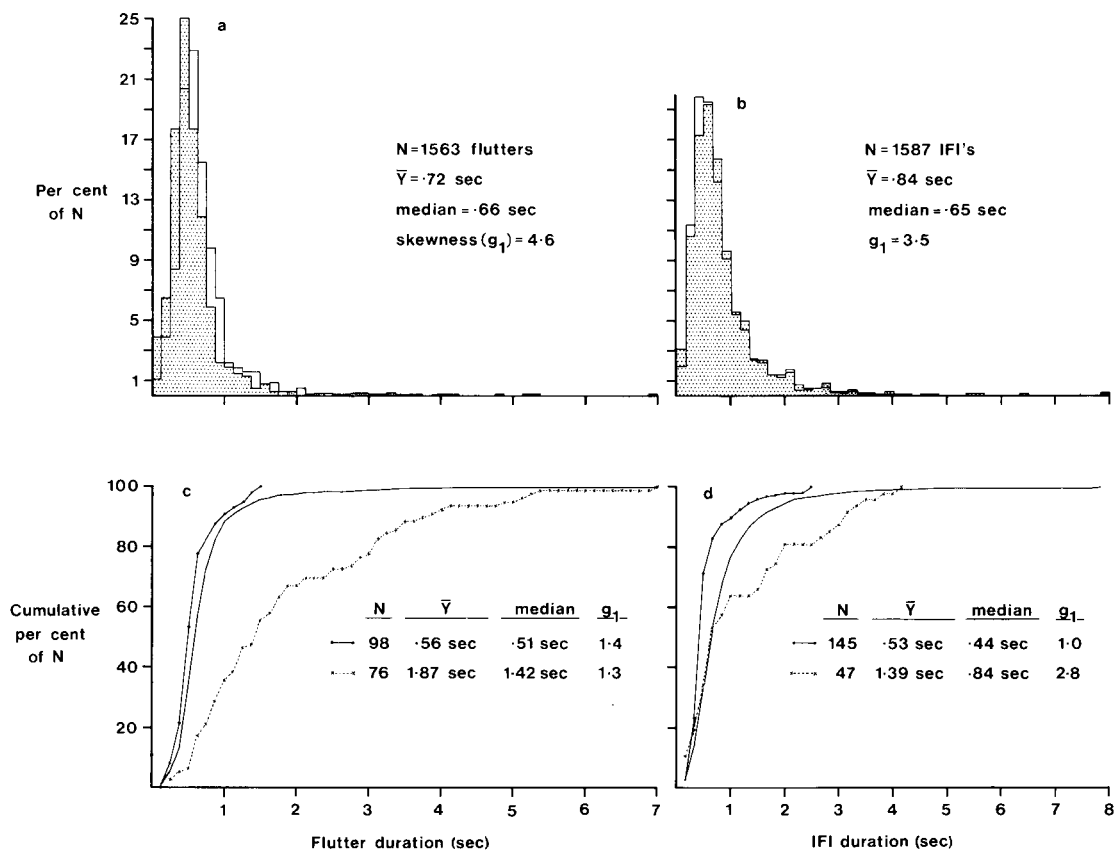


FIGURE 4. Frequency histograms (upper) and cumulative plots (lower) of the durations of Flutters (a, c) and Inter-Flutter Intervals (IFIs; b, d) in Display Flights by male Least Sandpipers. Frequency histograms for weighted data are stippled to distinguish them from those for raw data. Chosen extreme distributions and some descriptive statistics are shown in c and d. The central line in each of the cumulative plots represents all data summed.

h). There were 873 estimates of Flutter durations in low wind and 657 in high wind (by median test, $G = 0.49$, $df = 1$, $P < 0.5$). There were 899 estimates of IFI durations in low wind and 699 in high wind (by median test, $G = 0.34$, $df = 1$, $P < 0.5$). The combined data therefore suggested no systematic relationship of durations of Flutters and IFIs to wind velocity. If males were individually distinctive in the lengths of their Flutter and IFI phases, however, lumping their records could obscure systematic responses of particular males to changes in wind velocity. Analyses presented elsewhere suggest a weak trend toward brief Flutters in high winds, for individual males; IFI durations showed no systematic relationship to wind velocity (Miller 1977; see Fig. 5). My subjective impression was that males in DFs in high wind were frequently buffeted by gusts, and had to adjust their posture and direction by flexing or extending one or both wings, fanning and rotating the tail, and other movements.

Some unbroken PF sequences by different males under various wind conditions are sum-

marized in Figure 5. The top record is of a male filmed in DF in a high wind. He showed remarkable constancy in durations of Fluttering and IFI phases over the period depicted (about 140 each of Flutters and IFIs). Samples of records for three other males are shown in the lower parts of Figure 5. IFIs of male 75-07 varied markedly regardless of wind velocity, but the most striking irregularities in Flutter durations occurred at the lower wind velocity (sample (ii) at 10.6 km per h). Nevertheless, sustained periods of rhythmic Fluttering occurred in both samples: compare sample (i) at 10.6 km per h with the sample for 19.4 km per h. In general, durations of Fluttering by male 75-07 varied less and were briefer than were IFI durations. The opposite was true of male 76-18. The overall patterns of IFI durations for this male differed little between samples under different wind velocities. He had highly irregular Fluttering durations at the lower wind velocity (26.4 km per h) but IFI durations were much greater than those at 37.0 km per h only once. Fluttering durations of male 76-X were intermediate in

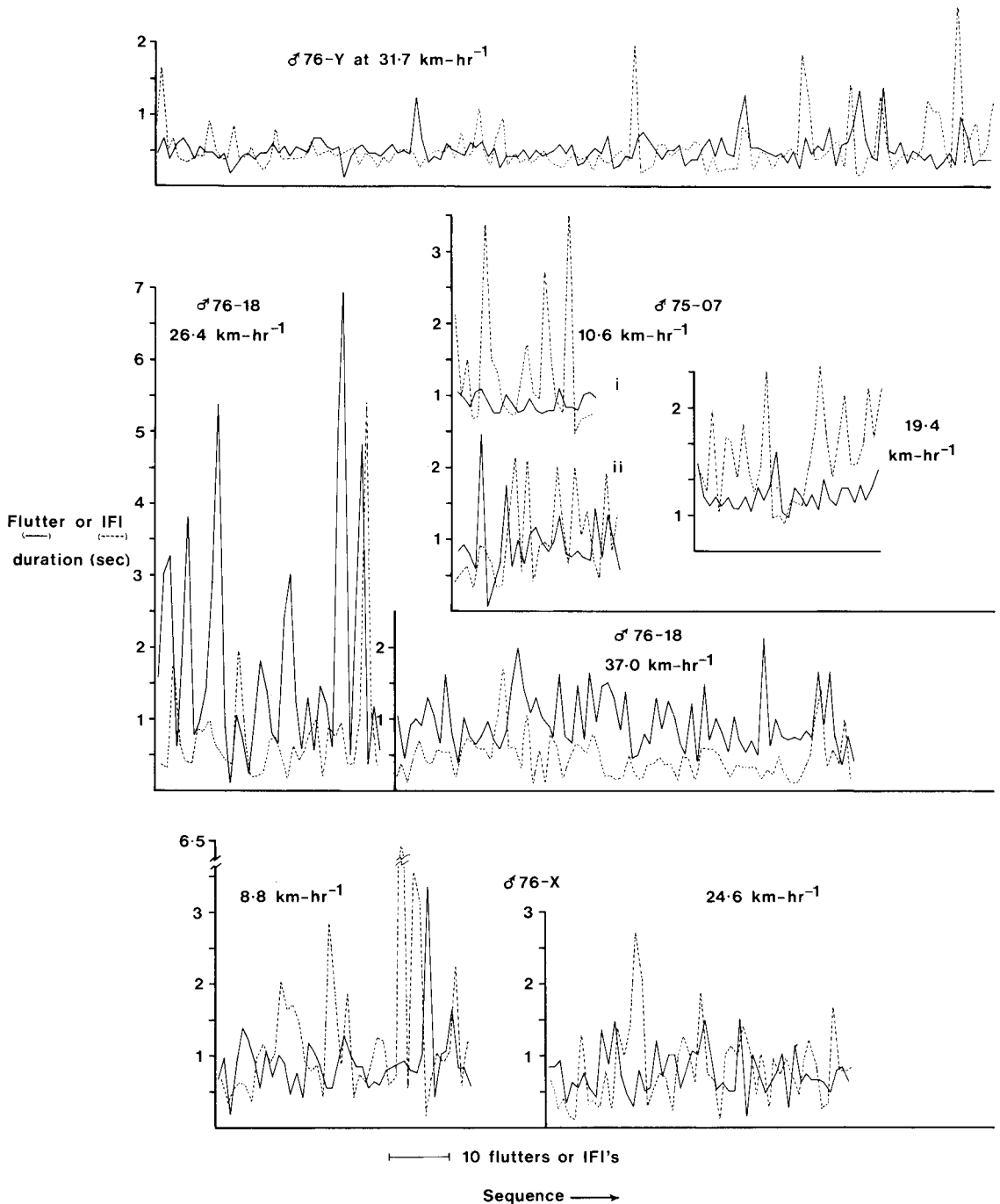


FIGURE 5. Plots of the durations of Flutters and Inter-Flutter Intervals (IFIs) over time, in chosen sequences of Punctuated Fluttering in Display Flights of male Least Sandpipers. The records are for the males referred to in Figure 5, plus one other. The wind velocity for each record is indicated.

certain respects. His Fluttering durations were only slightly longer in low than in high wind (this can be appreciated easily by scanning across both records at about the level of 0.5 s). His IFI durations were longer and more variable at 8.8 than at 26.4 km per h and were only slightly longer than Fluttering durations.

