

Functions of display flights by males of the least sandpiper, *Calidris minutilla* (Vieill.), on Sable Island, Nova Scotia

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Display flights (DF's) in the least sandpiper, *Calidris minutilla* (Vieill.), are described and their relations to ecological and social variables assessed. DF activity is highest in early spring and in the morning, and is low in strong winds and poor visibility (fog). DF's are given only by males and generally cease upon pairing. Unpaired males maintain exclusive DF areas from which they chase other unpaired males. Each male's DF area includes his eventual nest site, but only includes foraging and brood-rearing areas occasionally. Nesting areas are defended by males sometimes, but foraging sites and brood-rearing areas are not. The DF area of a paired male may be taken over by a later male who pairs and nests nearby, so nests may be quite close together; this suggests that the primary function of DF's in *C. minutilla* is not to space out nests to reduce predation. The ultimate function of DF's is probably mate attraction, and thus sexual selection has been an important force in their evolution. This may be true of scolopacids and charadriids, which nest at high latitudes, in general.

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On trouvera ici la description du vol de parade (DF) chez le bécasseau minuscule *Calidris minutilla* (Vieill.), ainsi qu'une évaluation des relations entre ce comportement et les variables écologiques et sociales. Les vols de parade sont fréquents surtout au début du printemps, le matin, et on en observe peu lorsque les vents sont forts et la visibilité faible (brouillard). Le vol de parade est l'apanage du mâle et il cesse ordinairement à la formation des couples. Les mâles non accouplés gardent des aires exclusives destinées aux vols de parade et ils en chassent les autres mâles non accouplés. L'aire que se réserve ainsi chaque mâle contient son futur site de nidation, mais ne contient que rarement les aires de recherche de nourriture et d'élevage des oisillons. Les aires de nidation sont parfois défendues par les mâles, mais pas les aires réservées aux autres fins. L'aire de vol de parade d'un mâle accouplé peut être occupée par la suite par un mâle non accouplé qui s'accouplera et fera son nid tout près, ce qui fait que les nids peuvent être très rapprochés; on peut conclure alors que la fonction principale des vols de parade chez *C. minutilla* n'est pas d'espacer les nids dans le but de diminuer la prédation. Le principal rôle de ces vols est probablement d'attirer un partenaire; conséquemment, la sélection sexuelle est un facteur important de l'évolution de ces vols. Ces données sont probablement vraies également des scolopacides et des charadriidés des latitudes élevées en général.

[Traduit par le journal]

Introduction

The 24 species of sandpipers in the subfamily Calidridinae (Scolopacidae) are small to medium, usually cryptically colored shorebirds which breed almost entirely in the world's subarctic and arctic areas (Larson 1957; Thomson 1964; Voous 1960). Most species exploit a fairly narrow feeding niche by probing soft substrates with their long bills, or by hunting visually for small invertebrates on the substrate surface (Baker and Baker 1973; Burton 1974; Ehlert 1964; Hoerschelmann 1970). Specialization for this manner of feeding has tied most calidridine species to certain ecological situations on both their breeding and wintering grounds, for

they generally prefer or must have access to soft substrate to feed.

Calidridines may maintain territories where they feed, mate, and nest if suitable feeding and nesting habitats overlap, but feeding and nesting areas are usually separate (see Discussion). This can vary geographically within a single species. For example, dunlin (*Calidris alpina*) in northern Alaska hold all-purpose territories until eggs hatch (Holmes 1966), but in Finland adults share undefended feeding sites up to several kilometres away from nesting areas (Soikkeli 1967). Mating systems may also vary geographically. In Canada, females of the sanderling, *Calidris alba*, rapidly lay two clutches, the first incubated by a male and the second by the female (Parmelee and Payne 1973). By contrast, in northeast Greenland mates share incubation at

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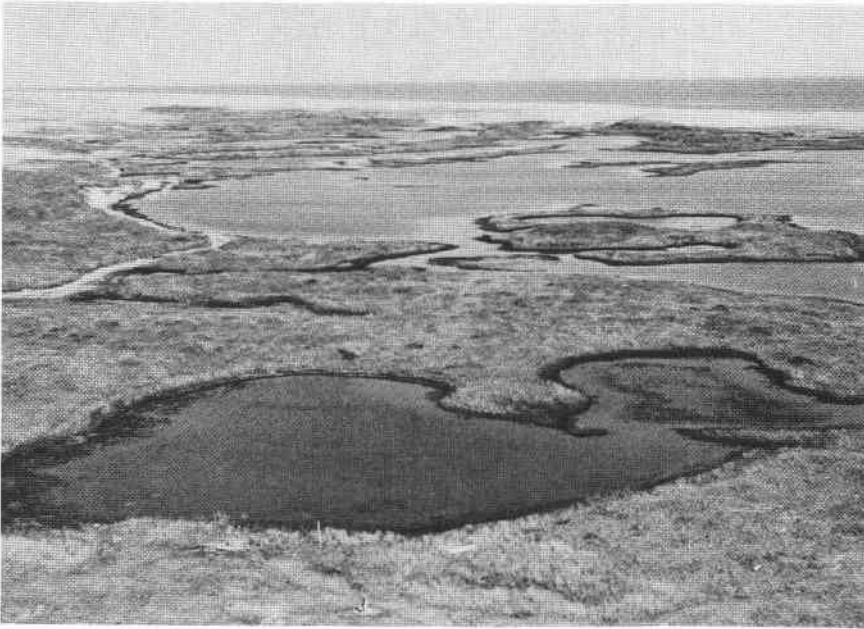


FIG. 1. Main study area on Sable Island, as viewed from the top of a 20-m light tower. Many birds foraged along the pond margins and nested in adjacent vegetation.

their single nest (Pienkowski and Green 1976; but see Meltofte 1976). Calidridines also show major species differences in social systems. The subfamily includes lek-forming species such as the ruff, *Philomachus pugnax* (Hogan-Warburg 1966; Rhijn 1973; Shepard 1975), polygynous species such as the white-rumped sandpiper, *Calidris fuscicollis* (Parmelee *et al.* 1968), and monogamous species like the stilt sandpiper, *Micropalama himantopus* (Jehl 1973). Because of these intra- and interspecific variations in social systems, and their relationships to ecological factors, the Calidridinae offer rich opportunities for sociobiological research (Pitelka *et al.* 1974).

The splendid review by Pitelka *et al.* (1974) shows that we have limited understanding of calidridine spacing systems and of the relationship of "territory" to the conspicuous aerial advertisement displays of males. In 1975 and 1976 I studied the least sandpiper, *Calidris minutilla* (Vieill.), on Sable Island, Nova Scotia, to document the breeding cycle and display behavior, and to evaluate the function of male display flights. I describe the breeding cycle elsewhere (Miller 1977). Here I describe briefly the motor patterns and prominent vocalizations associated with DF's, analyze the relationships of date, weather, and male breeding status to the incidence of DF's, describe the spatial relationships of DF's to feeding, nesting, and

brood-rearing locations, and review the functions of DF's and territoriality in the Calidridinae and related species.

Materials and Methods

Field work was carried out on Sable Island, Nova Scotia (43°57' N; 59°55' W), from 17 May to 23 July, 1975, and from 14 May to 3 August, 1976. I banded each of 210 birds with a unique combination of aluminum and color bands (122 chicks and fledglings, 40 adult males, 42 adult females, and 6 adults of unknown sex). I kept records on all banded birds plus about 12 others that could be identified by plumage, voice, or behavior.

Calidris minutilla is the only breeding calidridine on Sable Island. It nests abundantly in the vegetated environs of freshwater and brackish water ponds. The extensive complex of freshwater ponds between West Light and the meteorological station, and the adjoining nesting areas were chosen as the main study area (Fig. 1). Here the sand terrain is consolidated by a luxuriant growth of forbs, grasses, shrubs, and, along pond margins, cranberry (*Vaccinium macrocarpon*), sedges, and emergent rushes and mare's tail (*Hippuris vulgaris*). Vegetation around the ponds is the favored nesting habitat. It is kept quite short through intensive grazing by the island's resident wild horses, even at summer's peak. A large cranberry bog and extensive dry areas of juniper (*Juniperus horizontalis* and *J. communis*) mixed with black crowberry (*Empetrum nigrum*) are also favored by nesting sandpipers. Some nests occur in areas of sparse vegetation, consisting mainly of marram grass (*Amphiphila breviligulata*) and pearly everlasting (*Anaphalis margaritacea*). Representative photographs of habitat and a summary of weather during the years of study are in Miller (1977).

