

Habitat and breeding cycle of the Least Sandpiper (*Calidris minutilla*) on Sable Island, Nova Scotia

EDWARD H. MILLER¹

Biology Department, Dalhousie University, Halifax, N.S., Canada B3H 4J1

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Sable Island, Nova Scotia, is the southernmost significant nesting area of the Least Sandpiper. Many birds nest around a single pond complex, which supports a lush vegetation that is heavily grazed by horses. Nests occur there and in nearby dry, sparsely vegetated habitat. Birds start arriving by mid-May (males first), and clutches (including replacement clutches) are completed in a period of 4–5 weeks, from late May to late June. Most eggs are laid in the morning, at intervals averaging 1.2 days. Incubation increases gradually through laying and is ~100% beginning with the last egg. Incubation lasts 20–21 days. Nest and chick mortality is high, mostly due to predation by Herring Gulls (*Larus argentatus*). Mortality of siblings is contagious. Females which nest successfully begin to migrate south by late June, followed by successful males in early July; individuals of both sexes are seen for about 3 days after the completion of parental behavior. Unsuccessful breeders leave earlier, and fledglings later. On average, males are seen for about 10 days and females for about 7 days following final breeding failure. Adults and fledglings tend to flock assortatively in late summer. General features of the breeding cycle seem to be highly conservative throughout the species' range.

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L'Isle au Sable en Nouvelle-Ecosse est le site important de nidification du bécasseau minuscule le plus méridional. Plusieurs des oiseaux nichent près d'un complexe formé d'un étang entouré d'une abondante végétation qui est fortement broutée par les chevaux. On trouve aussi des nids dans un habitat adjacent à végétation clairsemée. Les oiseaux commencent à arriver vers la mi-mai, les mâles les premiers, et en l'espace de 4–5 semaines, soit de la fin de mai à la fin de juin, les couvées sont complètes, y compris les œufs de remplacement. Les œufs sont normalement pondus le matin, à un intervalle moyen de 1,2 jours. L'incubation est de plus en plus soutenue pendant la ponte et atteint à peu près 100% après la ponte du dernier œuf; elle dure 20–21 jours. La mortalité au nid et celle des oisillons est grande, particulièrement à cause d'un prédateur, le goéland argenté (*Larus argentatus*). La distribution de la mortalité des oisillons au sein d'une même famille est contagieuse. Les femelles qui ont réussi leur nidification migrent vers le sud à la fin de juin et sont suivies par les mâles au début de juillet; les individus restent sur place environ 3 jours après la fin de leur activité parentale. Les reproducteurs qui n'ont pas réussi quittent plus tôt et les jeunes plus tard. En moyenne les mâles restent 10 jours et les femelles 7 jours après leur dernier essai infructueux de reproduction. En fin d'été, les adultes et les jeunes ont tendance à former des vols distincts. La biologie de la reproduction de cette espèce varie peu sur toute son aire de répartition.

[Traduit par le journal]

Introduction

Knowledge of the annual cycle and breeding biology of sandpipers of the tribe Calidridini (24 species) has been extended greatly in recent years through field studies in their arctic and subarctic breeding areas. General ecological and social characteristics of the group are now known well enough to permit some syntheses on major adaptive trends (e.g., Burger and Olla 1983; Myers 1981a; Pitelka et al. 1974), and to allow more specific research questions to be asked (e.g., Ashkenazie and Safriel 1979b; Safriel 1975; Shepard 1975; van Rhijn 1973). Detailed documentation of many aspects of

natural history of the Calidridini is nevertheless largely incomplete, as is evident from the very general sorts of information on most species available to Pitelka et al. (1974) for their signal review. Indeed, the most notable publication on the Least Sandpiper before Jehl's (1970) paper is dated 1927 (Jehl 1968).

The Least Sandpiper (*Calidris minutilla*) is endemic to North America, where it breeds in a broad band from Alaska to Newfoundland. The southeasternmost limits of the breeding range are Cape Sable Island and Sable Island, Nova Scotia (Godfrey 1966), parts of mainland Nova Scotia (I. A. McLaren, personal communication), and Massachusetts (Anderson 1980). The species has been studied near Churchill, Manitoba (Jehl 1970, 1973; Jehl and Smith 1970), but its habitat relations and annual cycle on the breeding grounds remain inadequately documented. In this paper, I describe general features of nesting habitat and phenology on Sable Island, Nova Scotia,

¹Present addresses: Vertebrate Zoology Division, British Columbia Provincial Museum, Victoria, B.C., Canada V8W 1X4 (address to which all correspondence should be sent), and Biology Department, University of Victoria, Victoria, B.C., Canada V8W 2Y2.