The mean Flutter rate based on direct observations was 37.2 per min (Fig. 6), which is close to the figure of 38.5 obtained from data on mean durations of Flutters and IFIs from movie analyses (using data shown in Fig. 4, mean durations of Flutters plus IFIs = 1.56 s; $60/1.56 = 38.5$). Least Sandpipers near

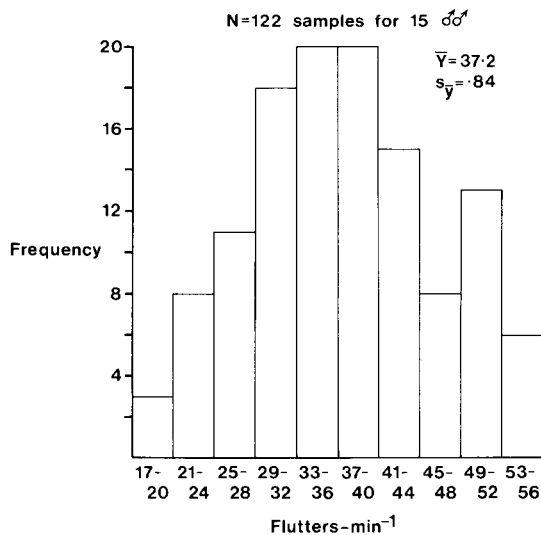


FIGURE 6. Frequency histogram of Flutter rate in Display Flights of male Least Sandpipers, on summed raw data.

Churchill and in the Yukon had a much lower rate of Fluttering, around 32.0 and 26.3 per min, respectively.

Data on rates of Fluttering by different males revealed individual differences in Flutter rates, and these remained fairly constant across the range of wind velocities sampled (Miller 1977). I often guessed correctly the identity of some displaying males before seeing their leg bands, just by observing their Flutter rates.

VOCALIZATIONS ASSOCIATED WITH DISPLAY FLIGHTS

Display Flight Vocalizations: description, individuality, variants, and sequences. Males in DFs emitted a rhythmically repeated monotonous call, the DFV (Figs. 7, 8, 9). Simultaneous sequences of DFVs and PF formed the longest and most conspicuous portions of DFs, and they sometimes continued for minutes without pause. Sequences of DFVs were occasionally given by males perched on the ground or up to several meters high on a prominence. Such sequences generally led to airborne DFVs in a standard DF. With this exception, DFVs were unique to DFs, and hence were given only by males.

The unweighted mean of the mean durations of DFVs for 22 males (totalling 866 DFVs) was 390 ms, with individual means ranging from 331 to 504 ms. Means of 880 interval durations between consecutive calls of 22 males (*Inter-call Intervals*, or ICIs) had an unweighted mean of 106 ms, and ranged from 79 to 131 ms. Thus calls occurred at a rate of about two per second; Dwight (1895: 18) estimated

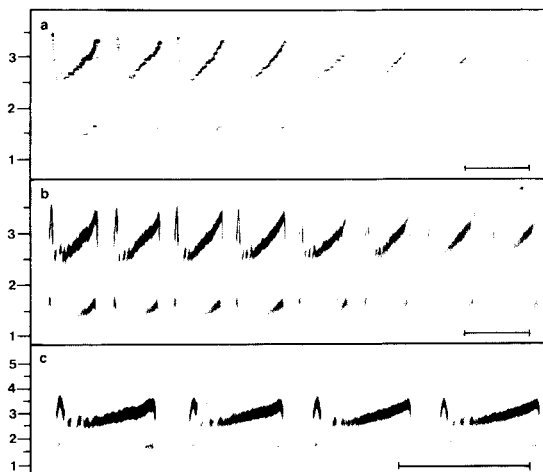


FIGURE 7. Sound spectrograms of Display Flight Vocalizations (DFVs) of male Least Sandpipers. A sequence of eight DFVs from a long series is shown in narrow (a) and wide (b) band representations. The first four of these are also shown in wide band representation on a different time scale (c). The time marker in the bottom right corner of each panel represents 500 ms. The frequency scale is in kHz. Analyzing filter bandwidths, 45 Hz (narrow) and 300 Hz (wide).

them to occur at about the rate of 130 per min on Sable Island. The fundamental frequency of DFVs was between 1 and 2 kHz, and was always much weaker than its first harmonic overtone (Figs. 7, 10). There was little detectable energy in higher harmonics on sound spectrograms. A typical DFV began with a brief high amplitude element that ascended and descended in frequency suddenly. This was followed by several briefer, lower amplitude and lower frequency elements, whose number and relative amplitude varied among males (Figs. 7, 8, 9). The last of these sometimes merged with the long final element. This last element rose slowly in frequency and amplitude; its maximal frequency and amplitude were near its end, and were about the same as for the lead element. Rhythmic amplitude modulations (AM) sometimes occurred in the first part of the last element (parts of Fig. 9), and rhythmic frequency modulation (FM) sometimes occurred throughout it (parts of Fig. 8).

A bivariate plot of durations of DFVs and ICIs revealed a clustering of most males, though a few males were extreme in one or both characteristics (Fig. 11). Nevertheless, using only these two temporal descriptors, many of the 22 males could be recognized: 13 males were distinguishable from all others, two were distinguishable from 20, three from 19, three from 18 and one from 16 (Fig. 11). Homogeneous subsets for ICI duration were larger and showed more overlap than did those for DFV duration

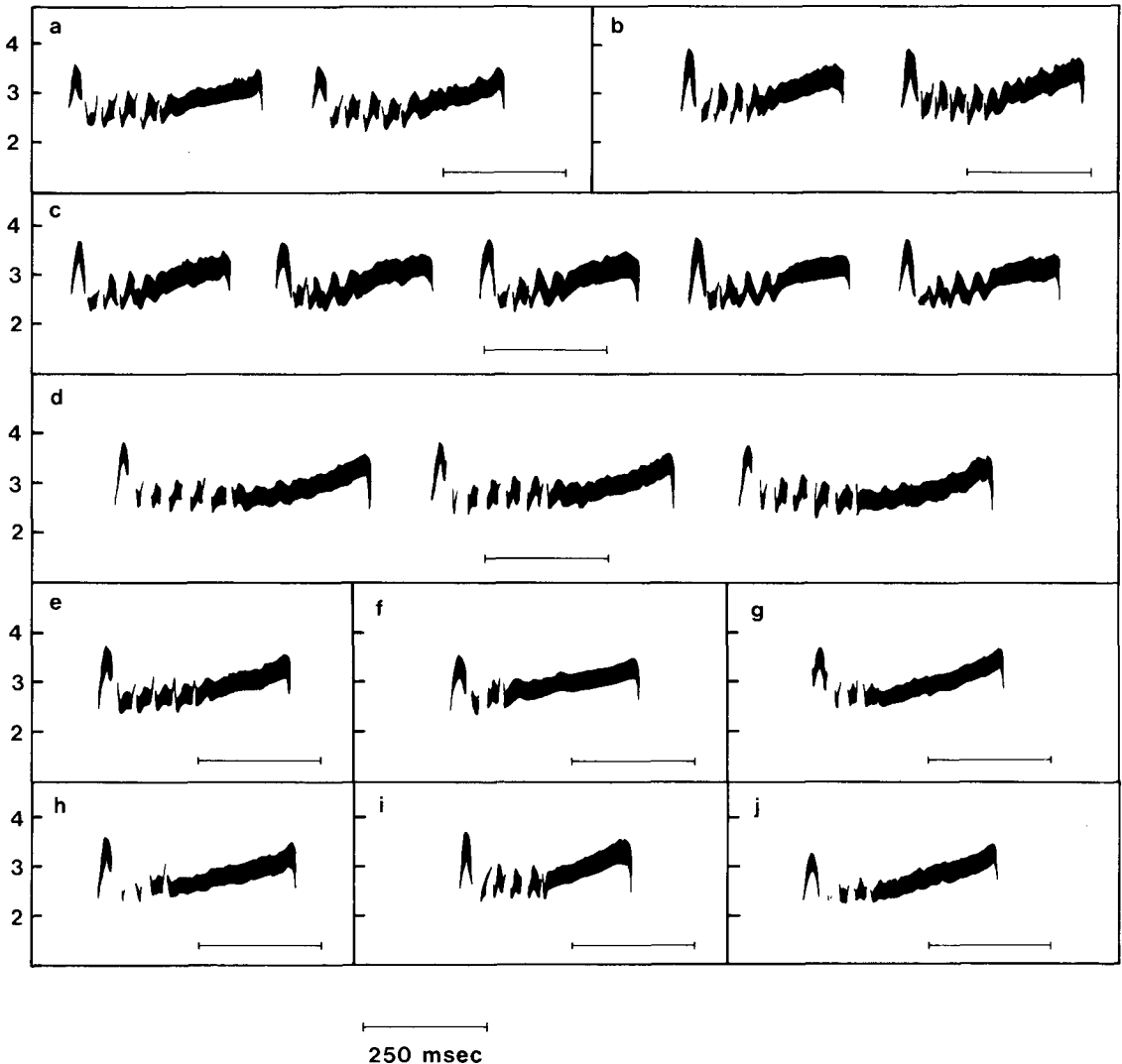


FIGURE 8. Examples of Display Flight Vocalizations (DFVs) and partial DFV sequences for 10 male Least Sandpipers (a-j). These are ink tracings of the first harmonic of the fundamental frequency, based on sound spectrograms. The frequency scale is in kHz. Analyzing filter bandwidth, 300 Hz.

(Fig. 11); this suggests that males exhibited greater individuality in duration of DFVs than of ICIs.

Song and Chattering: contexts of use. Least Sandpipers had a complex, rich vocalization that I term Song (Figs. 12-16). This was given occasionally during the course of DFs, but was most common around the time of descent from DFs, and during aggressive and sexual chases.

Spontaneous Song or Chattering was a normal part of pre-descent and descent phases of DFs, and occurred in periods of Parachuting Song embedded in DFs also. As will be described, the quality of DFVs changed during those phases and Song followed, generally during breakdown of PF, or during the Parachuting phase, or both (but before stoop descent).

If a male Parachuted all the way to the ground he sometimes sang until touchdown, or started Chattering as he neared the ground. Chattering generally became softer near the ground and then continued more loudly for a brief period on the ground, sometimes after a brief period of silence. Further Song was also sometimes given after landing.