I noted occurrences and locations of DF's by known males as opportunity permitted. If particular males were not seen in DF's on a given day, this did not necessarily mean that they did not

display that day, because the study area was large and I was always far from some display areas. On the other hand, DF's were sometimes given in response to human intruders, even during incubation when spontaneous DF's almost never occurred. I excluded from consideration all records of DF's which I judged might have been induced artificially.

I walked daily along predetermined routes among the ponds to search for banded birds in both years. Dates and locations for these sight records, excluding those that may have been of birds off their nests because of my presence, provide data on areas used by adults for raising broods and foraging.

In 1976 I obtained four measures of DF and song activity in five 30-min sample periods every 2 days. One sample fell in each of the time periods 0500–0800, 0800–1100, 1100–1400, 1400–1700, and 1700–2100 hours. For each minute in the samples I (i) counted all songs, and (ii) noted the number of different males giving display flight vocalizations (DFV's; see Results). At the end of each sample I counted the number of minutes in which I heard (iii) DFV's or (iv) songs. I timed durations of DF's as opportunity permitted, and noted the date and time of day for each. Weather data corresponding to the times of samples of DF–song activity and DF durations were supplied by Environment Canada, Atmospheric Environment.

Vocalizations were recorded at a tape speed of 19 cm s^{-1} with a Uher 4200 report stereo IC tape recorder and a Uher M517 dynamic microphone mounted on a Dan Gibson parabolic reflector. Sound spectrograms were prepared with a Kay Sona-Graph 7029A, using the FL-1 setting. The time markers for the sound spectrograms were established after measuring the revolution time of the drum ($= 1.65\text{ s}$ for the frequency range 80–8000 Hz, on the machine used).

Results

1. General Description of Display Flights (DF's)

Only males perform DF's. Typically, a male flies up from the ground at a steep angle and, as his altitude increases, his rate of ascent slows and his angle of ascent becomes gentler. He levels out about 15–20 m high. As a male's ascent becomes gentler, his normal flight pattern of rapid wingbeats is replaced by brief, alternating periods of rapid fluttering of the wings, and periods in which the wings are held motionless out to the sides (punctuated fluttering, or PF). PF is the dominant flight mode during DF's, as males hover at constant altitude over a small area. The alternating fluttering and nonfluttering periods of PF average 0.72 and 0.84 s, respectively (medians and N are 0.66 s and 1563, and 0.65 s and 1587, respectively; Miller (1977)).

Males in DF's often remain roughly stationary above a small area while in PF, then change the cadence of PF or cease PF altogether, while letting the wind carry them over another area where PF and hovering resume. Movements between areas are rapid and irregular, and may be in several steps. Displaying males commonly respond to an intruding man or dog by shifting the location of the DF quickly so that it is performed right above the intruder, often at unusually low altitude. A male may cover an area up to 200 m in diameter during a single

DF (this includes hovering areas and changes of location). DF's end with a breakdown of PF, a stepwise loss in altitude, and finally a steep descent which may be a slow parachuting or a rapid stoop. Stooping descent is commonest.

DFV's (Fig. 2) usually start just before maximal altitude is reached, but may begin even before a male leaves the ground. DFV's are repeated monotonously throughout a DF, and become louder and are delivered more rapidly just before descent. DFV's are usually replaced by song (Fig. 3) around that time. Song occurs before silent stooping descent, but may be emitted throughout a slow parachuting descent. A third type of call which often occurs around the time of descent is chattering (Fig. 4), and this often precedes or follows song. DFV's are virtually restricted to DF's, with some exceptions, but song and chattering occur in other contexts more frequently. Males sometimes give soft DFV's during ground courtship. Song and chattering are common when males chase females or other males in flight. Song is also a prominent part of ground courtship, and chattering occurs in a broad range of aggressive contexts.

DF's average 3.4 min in duration (median = 2.6 min, $N = 269$). More detailed descriptions and measurements are given elsewhere (Miller 1977).

2. Variation in DF and Song Activity

(a) Relationships of DF and Song Activity to Date, Time of Day, and Weather

I investigated the relationships of DF and song activity to date, time of day, and weather, through stepwise multiple regression. It was necessary to log-transform data on durations of DF's and on the two measures of song activity to meet assumptions about sampling error.

Durations of DF's plus all DFV and song activity measures show similar relationships to the independent variables (Table 1). All were high in the morning and in the early spring (their relationships to date probably would have been stronger had I adjusted the data to compensate for the low numbers of males present during the first samples in mid- to late-May). DF's were briefer and all activity measures were lower in high wind and poor visibility (fog).

Independent variables that were used in the initial analysis but that did not contribute substantially ($P \leq 0.10$) to the multiple regression solutions were omitted. These were barometric pressure, air temperature (dry bulb), air temperature (wet bulb), and change in barometric pressure in the hour before each activity sample. I had too few samples

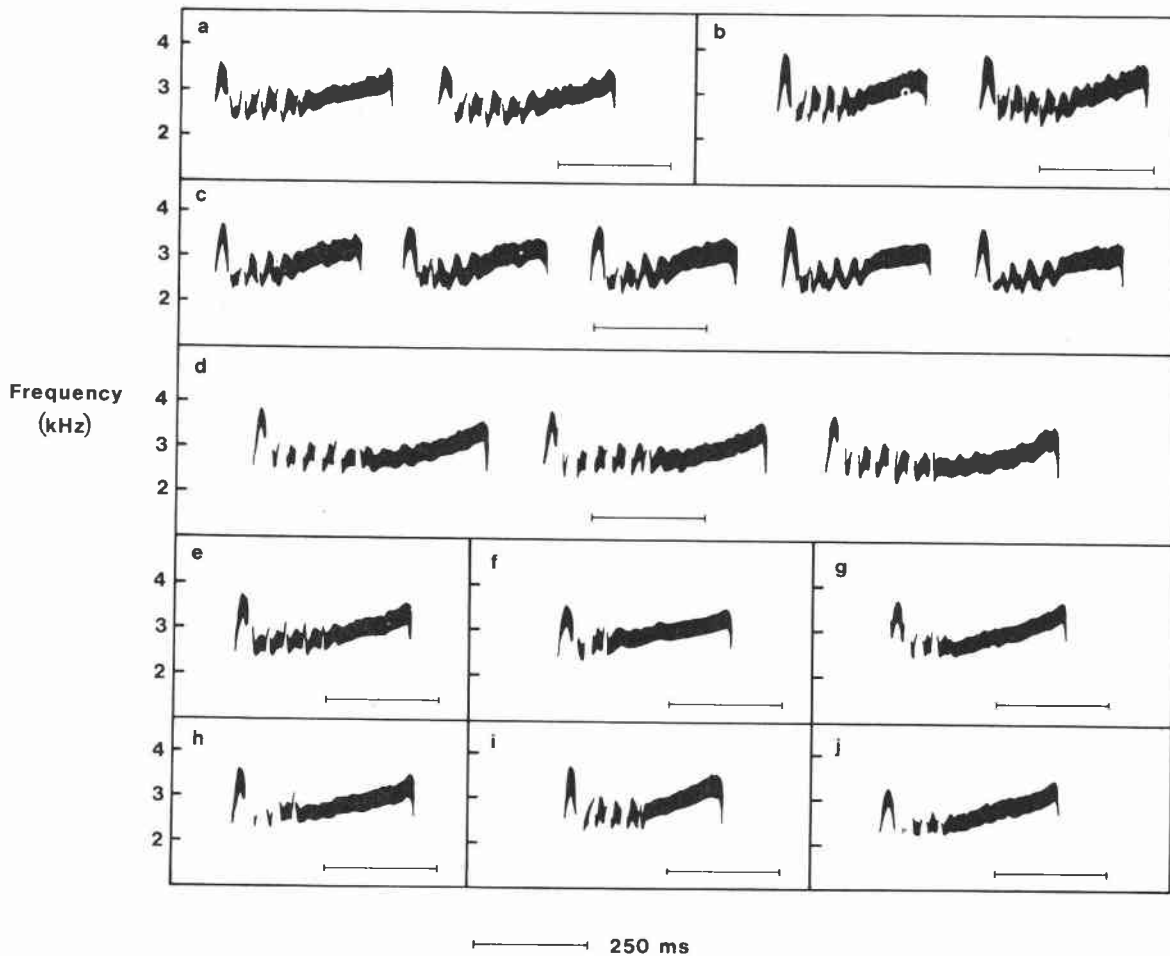


FIG. 2. Sound spectrograms of display flight vocalizations (DFV's) and brief DFV sequences, for 10 males of *C. minutilla*. These are ink tracings of the second harmonics; the first harmonics are faint. Analyzing filter bandwidth, 300 Hz.

during rain to enter precipitation as an additional independent variable, but heavy rain certainly depressed DF and song activity.

(b) *DF Activity, Fighting, and Mate Attendance by Males*

I have mentioned problems in assessing the occurrence of spontaneous DF's by males (see Materials and Methods). Nevertheless, measures of DF activity through the breeding cycles of individual males can be obtained by summing records on DF activity of males during six defined periods (prepairing, postpairing but before clutch completion, etc.; see Table 2). I computed these measures for known males by summing the number of days within each period on which DF's by the males were observed, then dividing these sums by the number of male-days in each period. The measures are listed in the first row of Table 2, and their relative magnitudes are shown in the third row.

Relative incidences in the bottom rows of Table 2 show the percentage of males seen displaying per day in each of the six periods; these were computed similarly.

A male's DF activity was highest before he paired. It declined sharply as soon as he started to consort with his future mate, and remained at a low level for the rest of his breeding cycle. Males that lost their clutches showed a slight resurgence of DF activity, even though those referred to in Table 2 renested with their original mates. Several other males were abandoned by their mates after gulls took their clutches; they resumed high levels of DF activity. The sharp decline in DF activity of newly paired males is accompanied by a sudden tolerance toward other males in DF's. Numerous times I watched males feeding peacefully with their new mates while an unpaired male called lustily in DF overhead, where the now-paired male displayed vigorously only a day or two earlier. Newly paired

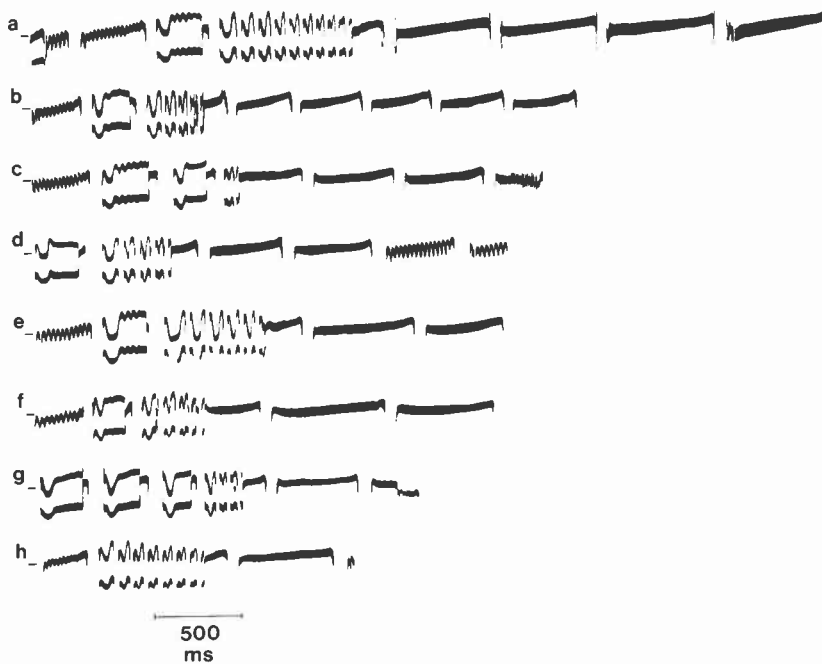


FIG. 3. Sound spectrograms of song associated with display flights, for eight males of *C. minutilla*. These are ink tracings of the first and second harmonics of all elements. The record for male *a* starts immediately from a display flight vocalization (see Fig. 2), the tail end of which is shown. The record for male *g* is incomplete; the initial few elements are unclear in the recording. Analyzing filter bandwidth, 300 Hz. Frequency markers, 3 kHz.

males tolerated unpaired neighbors and newly arrived males encroaching in DF's in the now-vacant airspace. This resulted in a certain amount of 'overlay' of DF areas which were defended asynchronously, *i.e.* by a succession of males (Fig. 5).

Overt fighting plays a role in the spacing system of *C. minutilla* but is not restricted to unmated males. Females fought rarely. One female, heavy with egg, attacked and drove away a female that was being courted by the first female's mate. Such altercations were brief and unsteretyped. Males fought more often and at length, especially when unpaired. Holmes (1973) gives good pictures and descriptions of fighting in a related species. A few newly arrived males fought frequently with established unpaired residents over several days, and at least one newly arrived male in 1976 fought at length to reestablish his 1975 territory, which necessitated compression of that held by the other male, his 1975 neighbor. From the resident's point of view this fighting was probably in defence of his DF area, and this seemed to be the rule for unmated males. Nevertheless, I saw a few bouts of vigorous prolonged fighting (occurring over several days for some male pairs) by paired *incubating* males; they actually left the clutch unattended for protracted periods while they fought. In all cases, the outbreak of fighting coincided with the onset of DF's by a

new male (presumed or known to be one of the fighters) in the former DF area of the incubating male. Some of these incidents may have resulted from the newly arrived males attacking the resident nesting males, with the latter responding in kind. Alternatively, the new males may have constructed nest scrapes too close to established nests and were attacked (unmated males construct "cock nests" (Miller 1977)), or they may have tended to land too close to nests after DF's: I caused one bird to leave its nest and walk close to another, which left its nest in turn and attacked the first. This is a partial explanation at most, for one nesting male left his foraging area several times to interact aerially with two new unpaired neighbors when they started DF's, and he fought with both of them extensively. To summarize, fighting is common among unpaired males, and seems to be associated simply with establishment and maintenance of DF areas. However, it also occurs in circumstances unrelated to DF activity, suggesting that it has broader functions than have DF's.

A newly paired male's attendance of his mate could reduce his DF activity. Members of undisturbed pairs spend most of their time together (Fig. 6). This is due mainly to assiduous attendance of females by their mates who follow them while feeding, fly after them when they change feeding

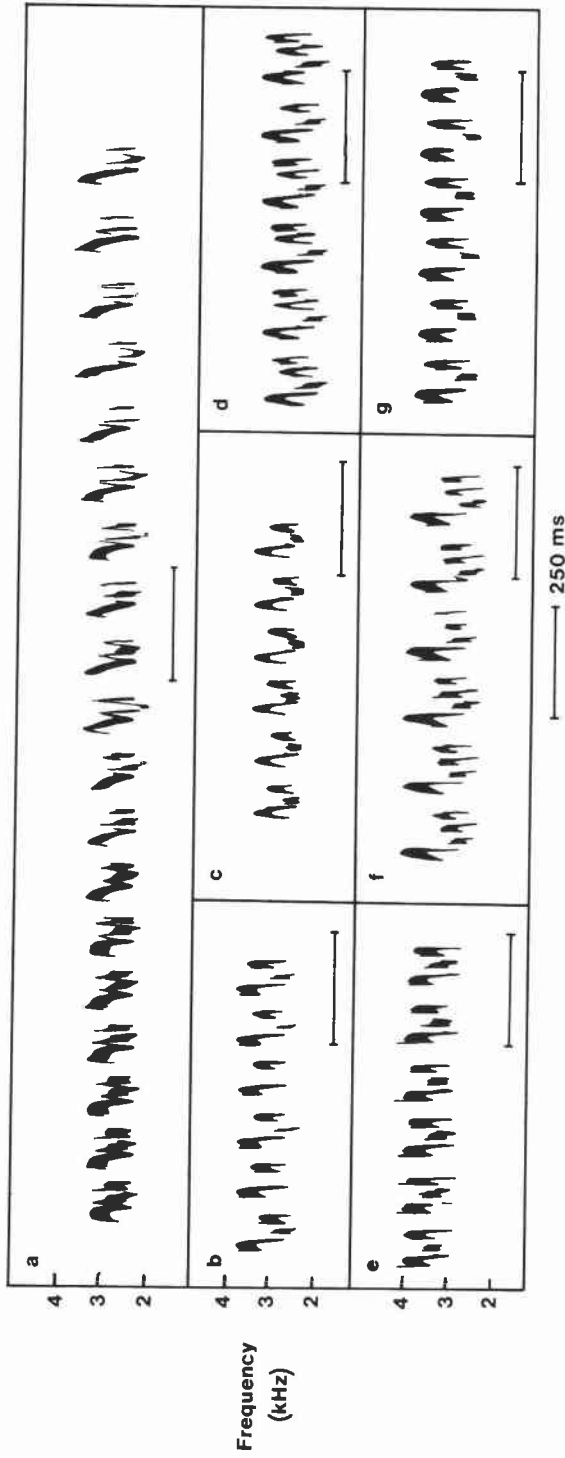


FIG. 4. Sound spectrograms of chattering, from seven males of *C. minutilla*. These are ink tracings of the second harmonics; the first harmonics are often faint. (a) Chattering immediately after song, during a pause in a fight on the ground. This sequence exhibits characteristic grading. (b) Chattering during descent from a display flight (DF), and following song (partial sequence shown). (c) Chattering during descent from a DF, and following song (partial sequence shown). (d) Chattering during a DF, and between songs (partial sequence shown). (e) Chattering following ground song, given in response to another bird (male?) swooping low overhead (partial sequence shown). (f) Chattering during slow flight over my head, possibly elicited by my presence in the male's DF area (partial sequence shown). (g) Chattering following a high-altitude aerial tussle with another male (partial sequence shown). Analyzing filter bandwidth, 300 Hz.