Most Chattering and Song was not spontaneous but was clearly elicited by the activities or presence of other males or females. This was true of Song in mutual BS and in most periods of PS embedded in DFs. Males on the ground gave Song, Chattering or DFVs (or all three) in response to calling by other males, or even in response to the sight of a neighboring male silently ascending into DF. Males in-

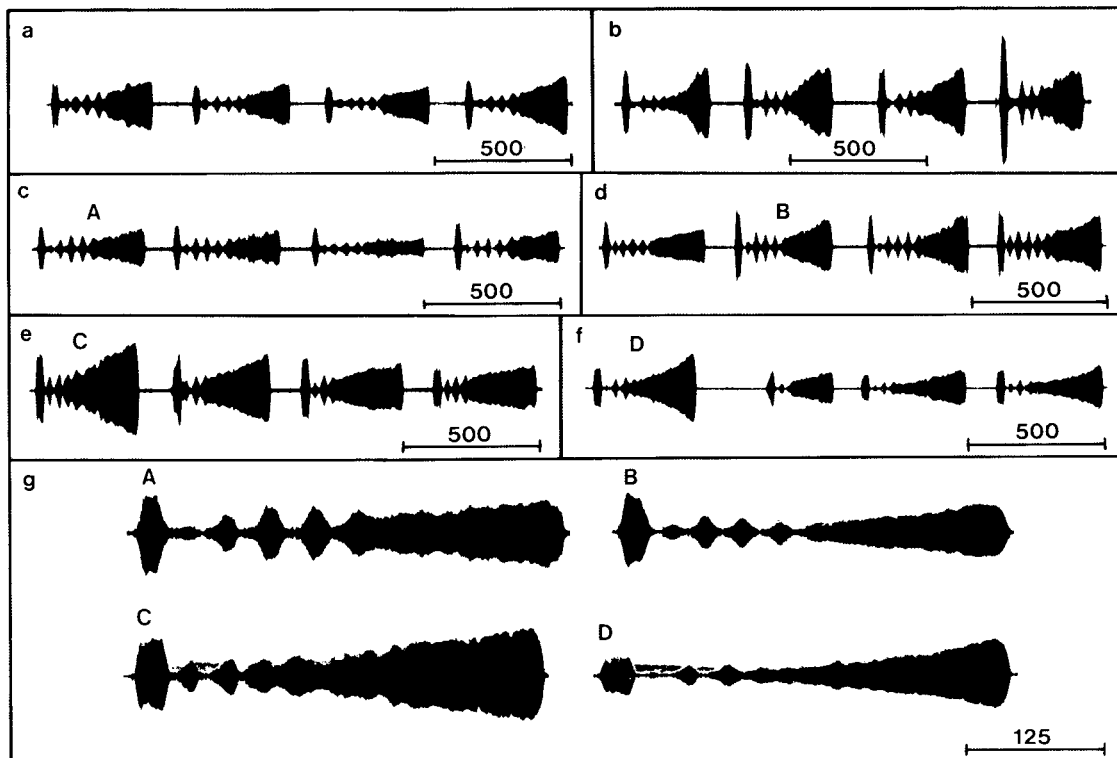


FIGURE 9. Oscillograms of Display Flight Vocalizations (DFVs) of male Least Sandpipers. Partial DFV sequences of six males are illustrated (a-f). g—Four DFVs on a different time scale. These correspond to the DFVs marked with the same letters (A-D) for males c, d, e, and f, respectively. Time markers are in ms.

variably gave Song (less frequently Chattering) as they leapt from the ground to chase intruders or to begin DF prompted by another male's DF. Males often gave Song or Chattering as they flew toward human intruders throughout the nesting cycle, even after the chicks hatched, although this was less common ("alarm" calls were more usual then). This is a common response of nesting shorebirds (Dixon 1918, Brown 1962, Portenko 1972).

Forms of Song were given by both sexes in certain contexts outside of DFs, e.g., in brooding chicks, in gathering chicks to be brooded,

and in ground courtship; these are described and discussed elsewhere (Miller, in press). Chattering seemed to be unique to males. For present purposes, it is sufficient to emphasize that Song and Chattering were prominent and integral parts of DF activity.

Description of Song. Songs were in the frequency band 1–4.5 kHz (Figs. 12, 13). Transitions from DFVs to Song were variable, but the first recognizable element of Song was usually one with rhythmic FM of a carrier frequency which rose from about 2.5 to 3.5 kHz. This element type had no detectable harmon-

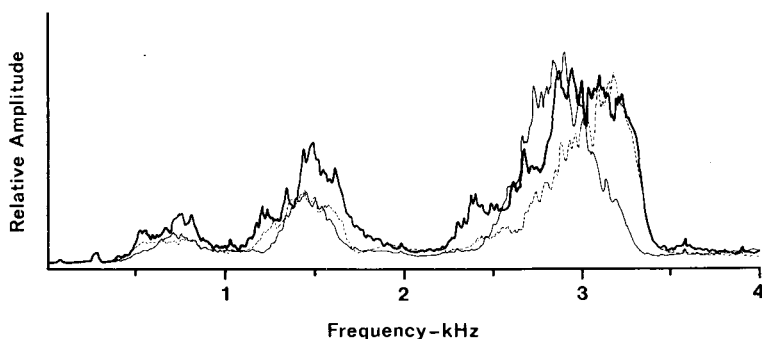


FIGURE 10. Power spectra of DFVs of three male Least Sandpipers from northern Manitoba.

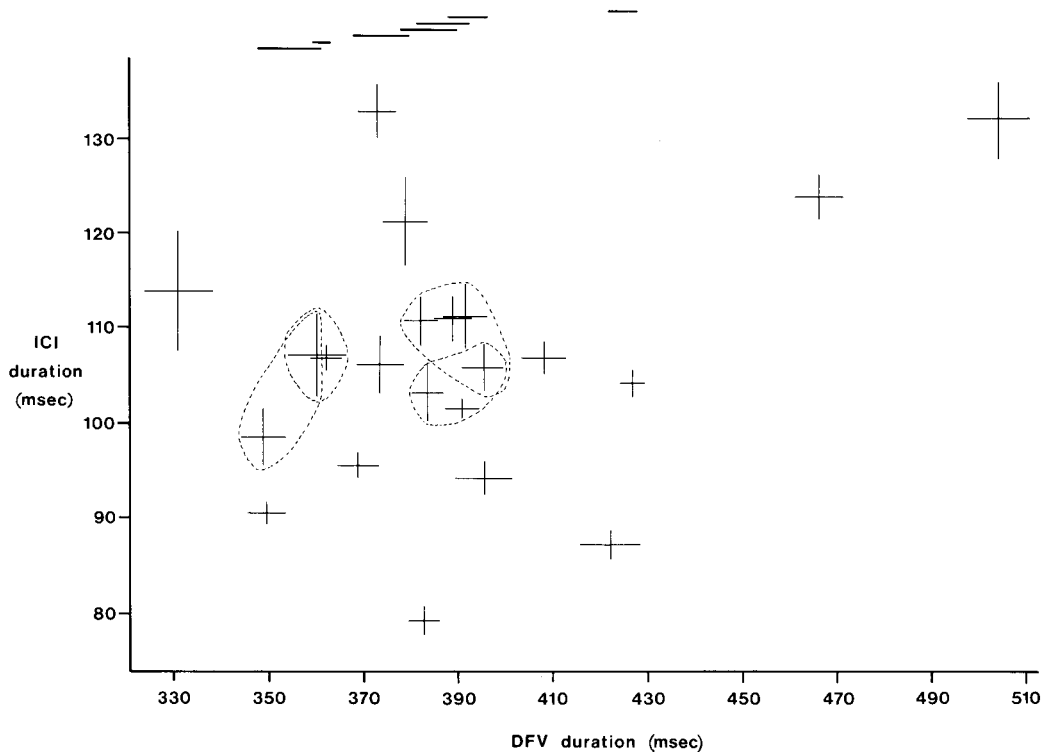


FIGURE 11. Bivariate plot of mean durations of Inter-Call Intervals (ICIs) and Display Flight Vocalizations (DFVs), for 22 male Least Sandpipers. The 95% confidence limits on the means are also shown. Homogeneous subsets on each of the two variables are shown above and to the right (by Student-Newman-Keul multiple range test, $\alpha = 0.05$). Those males that form homogeneous subsets with one another on both variables are enclosed by dashed lines.

ics, and lasted about 0.33–0.5 s (Fig. 12c, element A; Fig. 13, lead element in a, b, c, e, f and h). Usually only one of these elements occurred. Rhythmic AM occurred throughout it and was linked to FM (compare element A in Figs. 12c and 14a, and the same element type in Figs. 13a and 15a [A and B]). Otherwise the amplitude profile was marked only by a terminal amplitude peak (Fig. 14a, element A; Fig. 15a, elements A and B).

The element described was usually followed by a second type with a much lower fundamental frequency (around 1.5–2 kHz) and strong harmonic structure (Fig. 12c, elements B, C; Fig. 12f, elements A, B; Fig. 13a, third element; Fig. 13b, second element; etc. in Fig. 13c–g). This element started around 1.5–2 kHz, dropped in frequency just after its beginning, then increased to around its starting frequency, increased slowly or remained nearly constant in frequency, and ended with a sudden rise to a brief, non-harmonic ending around 3–3.5 kHz. Rhythmic FM often occurred between the early drop in frequency and the end (Fig. 12c, element B, Fig. 13a, c, e). The frequency spectrum of this element changed over its length; most energy was in the fundamental frequency, but its first harmonic overtone con-

tained more energy during the initial dip in frequency (Fig. 12c, elements B, C; Fig. 12f, elements A, B). Amplitude profiles of this element type varied greatly. Those for two consecutive elements of one male were different (Fig. 14a, elements B, C), although the first of these was similar to one of another male (Fig. 15a, element C). These differences were in the presence or absence of rhythmic AM. However, these elements plus those of a third male (elements A and B of Figs. 12f and 16) shared the feature of amplitude-frequency coupling for both rhythmic and non-rhythmic modulations (e.g., all examples showed an initial drop in frequency and amplitude, and all showed a terminal amplitude rise coincident with the sudden frequency shift then).