TABLE 1. Relationships of the durations of display flights (DF's) and of DF-song activity indices (INDEX's) in *C. minutilla* to date, time of day, and weather: results of stepwise multiple regression

Dependent variable ^{a,b}	Regression equation ^c	R ²	Contributions to R ² by independent variables ^d
log DF duration, s (N = 269)	$Y = 2.659 - 0.012 \text{ DATE} - 0.018 \text{ WIND} - 0.048 \text{ TIME} + 0.013 \text{ VISIBILITY}$	0.183	0.118, 0.034, 0.015, 0.015
INDEX 1 (N = 120)	$Y = 41.9 - 0.6 \text{ DATE} - 0.7 \text{ WIND} - 2.8 \text{ TIME} + 0.8 \text{ VISIBILITY}$	0.498	0.356, 0.051, 0.044, 0.048
INDEX 2 (N = 120)	$Y = 28.7 - 0.4 \text{ DATE} - 0.4 \text{ WIND} - 1.7 \text{ TIME} + 0.5 \text{ VISIBILITY}$	0.541	0.414, 0.045, 0.042, 0.039
log(INDEX 3 + 1) (N = 120)	$Y = 1.298 - 0.011 \text{ DATE} - 0.076 \text{ TIME} + 0.021 \text{ VISIBILITY} - 0.012 \text{ WIND}$	0.265	0.167, 0.042, 0.035, 0.021
log(INDEX 4 + 1) (N = 120)	$Y = 1.022 - 0.009 \text{ DATE} - 0.072 \text{ TIME} + 0.017 \text{ VISIBILITY}$	0.249	0.163, 0.051, 0.034

^aDecisions about whether or not to transform the dependent variable were made after examining residual plots from the UCLA program, BMD02R (revision of 26 June, 1969; see Draper and Smith (1967, chapter 3)). For the dependent variables finally chosen, the usual assumptions about error in regression analysis do not appear to be violated.

^bINDEX 1, no. of different males giving sequences of display flight vocalizations (DFV's) in a 30-min sample; INDEX 2, no. of minutes in which DFV's were heard in a 30-min sample; INDEX 3, no. of songs heard in a 30-min sample, irrespective of the identity of the caller; INDEX 4, no. of minutes in which songs were heard, in a 30-min sample.

^cDATE takes values from 01 (17 May, 1976) to 30 (05 July, 1976). TIME takes values from 1 (0500 hours) to 5 (1700 hours). Data on weather are from records of Environment Canada, Atmospheric Environment: WIND measurements are in knots (1 knot = 1.76 km h⁻¹); VISIBILITY takes values (in miles) of 0, 1/4, 1/2, 1, 1 1/2, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, and 2-10 (in 1-mile increments). Visibility greater than 10 miles is entered as 10 miles. The independent variables are listed in the order in which they were entered in the regression solution (see following footnote).

^dThe figures are listed in the order they appear in the regression equation. In the regression procedure used, the variable with the largest partial correlation coefficient is added first; the square of this value represents the proportional increment in explained variation, expressed as a proportion of variation unexplained by variables already in the equation. The values listed are the squares of partial correlations, hence minor reversals can occur (e.g. 0.044 precedes 0.048; see Kim and Kohout (1975)).

locations or if they flush for other reasons, and so on. The amount of time spent together by paired birds is highest in the first few days of their relationship and declines steadily thereafter (Fig. 6). One reason for this is the onset of egg laying, which entails some nest attendance by one of the pair (Miller 1977). Data adjusted for this factor are shown in Table 3. In theory mates could spend all time together when the eggs are uncovered ('free time'). However, males spent about 90% of their free time with their mates 9-10 days before completion of the initial clutch, about 50% in the 3rd and 4th days before clutch completion, and 0% in the last 2 days. The trend is the same for repeat nestings. Thus, males seem to have ample time in which they could resume DF activity after the early stages of pair formation.

3. Spatial Relationships of DF's to Nesting, Foraging, and Brood-rearing Areas

Males had favorite locations where they landed after DF's. Those whose DF areas overlapped pond areas generally landed on pond margins where they fed.

The relationships of DF areas to nest sites, foraging locations, and brood-rearing areas are shown in or can be inferred from Figs. 7 and 8. Each pair's nest site was within the area displayed over by the male previously, though nests were often near the peripheries of the areas. This was partly because males often displayed over open water adjacent to the land areas where they nested. Some males displayed only over dry heath or sparsely vegetated open sand where they nested, yet I could not always locate these males when searching their DF areas. I saw one such unpaired male foraging around the ponds several times in the period when he could usually be found displaying in his DF area. Thus some males did not occupy their DF areas continuously. Foraging areas were not defended by males or females, though individuals of both sexes showed preferences for particular feeding locations. Birds nesting near heavily used foraging areas tended to feed near their nests, and those nesting elsewhere tended to travel farther in order to feed (Fig. 8). Nests can be characterized in terms of how far the attending adults travelled to forage; mean, median, and maximal off-nest distances travelled by nesting adults to feed form very similar patterns, in which off-nest foraging distances increase from west (near favorite feeding areas) to east (Fig. 9). Pairs that nested near good foraging areas thus often fed in areas covered previously by the male's DF's, but this seemed to be just coincidental.

Broods were led from the nest by one or both

TABLE 2. Relationship of display flight activity (DF activity) to stage of the nesting cycle, in *C. minutilla*

	Stage of nesting cycle ^a					
	I	II	III	IV ^b	V	VI
DF days per male-day, in %	57.8	46.7	8.3	3.6	1.1	0.0
(No. male-days)	(128)	(15)	(144)	(84)	(380)	(173)
Relative incidence, in %	<u>100</u>	<u>81</u>	<u>14</u>	<u>6</u>	<u>2</u>	<u>0</u>
% of males seen displaying	91.7	46.7	57.1	50.0	7.7	0.0
(No. males)	(12)	(15)	(14)	(4)	(26)	(15)
Relative incidence, in %	<u>100</u>	<u>51</u>	<u>62</u>	<u>55</u>	<u>8</u>	<u>0</u>

^aI, before pairing; II, on day of pairing; III, between pairing and completion of initial clutch; IV, between loss of initial clutch and completion of replacement clutch; V, during incubation of definitive clutch; VI, during care of brood.

^bAll four males for which observations are available in stage IV remained paired with their first mates for the replacement clutch.

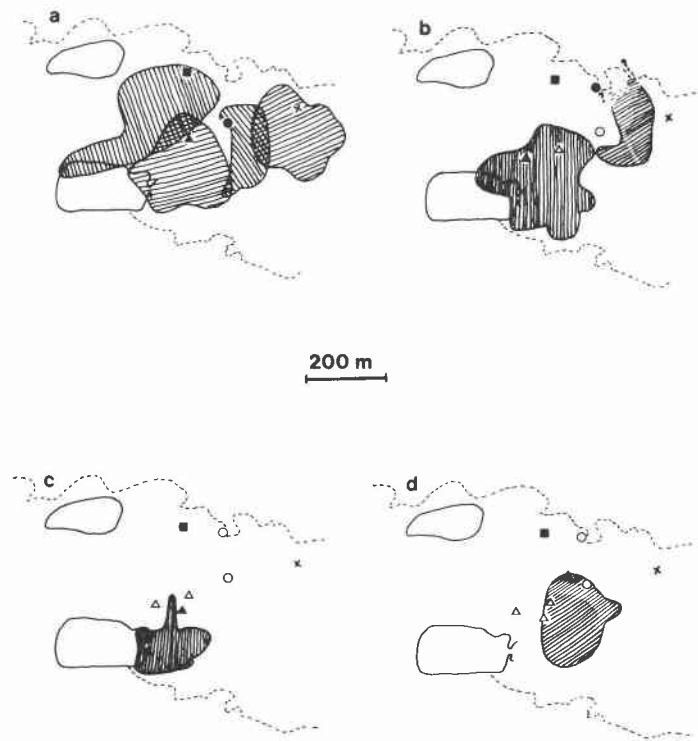


FIG. 5. Spatial relations of display flight areas (DF areas) to nest sites, and successive overlay of DF areas, in *C. minutilla*. The total areas covered by DF's of four males over a period of 4 days in mid-May are shown in *a*; their eventual nest sites are indicated. DF areas of two more males are outlined in *b*, and the nest sites of their predecessors are represented by hollow symbols. Nest sites of the two newcomers are represented by solid symbols corresponding to the symbols of the males whose DF areas they have taken over. Two more males are added successively in *c* and *d*, after pairing of the preceding males. The new males' nest sites are represented by solid symbols, and all preceding nest sites in the same region are represented by hollow symbols.