The next element type began in a very similar manner to the element just described, with a drop, then an increase in frequency at about the starting level; it was also very similar in frequency band, harmonic structure, and the common reversal of harmonic strength in the initial frequency dip (Fig. 12c, element D; Fig. 12f, elements C–E; Fig. 13a, fourth through twelfth elements; Fig. 13b, third through sixth elements; etc. in Fig. 13c–h). This element type undoubtedly had a common origin with the

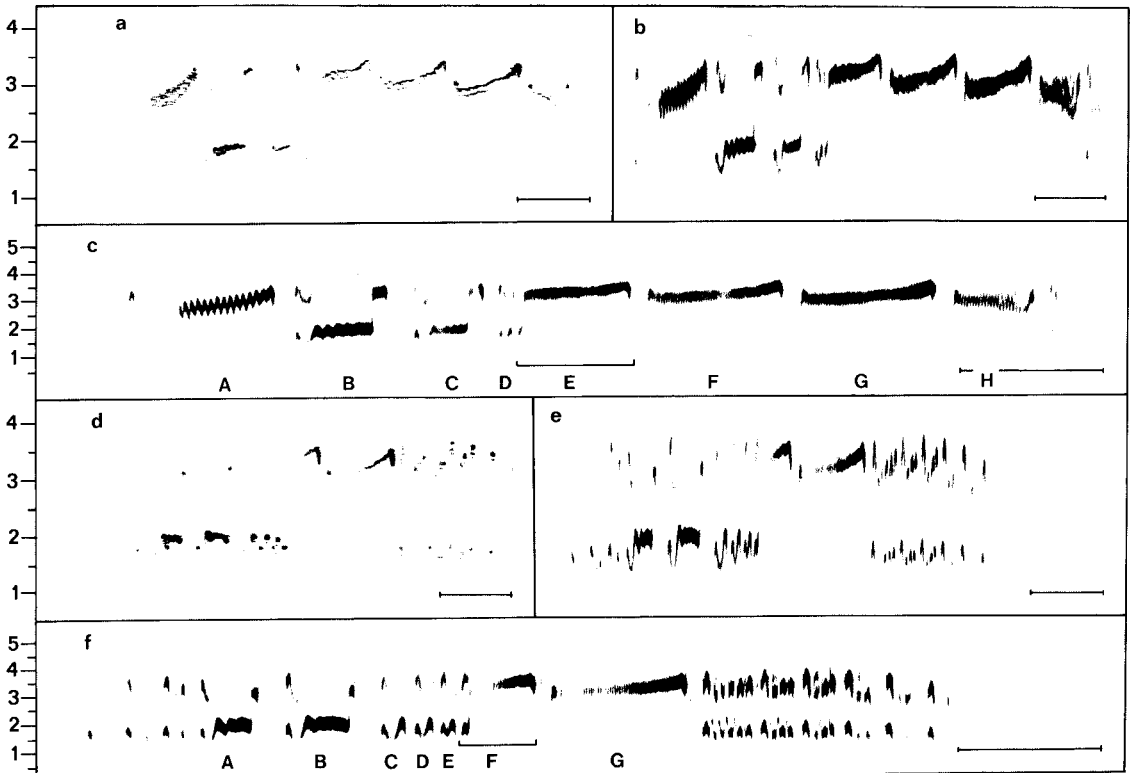


FIGURE 12. Sound spectrograms of Songs of male Least Sandpipers. a, b, c—One male's Song shown in narrow (a) and wide (b, c) band representations. Song elements marked "A" to "H" in panel c correspond to the oscillograms marked the same in Figure 14. An ink tracing of this Song is shown in Figure 13c. d, e, f—A second male's Song depicted in narrow (d) and wide (e, f) band representations. Song elements marked "A" to "G" in panel f correspond to the oscillograms marked the same in Figure 16. The Chattering which precedes element A and follows element G is also shown as oscillograms in Figure 16d, e and f. The time marker in the bottom right corner of each panel represents 500 ms. The frequency scale is in kHz. Analyzing filter bandwidths, 45 Hz (narrow) and 300 Hz (wide).

second element type, but is considered distinct here because it occurred in a graded series of varying length and did not end with a sudden upward frequency shift (except for the last one in each series; see below). Grading was apparent mainly as shortening on sound spectrograms, and also as declining amplitude in oscillograms (Fig. 15, elements D–L; Fig. 16, elements C–E). Amplitude profiles began as did the second element type, with a drop then recovery in amplitude. They thus had a dumb-bell shape overall, because of their brevity. At least one of these elements was in every Song examined. The series ended with a sudden upward frequency shift to the last element type (for comments on grading of this element type, see Miller 1979c).

The fourth type of Song element was about 3–3.5 kHz in frequency, and rose gently over its frequency range (Fig. 12c, elements E–G; Fig. 12f, elements F, G; Fig. 13a, last five elements; Fig. 13b, last six elements; etc. in Fig. 13 c–h). It had no detectable harmonic structure, and had a pulsed appearance on sound

spectrograms prepared on the range 80–8,000 Hz (Fig. 12c, f), because of rapid rhythmic AM (Fig. 14, elements E–H, Fig. 15, elements M–Q; Fig. 16, elements F, G). Amplitude increased strongly at the end.

Songs of most males had all four types of elements, in the order described. Two males each had one element type missing in their Songs (Fig. 13d, h). Songs of males varied mainly in the number of elements of the last type. Males tended to emit Songs in rapid succession and to add elements of that type, especially, when fighting or when chasing other birds in flight.

The integration of Song into DFs varied greatly. Some examples are shown in Figures 17 and 18. DFVs were briefer and delivered more rapidly as they blended into Song without pause (Fig. 17d) with normal pause (Fig. 17f, g-3) or with a long silent period. DFVs preceding Song sounded louder and more highly pitched than normal DFVs. DFVs just before Song were sometimes aberrant in form (Fig. 17c, g-2) or were followed by unusual

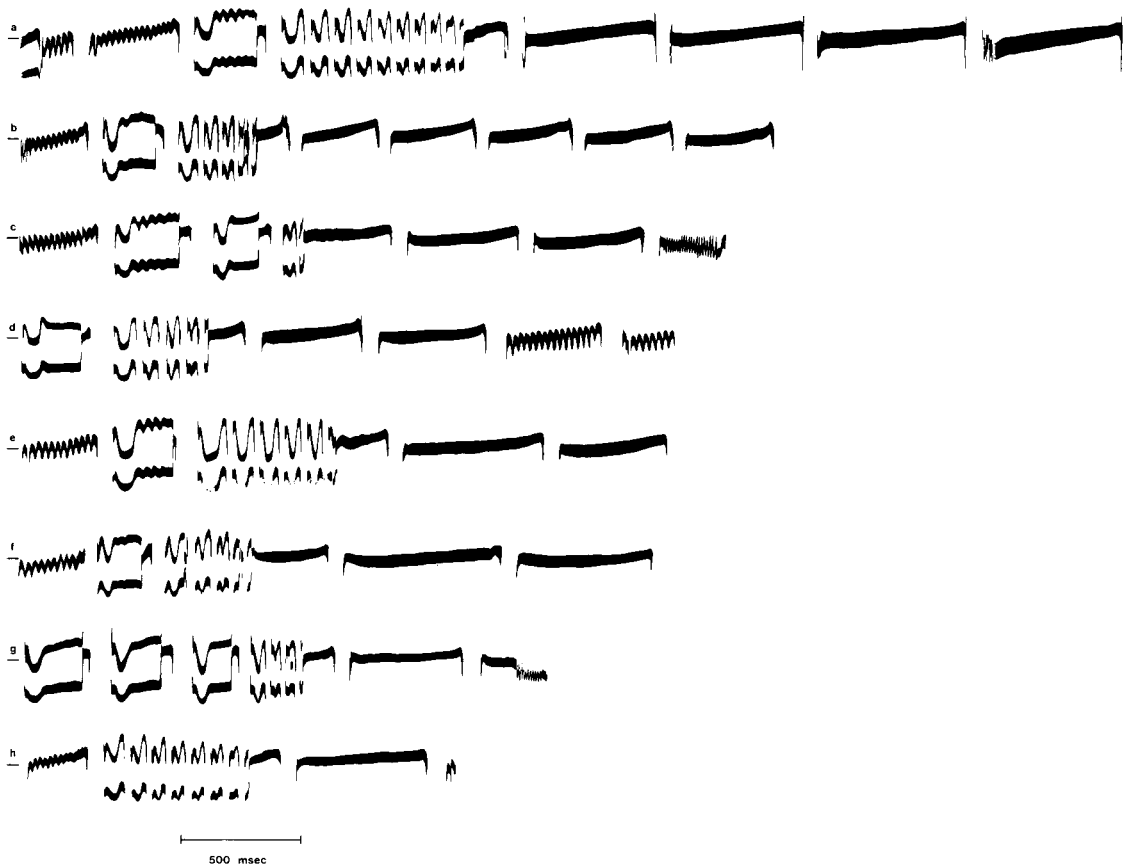


FIGURE 13. Examples of Song associated with Display Flights of eight male Least Sandpipers (a-h). Record g is incomplete; its initial elements are unclear on the tape. Record a starts immediately from a Display Flight Vocalization, only the terminal portion of which is depicted. These are ink tracings of the fundamental frequency and its first harmonic for all elements, based on sound spectrograms. The Song of male a is represented as oscillograms in Figure 15. The Song of male c is represented as sound spectrograms and oscillograms in Figures 12 a-c and 14, respectively. The dash at the beginning of each record represents 3 kHz. Analyzing filter bandwidth, 300 Hz.

elements that preceded Song (Fig. 17e, g-1, g-4). Chattering sometimes preceded Song. Transitions from Chattering to Song included some minor variants in form (Fig. 17a, b), but were generally less variable than were transitions from DFVs to Song.