parents, generally within about a day of hatching (Miller 1977). Most broods were led to and reared among the ponds where they remained until independence, but some broods were raised entirely in the drier juniper-crowberry areas (Fig. 7). Adults

which nested near the ponds often led the brood only a short distance from the nest to a nearby pond margin, where the family remained until the chicks become independent. In such cases the brood-rearing area was often in the former DF area of the

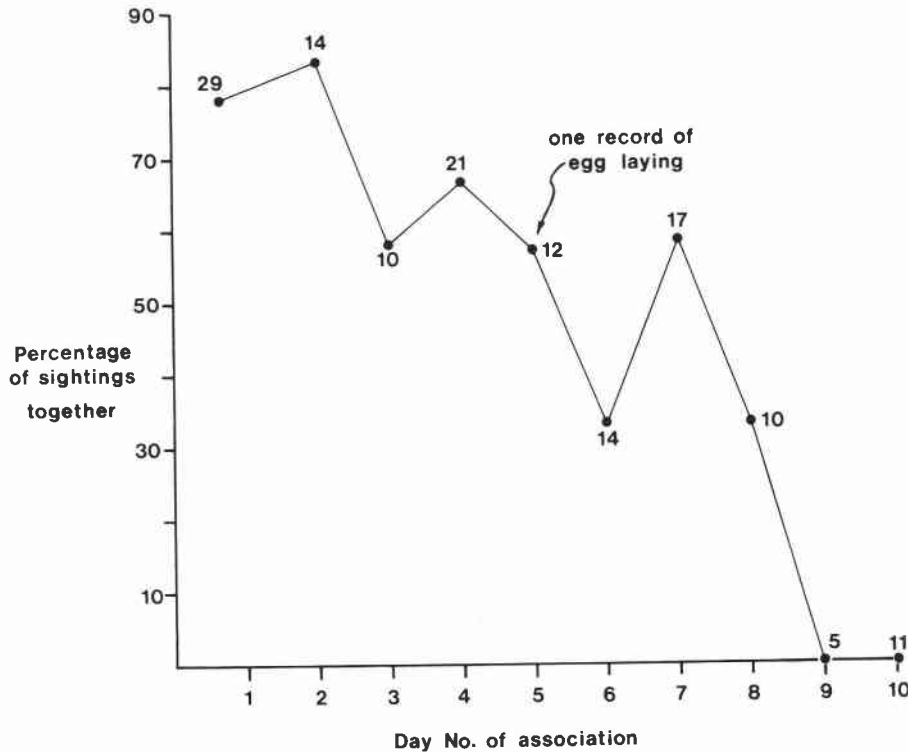


FIG. 6. Relationship of the percentage of time spent together by mates in *C. minutilla* to the length of their association (day No. 1 = 1st day of association, etc.). Sample sizes are shown by the points; they were computed as outlined in footnote a of Table 3. In the pairs under observation no eggs were laid earlier than day No. 5 of association.

TABLE 3. Summary of data on sightings of paired adults of *C. minutilla* whose egg-laying schedules were known, considered relative to the date of clutch completion (sample sizes are shown in parentheses (see footnote a))

No. of days before clutch completion	First nestings			Repeat nestings			Weighted means of columns C and F
	A, % of sightings together ^a	B, free time in % ^b	C, % A/B	D, % of sightings together ^a	E, free time in % ^b	F, % D/E	
1-2	0.0	33.5	0.0(13)	0.0	39.3	0.0(2)	0.0(15)
3-4	42.9	88.3	48.6(14)	22.2	87.9	25.3(9)	39.5(23)
5-6	85.7	100.0	85.7(21)	53.3	100.0	53.3(15)	72.2(36)
7-8	72.7	100.0	72.7(11)	66.7	100.0	66.7(3)	71.6(14)
9-10	88.9	100.0	88.9(9)	—	—	—(0)	88.9(9)

^aEntries in these columns represent the overall means for all sightings of paired birds, of the weighted percentages, % (no. of times female sighted with male)/(no. of times female sighted), and % (no. of times male sighted with female)/(no. of times male sighted). Taken together, these figures represent more accurately the amount of time spent together by pair members than could be achieved by using only the records for one sex. However, the numerator in the expressions is the same, so I have listed as sample sizes only the number of sightings of lone pair members.
^b'Free time' refers to the time not spent in incubation, all of which could in theory be spent with the mate. For days 1-2 and 3-4 before clutch completion, the free time represents the weighted percentages of time available, using figures on incubation attendance in Table 11 of Miller (1977).

male parent. Thus, brood-rearing and DF areas coincided only when nests were near areas favorable for rearing young. I never saw parents with broods defend space around them, but saw direct defence of young twice. One brood which was just leaving the nest attracted the attention of an unknown adult, which landed and started pecking at one of the chicks. After several seconds the parent

ran weakly toward the intruder, who flew away. In another case a strange adult attacked a 6-day-old chick and was attacked promptly by the chick's father. The strange bird returned several times to continue the attack and was attacked repeatedly by the father. Hamilton (1975), Graul (1975), and Oring and Maxson (1978) report similar attacks upon chicks in the American avocet, *Recurvirostra*

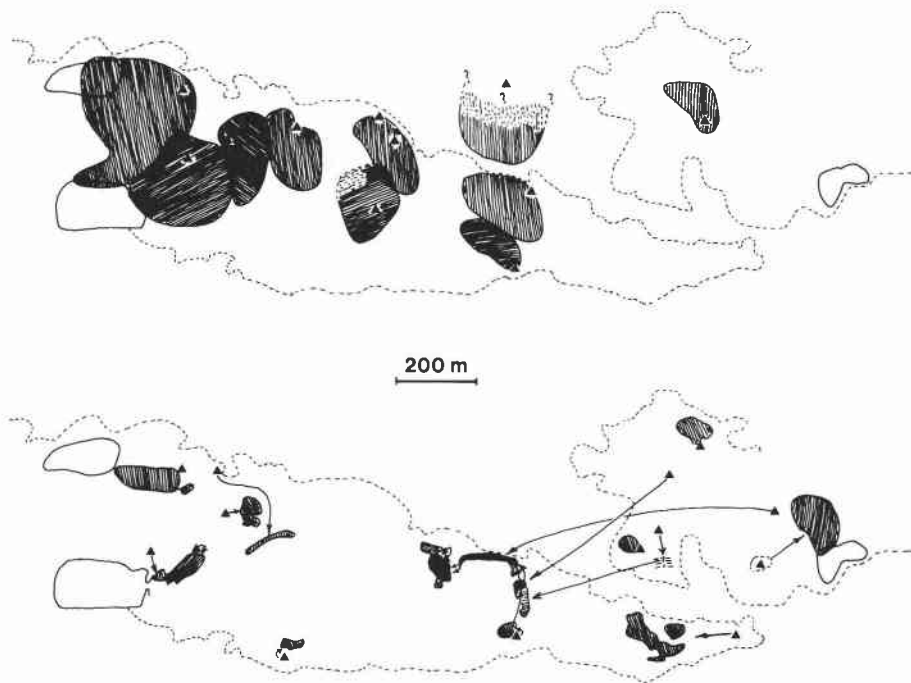


FIG. 7. Spatial relations of display flight areas to nest sites (triangles; upper diagram), and of nest sites to brood-rearing areas (lower diagram), in *C. minutilla*. Brood-rearing areas are joined by arrows to the corresponding nest sites, or are adjacent to nest sites. Areas of overlap between different families were usually asynchronous; such overlap is represented by cross-hatching (use by two families) or black (use by more than two families).

americana, the mountain plover, *Eupoda montana*, and the spotted sandpiper, *Actitis macularia*, respectively.

Records of nesting locations of birds that nested more than once are summarized in Fig. 10. Males renested in about the same place within and between years, regardless of whether they remated with the previous mate or took a new one. By contrast, females that changed mates between years nested much farther from their 1975 nest sites than did males that changed mates. These trends are consistent with a picture of males homing to nesting areas early in the spring, and pairing as soon as possible. Similar trends have been noted for other calidridine populations (Hildén 1978; Jehl 1970; Norton *et al.* 1975).

Three males reared broods in both years. One male reared his brood in the same location both years, but the others raised theirs in dry areas away from the ponds in 1976 (Fig. 10; I assume that the 1975 nest site of male No. 3 was near his 1976 nest site). In 1976 other males also reared broods in dry areas, especially in the juniper-crowberry heath, so those areas may have been particularly favorable for rearing chicks that year. Adults may thus respond facultatively to good areas for raising broods.

Discussion

1. The Functions of Display Flights in *C. minutilla* and Other Shorebirds

(a) The Timing of Display Flights in Relation to the Nesting Cycle

My observations suggest that display flights by males of *C. minutilla* function primarily to attract females: (1) DF's are given only by males; (2) DF's virtually cease as soon as a male starts to consort with his future mate, when (3) he usually becomes tolerant of other males encroaching in DF's; and (4) males whose nests are lost to predators and who are deserted by females early in the season reinitiate DF's. A male's DF's therefore define his ephemeral mating territory.

Most accounts of northern scolopacids in which males play a role in incubation and brood rearing indicate that males perform display flights predominantly or solely when unpaired or before full incubation starts (Bergman 1946; Hobson 1972; Holmes 1971, 1973; Jehl 1973; Lind 1961; Nethersole-Thompson 1951; Nettleship 1974; Parmelee 1970; Soikkeli 1967). In line with these trends, both Jehl (1973) and Parmelee (1970) report observations which suggest successive overlay of mating territories of males after earlier males were paired, in *M. himantopus* and *C. alba*, respectively. Tuck

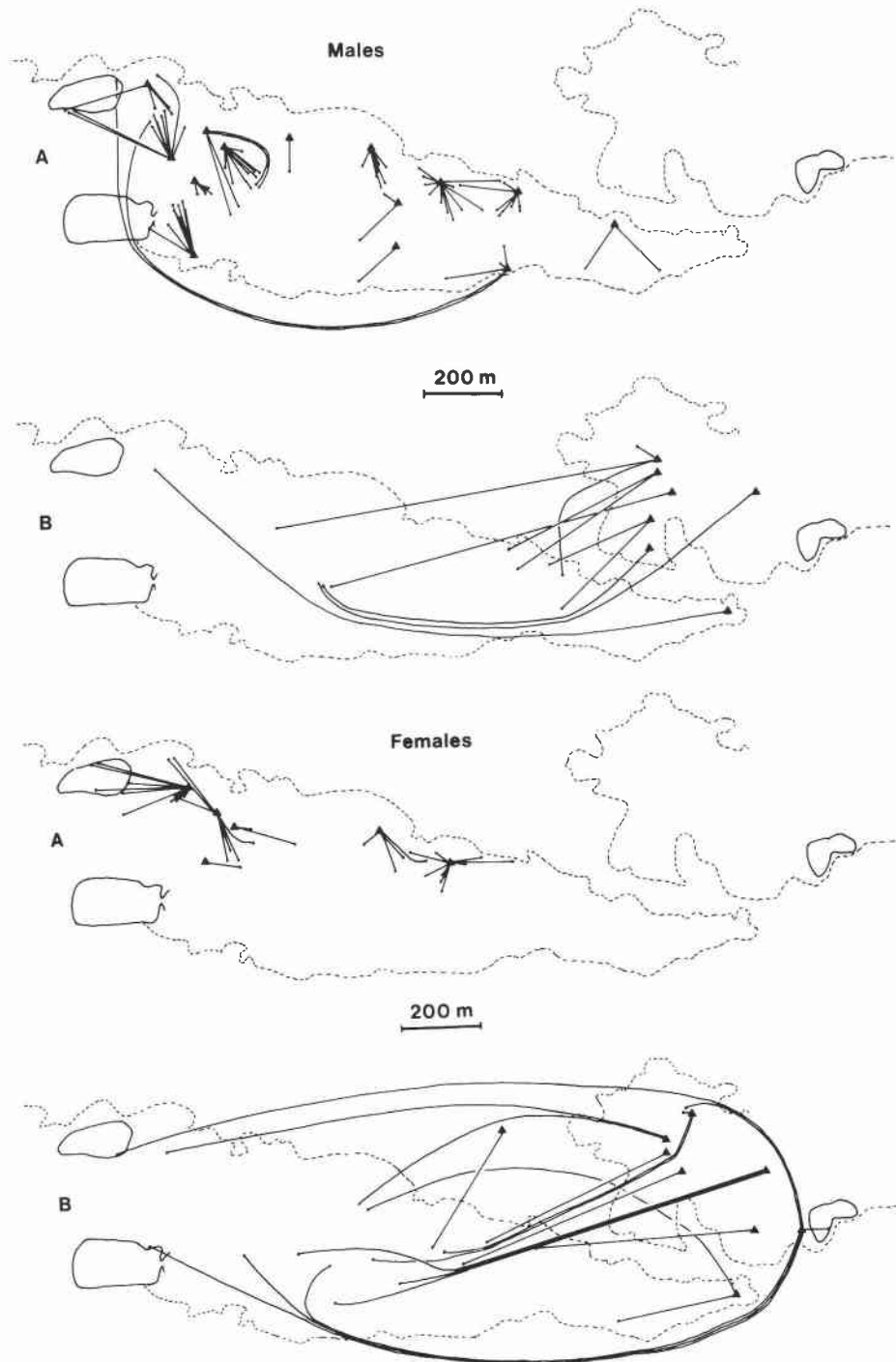


FIG. 8. Spatial relations of foraging areas to nest sites (triangles) in *C. minutilla*. Examples are for birds of each sex that nested near (A) and far (B) from their favorite foraging areas.

(1972: 139f) presents diagrams of territories of the common snipe, *Capella gallinago*, which strongly suggest the same.

There are some possible exceptions to these trends. Parmelee *et al.* (1967) mention that males of

M. himantopus may perform flight displays when not incubating, and Jehl (1973) reports a resurgence of flight song in this species when eggs start to pip (see also Buss 1951). Males of *C. alpina* in Alaska end territorial defence after hatching (Holmes 1966,

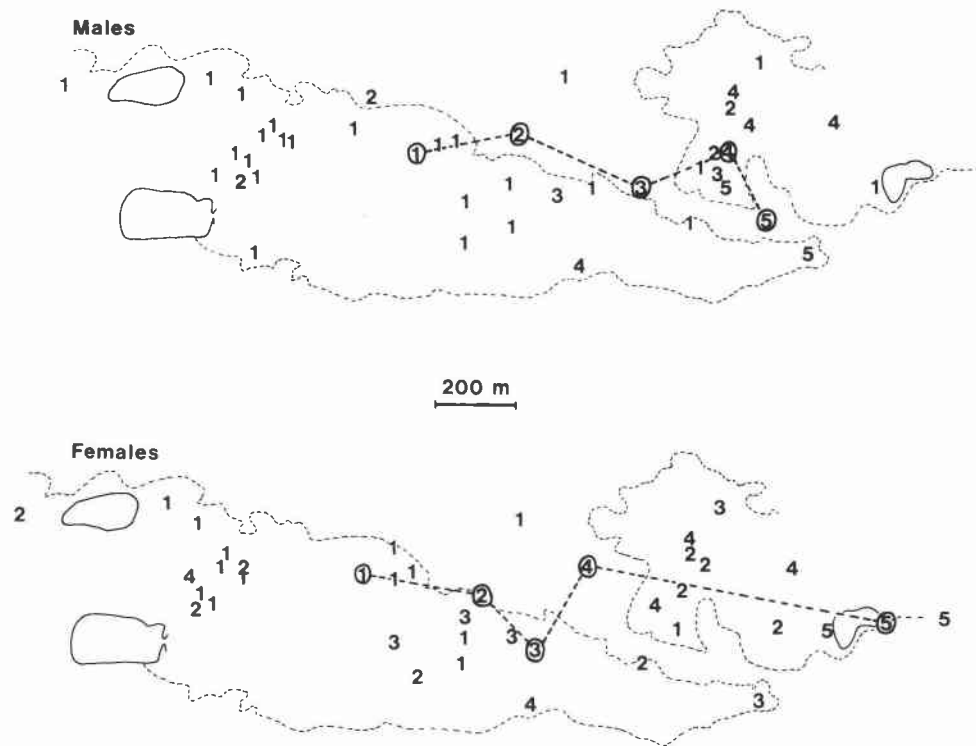


FIG. 9. Nest sites characterized by the maximal distances at which attending adults of *C. minutilla* were observed off the nest foraging. All foraging records for each sex were combined, and the ranges were divided into quintiles. Maximal distances travelled to forage by each nesting male and each nesting female were placed in the appropriate quintiles; these are indicated by numerals placed over the nest sites. For example, the male from the westernmost nest site had a maximal off-nest foraging record in the first quintile (lowest 20%) of all male maximal records; his mate was in the second quintile for all female maximal records. The centroids of each quintile are circled and joined by broken lines.