The manner in which Song ended depended largely on its context. Song was sometimes followed by resumption of DFVs that were aberrant in shape, and were brief and given in rapid but declining cadence (Fig. 18g-1). Some were followed by an aberrant DFV or two alone (Fig. 18d) or in transition to Chattering (Fig. 18b, f-6?, g-2?, h-1). Since Song was sometimes repeated several times without pause, it is not surprising that some Songs ended with aborted

introductory elements to further Song, and that those elements commonly led into Chattering (Fig. 18c, e-1, e-3). By far the commonest sequel to Song was Chattering, which was often introduced by various aborted elements of other derivations (as described) or of Chattering (Fig. 18e-2, f-1, f-2, f-3?, f-6?, f-7?, g-1, h-2, h-3). Even if silence followed Song, there was often a suggestion of one or a few Chattering elements immediately after the last Song element (Fig. 18f-4, f-5, h-4).

Description of Chattering. Chattering was a compound-repetitive call associated intimately with Song. It varied greatly among males, but usually consisted of triplets or quartets of elements repeated in loud rapid succession (Fig.

FIGURE 15. Oscillograms of a Song of a male Least Sandpiper. Elements marked "A" to "Q" correspond to the same calls in panels a to e of this figure. The element preceding "A" is a Display Flight Vocalization (DFV), and "A" starts with an incomplete DFV (see Fig. 13a, where this Song is shown as an ink tracing of a sound spectrogram). Time markers are in ms, except in panel a.

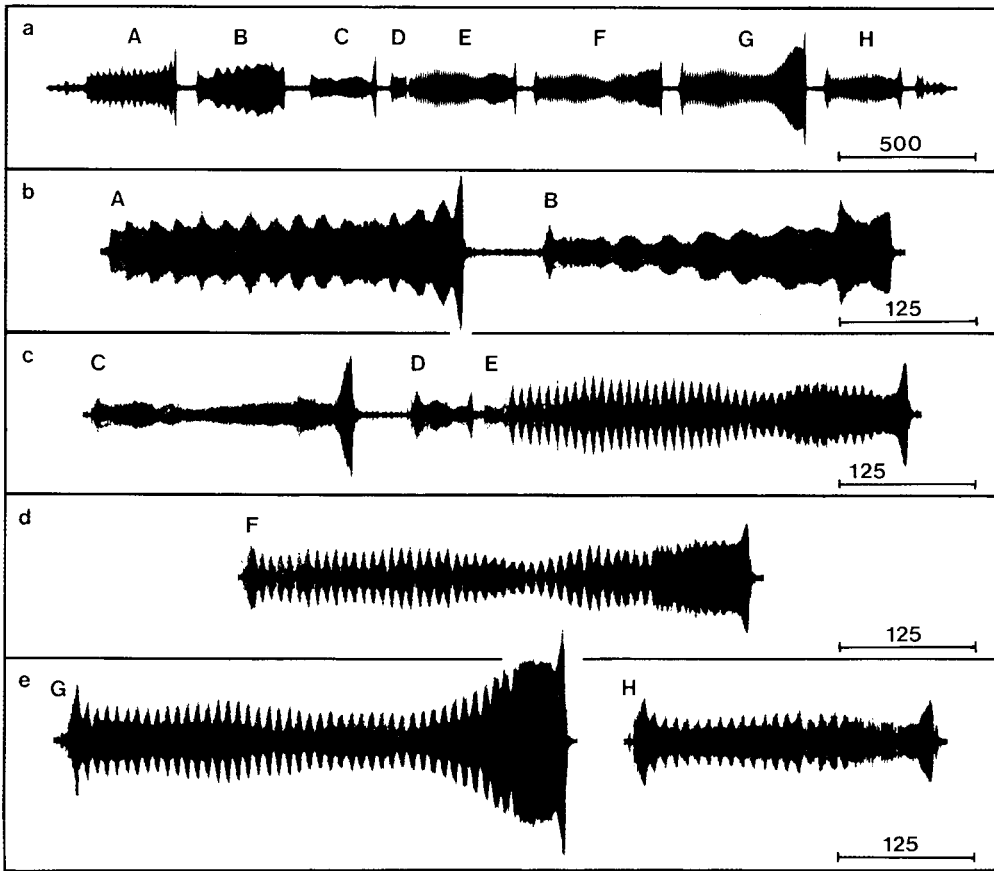
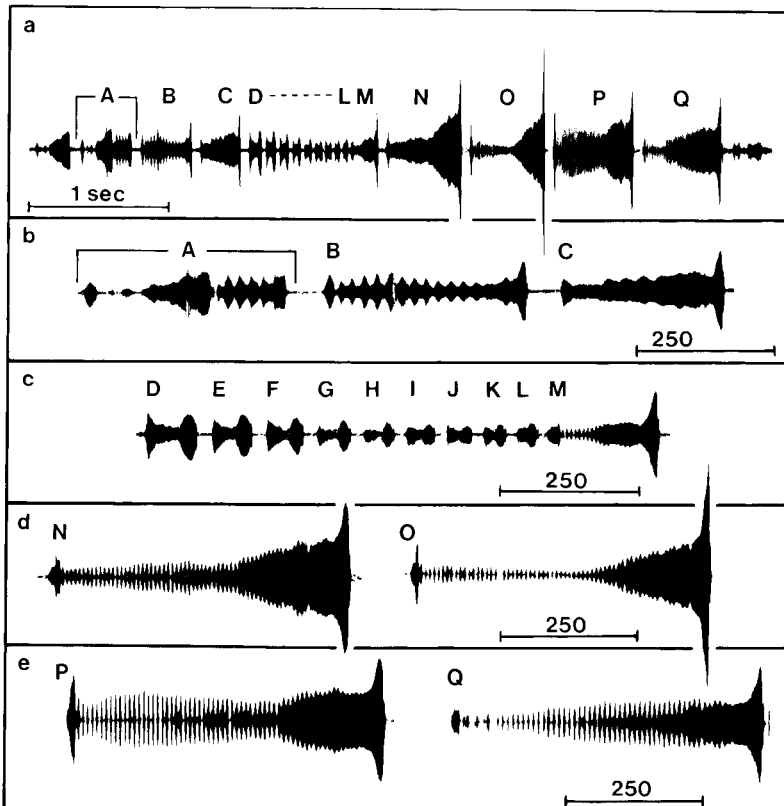


FIGURE 14. Oscillograms of a Song of a male Least Sandpiper. Elements marked "A" to "H" correspond to the sound spectrograms marked the same in Figure 12c, and also to the same calls in panels a to e of this figure. This song is also shown as an ink tracing of a sound spectrogram in Figure 13c. a—Entire Song. b—e—Song elements shown on a different time scale. Time markers are in ms.



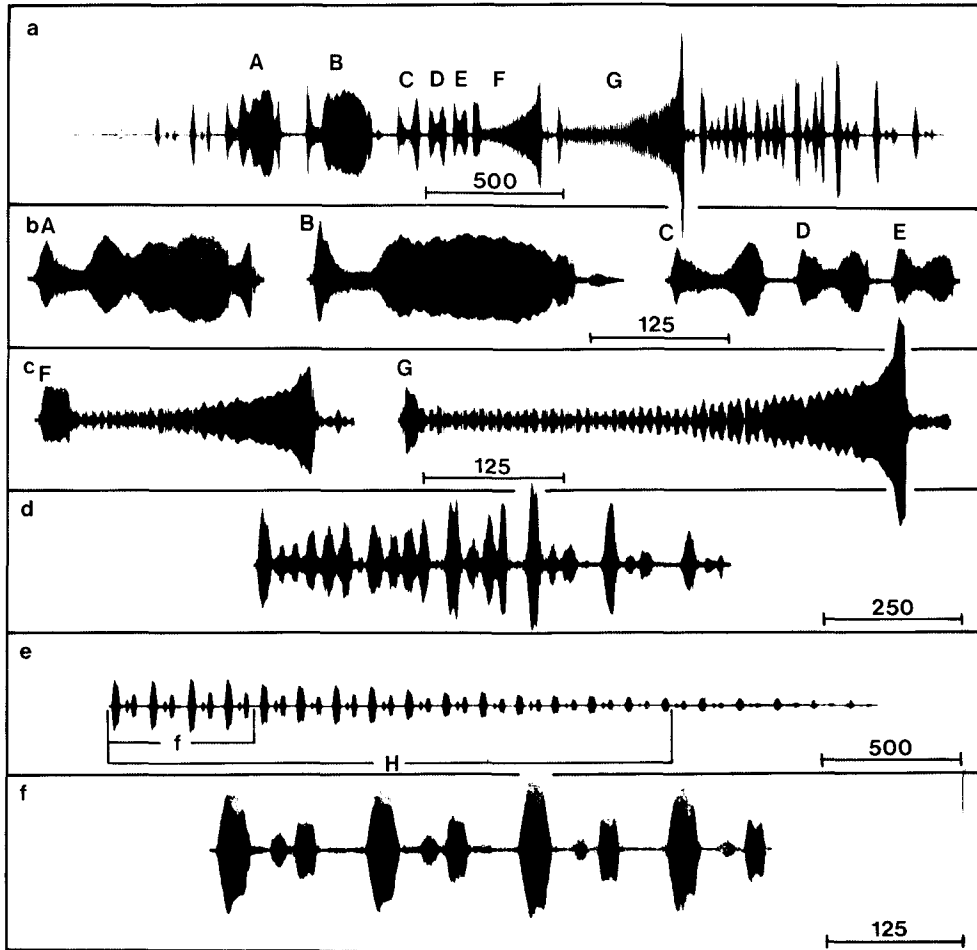


FIGURE 16. Oscillograms of Song and Chattering of a male Least Sandpiper. Elements marked "A" to "G" correspond to the sound spectrograms marked the same in Figure 12f, and also to the same calls in panels a to c of this figure. The entire Song is shown in panel a and its elements and subsequent Chattering are shown on different time scales in panels b, c and d. The terminal part of a long Chattering series by a different male is shown on two time scales in panels e and f. The Chattering sequences marked as "f" and "H" in panel e are shown as sound spectrograms in Figure 19b and c; the segment "f" also corresponds to panel f in this figure. Panel e is indicated as "e" in Figure 19b. Time markers are in ms.