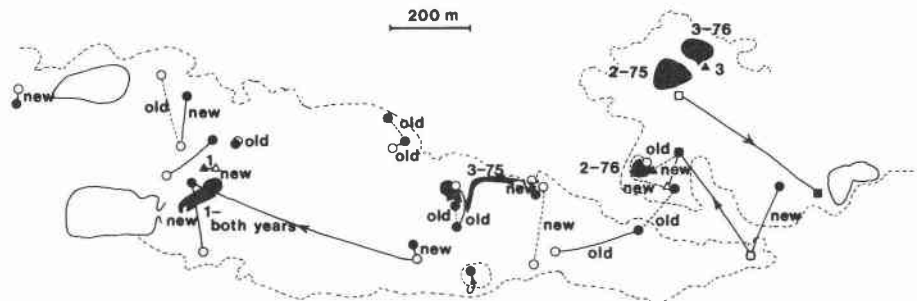


FIG. 10. Changes of nest sites within and between years, for *C. minutilla*. 1975 nest sites are represented by hollow symbols (○, male; □, female), and 1976 nest sites by solid ones (●, male; ■, female). For males, solid lines join changes between years, and broken lines join initial and replacement clutches in the same year. For females, solid lines with an arrowhead indicate changes between years. 'New,' new female taken as mate; 'old,' former female retained as mate. Three males raised broods in both years, and their nest sites are indicated (Δ, 1975; ▲, 1976). Two of them (numbers 1 and 3) are indicated further by numerals. Corresponding brood-rearing areas are indicated as 2-75, 2-76, 3-75, 3-76, and '1-both years.'

1970), and in one locality even show "more active displaying" late in incubation when many birds leave their territories to feed elsewhere (Holmes 1970: 306). In the Hudsonian godwit, *Limosa haemastica*, flight displays may reach a peak during full incubation (Hagar 1966). Unfortunately most authors make no distinction between events in the

breeding cycles of individual pairs and events in the breeding population as a whole, and this makes it difficult to appraise all reports. But certainly among the monogamous species of calidridines, only *C. alpina* in northern Alaska seems to depart from the trend for DF's to function mainly in the period of mate attraction. Additionally, females of *C. alpina*

may join in display flights (Sutton 1932), which may be unique within the Calidridinae.

The role of fighting in the social system of *C. minutilla* is not clear. Unpaired males fight, presumably to defend or acquire mating territories. Fighting by nesting males may function also to space out nests to reduce predation (see section (c), below).

(b) *The Relationship of Nesting Sites to Foraging Areas*

Pairs of *C. minutilla* on Sable Island may forage or rear the brood, or both, within the male's former DF area. This depends simply upon whether a nest is located conveniently, and neither foraging area nor brood-rearing area as such is displayed over or defended against conspecifics. Related species also forage or raise the brood near their nest sites if these are located near rich feeding areas (Mace 1971; Mason 1947; Nethersole-Thompson 1951; Parmelee 1970). Holmes (1966) reports opportunistic feeding off their territories by pairs of *C. alpina arctica*², a subspecies in which feeding usually occurs near the nest. In the whimbrel, *Numenius phaeopus*, near Churchill, good nesting habitat is poor for foraging, and vice versa, so only pairs in poor nesting habitat feed near the nest (Skeel 1976).

There is no general trend for shorebirds to nest particularly close to rich foraging areas. In virtually all populations of monogamous species of scolopacids and charadriids in medium to high latitudes, adults feed to a great (often unknown) extent away from the nest site, on undefended communal feeding grounds (Scolopacidae: Buss and Hawkins 1939; Hobson 1972; Holmes 1970, 1971, 1973; Jehl 1970, 1973; Keith 1938; Kistchinski and Flint 1973; Nethersole-Thompson 1951; Nethersole-Thompson 1934; Rowan 1930; Salomonsen 1950; Skeel 1976; Soikkeli 1967; Charadriidae: Dabelsteen 1978; Graul 1973; Lack and Lack 1933; Mace 1971; Mason 1947; Mayfield 1973; Oring, cited by Phillips 1972; Phillips 1973; Ratcliffe 1976; Sauer 1962; Simmons 1953, 1956; Smith 1969; Spencer 1953). Few exceptions occur. Males of the green and solitary sandpipers, *Tringa ochropus* and *Tringa solitaria*, hold joint feeding-nesting territories (Oring 1968, 1973) and there is occasional defence of feeding areas in the greenshank, *Tringa nebularia* (Nethersole-Thompson 1951) and willet, *Catoptrophorus semipalmatus* (M. A. Howe, in

litt.). Pairs of the piping plover, *Charadrius melodus*, hold feeding territories near and often contiguous to their nesting territories (Cairns 1977), and all-purpose territories are the rule in the Magellanic "plover," *Pluvianellus socialis* (Jehl 1975; temporary feeding territories may also be established). Nesting areas of the purple sandpiper, *Calidris maritima*, which abut on shoreline may be defended (Keith 1938; only early in the nesting cycle?).

Some of these species actively maintain territories in which the brood is reared (Cairns 1977; Jehl 1975; Wilcox 1959; see also Little 1967). Mace (1971) mentions the establishment of a defended territory around chicks in the killdeer, *Charadrius vociferus*, but in most species there is, if anything, little more than local defence of broods (e.g. Bergman 1946; Buss 1951; Nethersole-Thompson 1951, 1973; Spencer 1953).

Nesting areas bear little or no relationship to brood-rearing areas in high-latitude charadriids and scolopacids; as a rule, families leave the vicinity of the nest soon (generally within a few days) after hatching and gather in undefended locations which may be used communally. This generalization also applies roughly to Holmes's study populations of *C. alpina*. The usual pattern is for shorebird families to become sedentary after a few days or a week (Graul 1975; Hildén and Vuolanto 1972; Melfoite 1976; Mendall and Aldous 1943; Miller 1977; Norton 1973; Safriel 1975), though in some populations family groups continue to move around (Norton 1973; Wenstrom 1973).

I conclude that nest placement and spacing, at least on a local scale, are not influenced substantially by trophic considerations for adults or chicks in the vast majority of northern scolopacids and charadriids. Soikkeli (1967) reaches a similar conclusion for *C. alpina*. Nesting density is of course higher where rich areas are within feeding range of optimal nesting habitat (e.g. Ratcliffe 1976), and in such high-density situations uniform spacing of nests is expected (see next section). Holmes (1970) concludes that pairs of *C. alpina* in western Alaska hold smaller territories than do pairs in northern Alaska because of better feeding conditions. Yet the populations differ on a critical point: nesting adults of *C. a. pacifica* feed off territory, especially late in incubation, whereas those of *C. a. arctica* do not (Holmes 1970). Soikkeli (1967) provides other arguments against food being an important ultimate factor affecting spacing behavior of *C. alpina*, but all do not apply equally well to the various populations that have been studied.

²Browning (1977) discusses North American subspecies of *C. alpina*.

(c) *The Relationship of Territoriality and Nest Spacing to Predation*

Northern shorebird populations show many adaptations to minimize nest predation: camouflaged nests and eggs, cryptic plumage and nesting behavior, distraction behavior, and so on. Many authors have suggested that uniform spacing of nests is also an adaptation to this end, and is effected through aggressive behavior among nesting pairs. DF's space out pairs nesting synchronously where mating and nesting areas overlap (cf. *C. alba*, *T. nebularia*, and lek species, where they do not; see next section), and this may space nests sufficiently so that further spacing mechanisms are unnecessary (Holmes 1966, 1973; Jehl 1973; Skeel 1976; see also Ratcliffe 1976). Only Skeel (1976) has tested the spacing of nests of a shorebird species for randomness statistically: she found that nests of *N. phaeopus* were significantly evenly distributed. Undoubtedly tests on other published distributions (e.g. Ratcliffe 1976) would agree. But are nests spaced uniformly to reduce nest predation or as a simple consequence of the regular spacing of mating territories held previously? Soikkeli (1967) doubts that territorial behavior decreases susceptibility of nests to predation because northern scolopacids are not interspecifically territorial and also because dense mixed-species nesting associations occur (see Young 1976). My data on *C. minutilla* are not enlightening: successive overlap of mating territories, with consequent close positioning of nests, would be expected in populations exposed to little nest predation, as was true for *C. minutilla* on Sable Island in historic times (Miller 1977). However, the trends on DF's and spacing which I have reviewed agree closely with my observations, and I conclude with Soikkeli that the ultimate significance of "territoriality" in most species of calidridines is in pairing and "reducing fighting in courtship activities" (Soikkeli 1967: 194). This mating competition results in even spacing of nests that obviates the need for major nest-spacing adaptations. Local defence of nests by incubating shorebirds (Cairns 1977; Hays 1972; Lack and Lack 1933; Nethersole-Thompson 1951, 1973; Parmelee *et al.* 1967; Spencer 1953; this study) is surely a very primitive response, and may be the only additional mechanism required to reduce risks from predation that result from neighbors nesting too close.

(d) *Relationship of Display Flight Activity and Duration to Date, Time of Day, and Weather*
The decline in measures of DF and song activity

in *C. minutilla* as the season progressed is explained by declining durations of DF's and the cessation of DF's by nesting males. Only Sheldon (1967) presents comparable seasonal data for a scolopacid: mean duration of display flights in the American woodcock, *Philohela minor*, showed no seasonal trends.

Calidris minutilla on Sable Island had highest DF and song activity in early morning, when DF durations were greatest; all measures declined over the day. Display flights by males of the sharp-tailed sandpiper, *Calidris acuminata*, are commonest in early morning or evening (Flint and Kistchinski 1973). For the knot, *Calidris canutus*, Manniche (1910: 132) reported that "singing" was most frequent in the afternoon, though Berula "was unable to note any regularity or relation to the time of day" (quoted by Pleske 1928: 269). Males of species with evening or nocturnal displays show strong diel rhythms in display (e.g. Nemetschek 1977; Wishart and Bider 1977). Males of *C. gallinago* display mainly after sunset and secondarily just before sunrise, though this is modified by the amount of moonlight (Tuck 1972).

High winds depressed DF and song activity and caused abbreviation of DF's in this study. High winds seem to be a deterrent to display flight activity in shorebirds in general (Dabelsteen 1978; Flint and Kistchinski 1973; Marcström 1974; Nechaev 1973; Parmelee 1970; Parmelee *et al.* 1968; Tuck 1972), and also lead to shortened displays in *Ph. minor*, at least (Pitelka 1943). Fog or mist are likewise widely effective in reducing display flight activity (Dabelsteen 1978; Marcström 1974; Nechaev 1973), and Tuck (1972: 51) states that "when dense fog rolls in...performing snipe drop out of the sky immediately."

I detected no relationship of changes in barometric pressure to DF and song activity in *C. minutilla*, but in *C. gallinago* low levels of display portend the approach of a low pressure system, and conversely high levels of display occur as high pressure areas approach (Tuck 1972). Males of *C. minutilla* on Sable Island experience fairly mild weather in general, and their DF and song activity are affected by prevailing temperatures little. Display flight activity in scolopacid populations subjected to more extreme temperatures may be depressed by cold weather (Marcström 1974; Nechaev 1973; Parmelee *et al.* 1968; Pitelka 1959).

2. *The Relationship of Intersexual Selection to Mating Territories in C. minutilla*
Males holding mating territories, even in

monogamous species like *C. minutilla*, are exposed to intersexual selection (Darwin 1874). "It is perfectly clear that if a female ... does not want to pair with any given male, he has no possible means of forcing her to do so. He can only ... attempt to persuade her (by means of his display), and if she is very unfavourable to his suit, she can even prevent him from doing this, by flying off directly he begins" (Huxley 1912: 654). We must therefore ask what properties of males of *C. minutilla* and of their DF areas are most attractive to unpaired females, such that tenured males are preferred as mates and come to nest early? In this discussion I will disregard the importance of familiarity with previous mates in promoting reunion and rapid nesting effort (see Jehl 1970).

Calidris minutilla on Sable Island is single clutched and monogamous, and males play a major role in incubation and are mainly responsible for raising the brood (Miller 1977). A prospecting female should therefore choose a male that will be a good father to her chicks and a good mate, and that is genetically desirable as a sire of her offspring. Females may be able to appraise such qualities indirectly, by predicating mate choice upon two related general characteristics: resource-accurring ability (Trivers 1976), and success in intramale competition (Bartholomew 1970; Darwin 1874; Huxley 1938; McLaren 1967; Miller 1975a, 1975b; Waage 1973). A male's 'quality' is reflected in his physical characteristics, behavior, and proven ability to acquire an object of contest, such as a mating territory. All else being equal, females should mate with males in areas of high intramale competition (McLaren 1967); limited evidence supports this (Coulson and Hickling 1964; Floody and Arnold 1975; Lisitsyna 1976; Miller 1975a). The seeking of such areas by unmated females should facilitate their choice of mate, for a certain amount of "sorting out" has already been done for them (Cronin and Sherman 1976; Darwin 1874; Emlen 1976; Emlen and Oring 1977; Lill 1974b; Miller 1975a; Payne and Payne 1977; Selander 1972). This may be particularly important in species with brief breeding seasons, for which rapid mate choice and early nesting are advantageous. In monogamous species like *C. minutilla* such a mechanism would be most pronounced early in the season, when the fittest "choosiest" females are prospecting for mates (Burley 1977).

The preceding remarks suggest that females of *C. minutilla* use success in intramale competition as a criterion when choosing mates. Females may also choose preferentially as mates those males with DF areas over preferred nesting habitat, but suitability

of DF areas for foraging is probably relatively unimportant in *C. minutilla* and most other shorebirds (see Discussion, part 1(b), above; but see Holmes (1973) and Mace (1971)). The mating system in *C. minutilla* thus comes close to being 'non-resource-based,' and females should assess characteristics of males closely (review by Cronin and Sherman (1976), see also Lill (1974a, 1976)). Accordingly, many bird species with 'non-resource-based' mating systems show pronounced sexual dimorphism. In monogamous calidridines like *C. minutilla*, however, females probably select against showy males; males share incubation and brooding, so should be the same size and color as females. It is therefore interesting to note that the spring plumage of females of *C. minutilla* on Sable Island and in northern Manitoba is distinctly warmer and richer than that of males (personal observations); a similar sexual difference occurs in *C. pusilla* (Sutton 1932). Monogamous calidridines also show slight reversed sexual dimorphism in size (females larger than males: review by Pitelka *et al.* (1974)), and Jehl (1970) provides evidence of negative assortative mating by size in some species (see also Ankney 1977). Jehl (following Hamilton (1961) and Hamilton and Barth (1962)) suggests that sexual dimorphism in size in calidridines may facilitate sexual recognition and rapid pair formation, which are important in species with brief breeding seasons. Jehl's interpretation implies that sexual dimorphism should be less pronounced in calidridine populations with longer nesting seasons, like *C. minutilla* on Sable Island or *C. alpina* in Finland or western Alaska. This is not supported by available measurements (*e.g.* Browning 1977; Miller 1979; Soikkeli 1974), so if intersexual selection is maintaining sexual dimorphism in *C. minutilla* and relatives, it is for reasons other than those advanced by Jehl. In any case, limits to sexual dimorphism in these species are probably set strictly by the shared parental roles.

Males of *C. minutilla* on Sable Island that have mating territories away from feeding ponds do not occupy them continuously. Similar observations on discontinuous attendance of mating territories have been reported for *C. alba* (Parmelee 1970), Temminck's stint, *Calidris temminckii* (Southern and Lewis 1938), and *V. vanellus* (Dabelsteen 1978; see also Bengtson and Fjellberg 1975). Given emancipation of males from nesting and parental duties, it would seem to be a simple evolutionary step to a mating system such as that in *Ph. minor*, in which males occupy exclusive mating territories for part of each day, and retire to undefended feeding grounds for its remainder (Mendall and Aldous

1943). This may already occur to some extent in the two polygynous species *C. fuscicollis* and the pectoral sandpiper, *Calidris melanotos* (Parmelee *et al.* 1968; Parmelee *et al.* 1967; Pitelka 1959).

Males of *C. minutilla* show a sharp drop in DF activity during early pair formation, when they also spend most of the time with their mates. This may be mate guarding (Arnold 1976; Parker 1974), an interpretation consistent with reduced attendance of females by males as clutches approach completion. Close prenesting attendance of female shorebirds by their mates has also drawn comment from Kistchinski and Flint (1973), Nethersole-Thompson (1951), and Parmelee (1970). This may not be true of *C. temminckii* and *E. montana*, both of which have complex nonmonogamous mating systems (Graul 1973; Hildén 1975).

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