12 d-f; Figs. 16-20). Most Chattering showed less energy in the fundamental frequency than in its first harmonic overtone (Fig. 19). It was the most variable call emitted by males in DFs, and showed strong changes in amplitude, frequency, and harmonic content even within single series (Figs. 16-20). However, such changes were gradual, and prolonged series of loud Chattering usually varied little; they were particularly constant in the intervals between elements and in the relative amplitudes and frequencies of the elements. The latter two characteristics plus the number of component elements per compound unit of repetition were characteristic of individual males, though the number of elements per compound unit varied with behavioral context; e.g., the number of elements was high just before and after Song (Fig. 12d-f; Fig. 16a, d; Fig. 17; Fig. 18).

I have described transitions between Song and Chattering. Chattering sometimes also graded directly into DFVs and vice versa (Fig. 17h). DFVs that blended into Chattering or followed it were less aberrant than were those that preceded or followed Song, but their duration and cadence followed the same trends: DFVs were briefer and of faster cadence immediately before and after Chattering, and were increasingly normal as they fell away to either side of it.

DISCUSSION

The foregoing descriptions should facilitate recognition and description of similar and different display components in aerial displays of related species. Few adequate descriptions of relevant displays of calidridines and other charadriiform species have been published

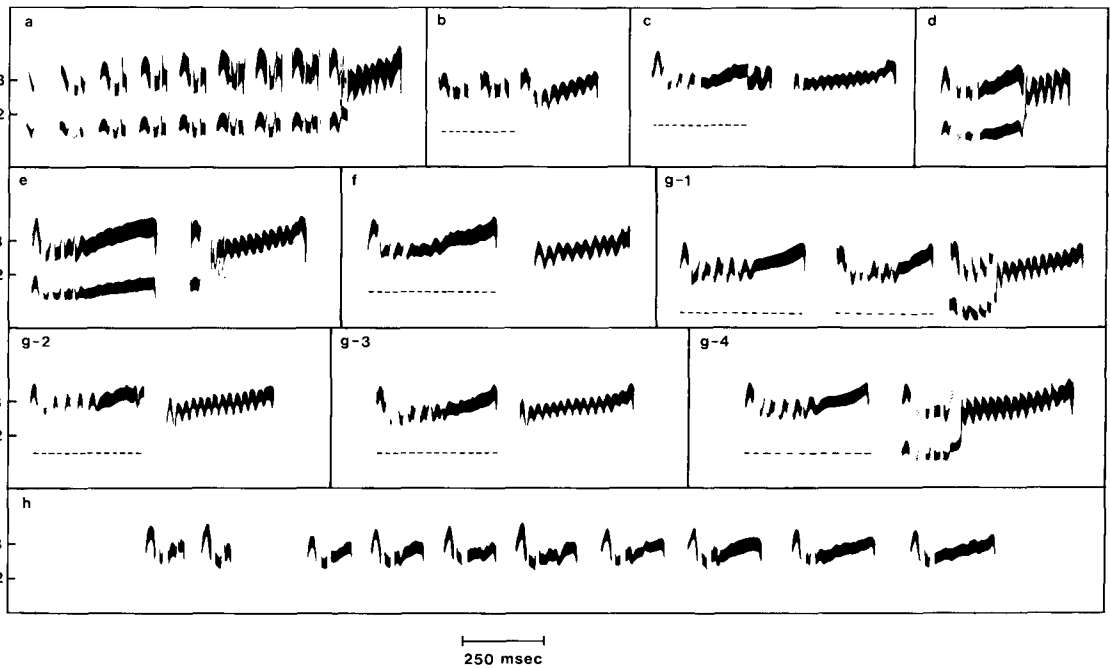


FIGURE 17. Beginnings of Song by six male Least Sandpipers (a–g), and transition from Chattering to Display Flight Vocalizations (DFVs; h). These are ink tracings of the fundamental frequency and its first harmonic, based on sound spectrograms. The fundamental is replaced by a dashed line where it was either too faint to portray or was not involved in transitions; it is omitted altogether from panel h, though it is present for that entire series.

a—Early descent from Display Flight (DF); the rhythm of Punctuated Fluttering was broken, but the Song occurred before stooping descent. b—During descent from DF. c—Brief Parachuting Song embedded in DF. d—During slowing-down of DF (i.e., lengthening of Inter-Flutter Intervals), with slight loss of altitude. e—Preceding descent from DF, with Chattering. h—Transition from Chattering to DFV's, about 10 s after Song during the same DF.

Frequency markers are in kHz. Analyzing filter bandwidth, 300 Hz.

(acoustic displays are reviewed by Miller [in press]). Most of the following discussion deals with convergent and adaptive features of aerial displays of the Least Sandpiper, and evaluates the homologous status of only some display characteristics in the species.

CONVERGENCE AND ADAPTATION IN DISPLAY FLIGHTS

Birds that inhabit open country commonly perform aerial displays in long-distance signalling, since the higher they are, the farther sounds will carry (Armstrong 1963). Altitude also increases a bird's visual conspicuousness, and the distinctive flight pattern of male Least Sandpipers in Display Flight is detectable over long distances. Considering this relationship of transmission distance to display height, it is unsurprising that display height varies inversely with breeding density among species. For example, the Red Knot (*Calidris canutus*) nests at low densities, and male knots have very high aerial displays (Manniche 1910, Nettleship 1974). Height of aerial display is greatest in the Stilt Sandpiper (*C. himantopus*), lower in the Dunlin (*C. alpina*), lower yet in Least Sandpiper, and lowest in the Semipalmated

Sandpiper (*C. pusilla*) in northern Manitoba, while breeding density increases in the same order (pers. observ.). Display height is low in the semi-colonial Western Sandpiper (*C. mauri*; Holmes 1971, 1973), and in the densely nesting Temminck's Stint (*C. temminckii*), a species which also relies heavily on song posts (Hildén 1965, 1975, 1978, 1979). I know of no data on the relationship of breeding density to display height within species.

The long broadcast distances for species with medium to low breeding densities must set some limits to the structure of aerial displays. Such displays must be obvious, stereotyped, redundant, and physically adapted to withstand attenuation and environmental degradation, for maximal transmission and accurate reception to occur. Features of the main part of the DF of *C. minutilla* illustrate some conformity with these points. First, the distinctive pattern of Punctuated Fluttering during DFs is visible over long distances, and is stereotyped and redundant through its rhythmical repetition. Furthermore, the approximately stationary position of displaying birds aids receivers in locating them. The same points apply to Display Flight Vocalizations. Redun-

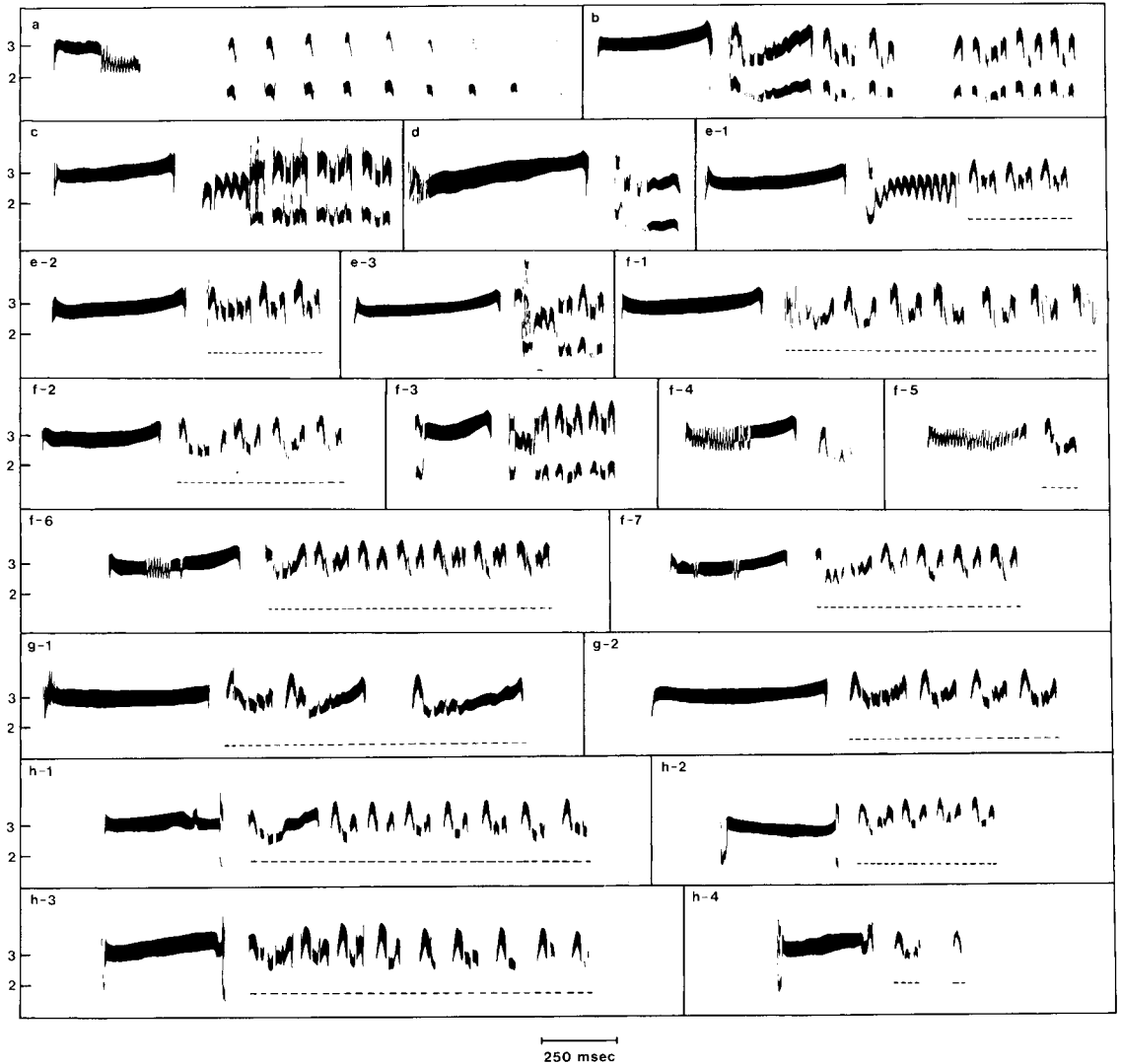


FIGURE 18. Endings of Song by eight male Least Sandpipers (a-b). These are ink tracings of the fundamental frequency and its first harmonic, based on sound spectrograms. The fundamental is replaced by a dashed line where it was too faint to portray.

a—During joint Butterfly Song (BS) descent with a neighbor. **b**—In descent; Chattering continues beyond the sequence illustrated. **c**—During BS about 1 m high, after a leap from the ground in response to audible Display Flight (DF); four further triplets of Chattering conclude this record (not illustrated). **d**—Slowing-down in DF (i.e., lengthening of Inter-Flutter Intervals), with a slight loss in altitude. **e-1**—During DF, in response to a pair flying into the DF area of the calling male. **e-2**—During descent from DF; Chattering continues beyond the sequence illustrated. **e-3**—Song in DF long before descent starts. **f-1**—Spontaneous Song during DF; silence follows the record shown. **f-3**—Song during mutual BS descent with a neighbor; Chattering continues beyond the sequence illustrated. **f-4**, **f-5**—Silence follows the records shown. **f-6**—Song during high altitude aerial tussle with another (presumed) male; Chattering continues beyond the sequence illustrated. **f-7**—Song during high altitude aerial tussle with another (presumed) male; Chattering declines then stops shortly after this record. **g-1**, **h-1**—Silence follows the records shown. **h-2**—Chattering continues beyond the sequence illustrated. **h-3**—Song early in descent from DF. The rhythm of Punctuated Fluttering was broken, but the Song occurred before stooping descent. **h-4**—During DF; silence follows the record shown.

Frequency markers are in kHz. Analyzing filter bandwidth, 300 Hz.

dancy in both cases is manifest not through the correlation of parts of a complex pattern, but rather through rhythmical repetition of a simple one. This reflects the simple, unchanging information content of DFs over most of their course.

Rhythmically repeated, simple calls occur in

lengthy aerial displays of many taxa, including Furnariidae, Motacillidae, and Charadriidae (pers. observ.). Such widespread convergence suggests adaptiveness, which may lie in the opportunities of signal averaging afforded to listeners, in an environment that severely degrades sounds because of wind and tempera-

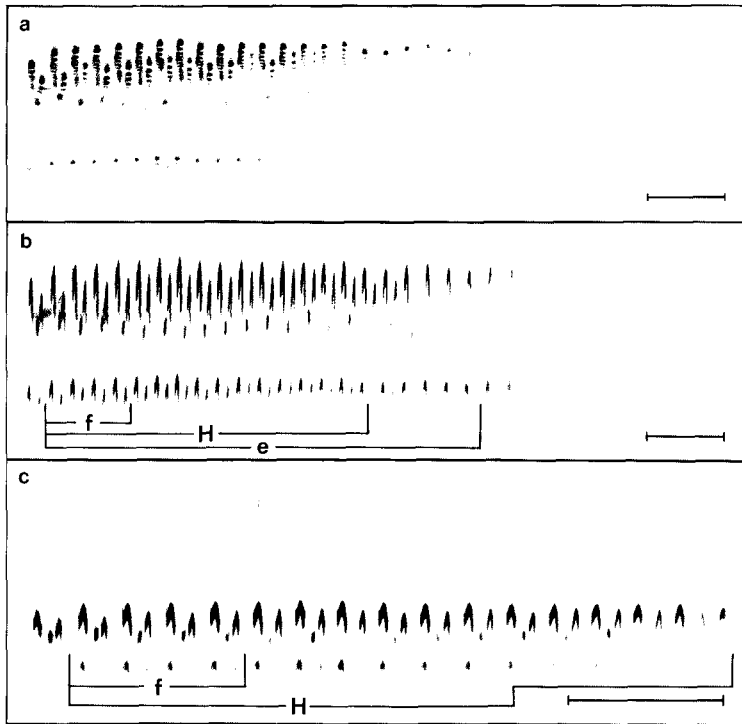


FIGURE 19. Sound spectrograms of Chattering by a male Least Sandpiper. A sequence is shown in narrow (a) and wide (b, c) band representations. Segments marked “e” and “f” correspond to the oscillograms in Figure 16e and f, respectively; the segment marked “H” corresponds to the segment marked the same in Figure 16e. These letters also correspond to the same segments in panels b and c of this figure. The time marker in the bottom right corner of each panel represents 500 ms. The frequency scale is in kHz. Analyzing filter bandwidths, 45 Hz (narrow) and 300 Hz (wide).

ture (see Schleidt 1973, Wiley and Richards 1982). One feature of DFVs themselves, which is probably adaptive, is their relatively narrow band structure. This characteristic minimizes differential frequency attenuation, with the re-

sult that spectral structure remains fairly constant regardless of transmission distance. Also, this represents efficient “packaging” of energy into calls (see Miller and Baker 1980). Most features of the calls themselves are less readily

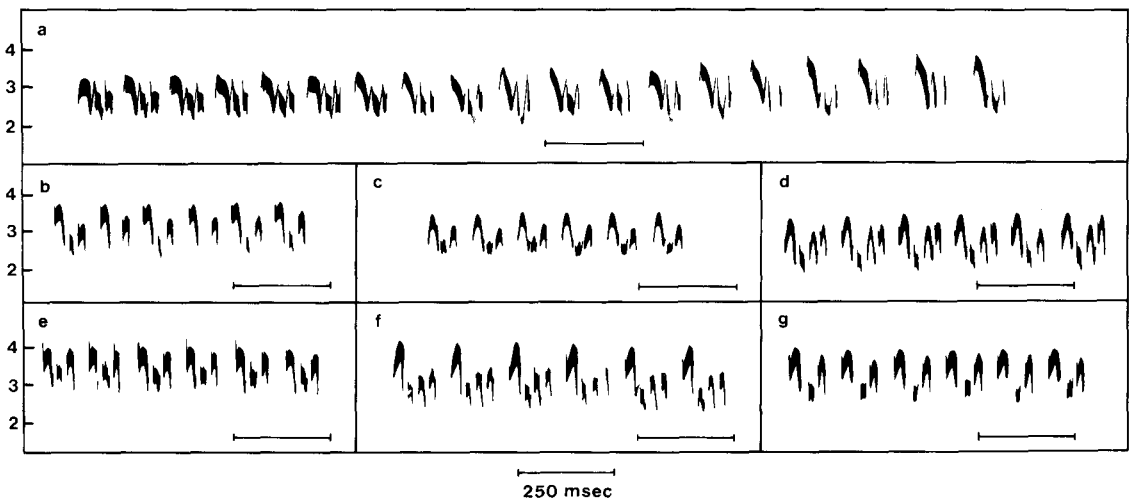


FIGURE 20. Examples of Chattering from seven male Least Sandpipers (a-g). These are ink tracings of the first harmonic of the fundamental frequency, based on sound spectrograms. Frequency markers are in kHz. Analyzing filter bandwidth, 300 Hz.

interpreted, however (see Wiley and Richards 1982):

1. The frequency spectra of DFVs of Least Sandpipers and other calidridines (including syntopic species) vary substantially (see Kroodsma and Miller 1982). This would not be expected if spectra were closely adapted to long-distance transmission in such simple, similar habitats.

2. Frequency modulation is a good way to encode information for long-distance signaling, and amplitude modulation is a poor way, because of its high susceptibility to environmental degradation. Both increase gradually over the course of DFVs, and FM is also expressed in the lead element of DFVs, with AM in comparable or greater detail in the subsequent soft, brief elements. Thus, patterns of AM and FM in DFVs do not differ in a way predicted by signal detection theory.

In an adaptational perspective, several alternative explanations for these observations can be proposed. First, calidridine sandpipers differ in their breeding densities, so the frequency spectra of their long-distance calls may reflect close adaptation to species-typical spacing patterns and microhabitat. Wasserman (1979) and Gish and Morton (1981) have documented adaptive differences for maximal transmission in song of White-throated Sparrows (*Zonotrichia albicollis*) and Carolina Wrens (*Thryothorus ludovicianus*) between habitat types and from different parts of the species' range, respectively. Second, different features of DFVs may encode different sorts of information, some for nearby neighboring males, others for more distant, anonymous receivers. Call characteristics that are important for individual identification among neighbors may be degradable or not. Hence, they may apply to such features as temporal patterning and amplitude envelopes of the soft, brief intermediate elements of DFVs, as well as to gross temporal patterning within DFV-calling sequences. Call characteristics may also be designed to provide information to receivers about their distance from callers (though such information must be very approximate in an environment so physically variable because of turbulence, etc.), and such information can come from sound features that degrade predictably with distance. Evidence for differential responsiveness of receivers to songs with different levels of natural degradation has been provided by D. G. Richards (review in Wiley and Richards 1982). In summary, long-range acoustic signals like DFVs are probably adapted for transmission over optimal, not maximal, distances to biologically relevant receivers (Lemon et al. 1981), and particular sound

characteristics probably vary in what those distances are. Experimental evidence is needed to evaluate further the adaptiveness of DFV structure.

The adaptive significance of other display components of DF's can not be evaluated in a similar way, because they are not used in simple long-distance communication, with likely adaptations to the physical environment. Song, Chattering, and associated visual displays by males presumably evolved through sexual selection, as have DFVs and Punctuated Fluttering. Unlike the latter two components, they are often transmitted over short distances to particular receivers of known sex, identity, and pairing status, and they encode more complex messages, and can assume more complex and variable form than can DFVs. All are emitted during major changes in locomotion, including ascent into DFs and descent from them, as well as during diverse aerial approach behavior toward males or females. Descents from DFs show particularly striking visual and acoustic displays, a seemingly universal characteristic in waders (see next section). In brief, DFVs and Punctuated Fluttering encode non-behavioral information about a male's pairing status, individual identity, and location, and they encode general sorts of behavioral information about a male's activity and attentiveness. More complex display components differ primarily in also encoding behavioral information about locomotory, approach, and interactive behavior (see Smith 1977). It is these messages that have molded the complexity of Song and Chattering and the graded nature of Chattering, under the influence of sexual selection.

HOMOLOGIES OF VISUAL COMPONENTS

For homologies to be useful in suggesting affinities, they must represent shared derived states (synapomorphies), and not shared ancestral or uniquely derived ones (symplesiomorphies and autapomorphies, respectively; Eldredge and Cracraft 1980).

Visual displays associated with DFs in Least Sandpipers show strong similarities to some sketched by Drury (1961), notably Stooping descent, Parachuting, and Punctuated Fluttering. The first of these is widespread in aerial display of birds, and has probably arisen a number of times. Stooping is apparently ubiquitous in waders, and provides little insight into relationships. Parachuting and Butterfly occur sporadically in Calidridinae, the former in Least and White-rumped sandpipers, the latter in the same two species plus Baird's Sandpipers (Drury 1961). The seemingly re-

stricted occurrence of these two visual displays may just reflect inadequate description, so evaluation of their ancestral/derived status must wait.

Punctuated Fluttering occurs in various wader species outside the Calidridinae, including the American Woodcock (*Scolopax minor*; Brewster 1894), the Willet (*Catoptrophorus semipalmatus*; Vogt 1938, Sordahl 1979), the Upland Sandpiper (*Bartramia longicauda*; Ailes 1976, pers. observ.), and the Little Curlew (*Numenius minutus*; Labutin et al. 1982). It is also probably homologous to a component of aerial displays in certain Tringinae and curlews (*Numenius*), in which fluttering occurs during rises and gliding occurs during falls (Rowan 1929, Grosskopf 1963, Bicak 1977, Glutz von Blotzheim et al. 1977). Thus, Punctuated Fluttering is plesiomorphous within the Calidridinae.

A distinct form of aerial display in Calidridines has been mentioned by several authors, though I have never seen it in Least Sandpipers. Male Western Sandpipers take flight with a "slow but deep wingbeat," then, at an altitude of about 5 m, slowly patrol the territory (Holmes 1973: 109). Slow wing beats also occur in Baird's Sandpiper (Drury 1961, Holmes and Pitelka 1964, Holmes 1973), Dunlin (Cramp et al. 1983), the Little Stint (*Calidris minuta*; Cramp et al. 1983), the Curlew Sandpiper (*Calidris ferruginea*; Holmes and Pitelka 1964), and the Purple Sandpiper (*Calidris maritima*; Swanberg 1945, Bengtson 1970, Cramp et al. 1983). Portenko (1972: 359) described males of the Rufous-necked Sandpiper (*Calidris ruficollis*) as "slowly beating their wings like a bat that had just taken flight," while flying low above the ground. Comparable displays also occur in Common Snipe (*Gallinago gallinago*), Eurasian Woodcock (*Scolopax rusticola*), Charadriidae, Haematopodidae, Laridae (jaegers, *Stercorarius*), and Thinocoridae, at least (Drury 1961, Andersson 1973, Maclean 1969, Shorten 1974, Glutz von Blotzheim et al. 1975, Miller and Baker 1980, Phillips 1980, pers. observ.). The display is thus plesiomorphous within the Calidridinae, and its absence in the Least Sandpiper is apomorphic.

The kind and amount of movement during Display Flights varies greatly across species. Considering such variations, it is easy to visualize the evolutionary elaboration of flight path for display purposes. In Charadrioidae, DFs include simple ascent followed by gliding descent (Thinocoridae; Maclean 1969, pers. observ.), Punctuated Fluttering and treading (certain species discussed in this paper), regular intermittent dives (snipes; Kliebe 1974,

and references given below; Little Curlew; Labutin et al. 1982), patrol flights (turnstones; Bergman 1946, Nettleship 1973; R. E. Gill, pers. comm.), switchback flight paths (Green-shank, *Tringa nebularia*; Nethersole-Thompson and Nethersole-Thompson 1979), undulating flight (Lesser Yellowlegs, *Tringa flavipes*, and Redshank, *Tringa totanus*; Grosskopf 1963, Rowan 1929), and numerous other elaborate variants (e.g., Pitelka 1943, von Frisch 1956, Lind 1961, Haverschmidt 1963, Glutz von Blotzheim et al. 1975, 1977, Dabelsteen 1978, Allen 1980). The evolutionary origins of many such variants may lie in the correlation between Display Flight termination and display complexity. For example, most calidridines have fairly simple flight paths in DFs (exceptions are the Spoonbill Sandpiper [*Eurynorhynchus pygmeus*] and Red Knot; Dixon 1918 [but see Portenko 1957], Nettleship 1974). The most complex motor patterns occur during terminal dives, which are almost always accompanied by Song, the most complex vocal utterance associated with DFs. Terminal dives and flourishes appear to be given by all or nearly all wader species. Ritualization of these during Display Flights would seem to be a straightforward process, and has probably occurred in various groups, including lapwings, godwits, tringines, and snipes. In the latter, ritualization of terminal diving has promoted the evolution of non-vocal acoustic displays, based on vibration of the outer rectrices in the air current modified by the set wings (Tuck 1972, Rutschke 1976, Reddig 1978, Sutton 1981; see also Labutin et al. 1982). It is probably safe to consider simple flight paths, without embedded dives, to be plesiomorphous within the Calidridinae.

The tail is not an important visual display feature in Display Flights, despite its obvious functional correlation with them. This is presumably because of its inconspicuousness and its involvement in stabilizing adjustments under windy conditions. In the Least and Upland sandpipers the tail is spread only as necessary to adjust position (Ailes 1976). Spreading occurs consistently during the descent phases of undulating flight in the Lesser Yellowlegs (and probably in other species, whose displays are yet undescribed), but this also appears to be simply for aerodynamic reasons, probably to slow the descent (Rowan 1929). Future observations may disclose display functions of the tail in DFs of some calidridines. If so, such states must be considered apomorphic.

To summarize, the Least Sandpiper exhibits plesiomorphy in Display Flights in Punctuated Fluttering, simple flight pattern with no ritualized embedded dives (occasional brief and

variable Song or Chattering false descents are embedded), and lack of display use of the tail. It is apomorphic in lacking "bat display."

HOMOLOGIES OF ACOUSTIC COMPONENTS

The few published accounts of aerial displays in waders, particularly calidridines, preclude comprehensive assessment of homologies of Song and Chattering and of the ancestral/derived status of particular features of Display Flight Vocalizations at present.

Homologues to DFVs may occur even in distantly related groups. Thus, the distinctive long call of curlews is probably homologous to the DFV of calidridines, because of its simplicity, repetitiveness, physical features, and association with Display Flights (Forsythe 1967, 1970, Skeel 1976, 1978, Glutz von Blotzheim et al. 1977). Male Willets emit a repeated "pill-will-willet" during DFs, a call which is also a likely homologue of the DFV of calidridines (Vogt 1938, Sordahl 1979). Finally, godwits (*Limosa*) utter simple, repeated calls in the prolonged circling phase of their aerial displays (Bent 1927, Lind 1961, Hagar 1966, Nowicki 1973). DFVs are thus plesiomorphous within the Calidridinae, and their absence in certain species is apomorphic.

Convergence, though, is partly responsible for the loss of Display Flight Vocalizations. The lekking Buff-breasted Sandpiper (*Tryngites subruficollis*) has a silent flight display which is simply ritualized flutter-fighting, and it utters only soft "tick" sounds during mate-attraction displays on the ground (Parmelee et al. 1967, Sutton 1967); males of the Ruff (*Philomachus pugnax*) have a similar flight display and are silent on their lekking hills (Hogan-Warburg 1966, van Rhijn 1973); the related Sharp-tailed and Pectoral sandpipers (*Calidris acuminata* and *C. melanotos*) utter entirely different kinds of calls during low, rapid display flights over their mating territories (Pitelka 1959, Flint and Kishchinskii 1973, Myers 1982) (are these derivatives of DFVs?); and White-rumped Sandpipers possess a well-developed hovering flight but also produce unique calls during it (Sutton 1932, 1961, Drury 1961, Holmes and Pitelka 1962; however, the "territorial song" shown as a sound spectrogram in Fig. 91 of Glutz von Blotzheim et al. [1975] is certainly suggestive of DFVs). The absence of DFVs in these species is partly due to an increased emphasis on visual signals, promoted by the moderate- to high-density breeding conditions which characterize these polygynous forms. At least some calidridine species are polygynous and possess DFVs (e.g., Curlew Sandpipers [Holmes and Pitelka 1964]), but most species that have DFVs are monoga-

mous and nest at moderate to low population densities.

CONCLUDING COMMENTS

Inference about adaptations in the structure of Display Flights is simplest for those characteristics which encode simple behavioral information, and which are transmitted over long distances: Punctuated Fluttering and approximately stationary position. The significance of the form of Song and Chattering lies in their proximate effects on receivers, not on effective transmissibility, and assessment of their adaptiveness depends upon which paradigm of communication one is working within (Marler 1967, Beer 1977, Smith 1977, Dawkins and Krebs 1978, Morton 1982). Different paradigms predict different evolutionary modes and patterns, and these are of varied significance for the origin and evaluation of homologies. For example, predictions of signal structure based on models of maximal vs. optimal transmission differ, as do those based on models of deceptive (manipulative) vs. non-deceptive communication. In this paper, I have adhered to the view that signals are adaptive in structure, largely for consistency. It seems best to sidestep these admittedly crucial issues at present, and await further information on adaptive radiation of calidridine Display Flights from future studies.

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Vertebrate Zoology Division, British Columbia Provincial Museum, Victoria, British Columbia V8V 1X4, Canada and Biology Department, University of Victoria, Victoria, British Columbia V8W 2Y2 Canada. Received 1 April 1982. Final acceptance 26 October 1982.

APPENDIX. Abbreviations used in the text for features of the Display Flight and vocalizations of the Least Sandpiper.

AM	Amplitude Modulation
BS	Butterfly Song
DF	Display Flight
DFV	Display Flight Vocalization
FM	Frequency Modulation
ICI	Inter-call Interval
IFI	Inter-Flutter Interval
PF	Punctuated Fluttering
PS	Parachuting Song