TABLE 1. Summary of data on temperature, precipitation, wind velocity, and sunshine during this study (May–July, 1975 and 1976). These figures are based on hourly records compiled at the Sable Island meteorological station^a

| | Daily temperature, °C | | | Total precipitation, mm | Mean wind velocity, km·h ⁻¹ | No. of hours of bright sunshine |
|------|-----------------------|------------------------|------------------------|-------------------------|--|---------------------------------|
| | Mean | Mean maximum | Mean minimum | | | |
| 1975 | | | | | | |
| May | 6.3 | 8.6(14.4) ^b | 3.9(-2.2) ^c | 121 | 19(56) ^d | 192 |
| June | 9.4 | 12.0(17.2) | 6.8(4.4) | 49 | 17(53) | 180 |
| July | 15.3 | 17.7(22.1) | 12.8(8.3) | 83 | 17(44) | 78 |
| 1976 | | | | | | |
| May | 7.6 | 10.1(13.7) | 5.1(2.3) | 80 | 25(53) | 193 |
| June | 11.1 | 13.9(17.7) | 8.2(3.9) | 46 | 21(62) | 138 |
| July | 15.4 | 18.1(21.3) | 12.7(9.4) | 88 | 16(56) | 152 |

^aEnvironment Canada, Atmospheric Environment.

^bMaximum temperatures recorded are given in parentheses.

^cMinimum temperatures recorded are given in parentheses.

^dMaximum hourly records are given in parentheses, excluding gusts.

where the Least Sandpiper is an abundant breeding species (McLaren 1981; Miller 1977, 1979a, 1979b, 1983). This location is of particular interest because its habitat and moderate climate are so different from elsewhere throughout the nesting range of this and most related species of Calidridini. The Spotted Sandpiper (*Actitis macularia*) is the only other species of shorebird which nests on Sable Island; Semipalmated Plovers (*Charadrius semipalmatus*) no longer nest there (McLaren 1981).

Nomenclature used for shorebirds follows Gochfeld et al. (1983). Plant names follow Roland and Smith (1969).

Materials and methods

Fieldwork 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 210 birds, consisting of 122 chicks plus fledglings, and 88 adults (40 males, 42 females, 6 of unknown sex). Each received a unique combination of aluminum and color bands (red, light blue, yellow, and black; supplied by A. C. Hughes, Middlesex, England). Fast-drying epoxy was applied to each color band. Some birds were mist-netted in early spring 1975, but most were caught at their nests with a simple drop trap.

To estimate seasonal trends in population composition and size, in 1976 I walked daily along all pond margins in predetermined routes, counting and identifying all Least Sandpipers seen on the ground except those known or judged to be off their nests because of my presence. Sandpipers sighted at other times were not included in these counts, but were noted for other purposes (e.g., to assess seasonal changes in flock size).

Specific details of data collection and analysis are treated below, where appropriate.

Results

Environment and habitat

Temperatures during May of both years were cool, but rarely fell below freezing (Table 1). Weather was cooler and wetter in May and June 1975 than in the same months of 1976, and fog was more common in July 1975 than in July 1976 (correspondingly in July 1975 there were fewer hours of sunshine; Table 1).

Least Sandpipers nested abundantly in the vegetated environs of freshwater and brackish water ponds, toward the west end of the island (see Fig. 1 of Miller 1979a). Here the sand terrain was 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*). Most vegetation around the ponds was kept quite short through intensive grazing by the island's resident wild horses, even at summer's peak, and was used as nesting habitat by most sandpipers. A large cranberry bog and extensive dry areas of juniper (*Juniperus horizontalis* and *J. communis*) mixed with black crowberry (*Empetrum nigrum*), were also favored by nesting sandpipers (Figs. 1 and 2). Some nests occurred in areas of sparse vegetation, consisting mainly of marram grass (*Ammophila breviligulata*) and pearly everlasting (*Anaphalis margaritacea*) (Fig. 2).

Most nests (24) were in lush vegetation around the ponds, and 15 were in low-lying moist areas, often near pond margins. Eighteen other nests were situated in extremely dry sparsely vegetated sandy areas (Fig. 2), small patches of lush vegetation in predominantly dry sandy locations, and in vegetation intermediate between lush and sparse. Nine nests were in the dry juniper-



FIG. 1. Dry juniper-crowberry nesting habitat, with a small dry cranberry bog in the foreground. (Photograph courtesy of the Nova Scotia Museum; August 1976).



FIG. 2. Sparse nesting habitat, typified by scattered marram grass and pearly everlasting. A single nest was located in about the center of the area shown here (25 June 1975).

crowberry habitat (Fig. 1). Most nests were in or near some small irregularity in vegetation or terrain. Examples included nests in small patches of vegetation that differed from surrounding vegetation (often lush), or on the sides of small knolls, or near horse droppings. No nests were on steep slopes, though these were common.

Nests were lined with materials that were available in the immediate vicinity (Fig. 3). Some materials were

nevertheless strongly favored, chief among these being the aromatic dead leaves of the Bayberry (*Myrica pensylvanica*), which commonly lined the bottom of nest cups (Fig. 3).

Population trends and composition

Daily counts for 1976 are summarized in Fig. 4. Birds were present when I arrived on the island in both years

(17 May 1975, 14 May 1976). In 1976 numbers increased rapidly into the 1st week of June, after which they fluctuated irregularly. The decline in total count after the 1st week of June is attributable in part to incubation activities of many birds, and in part to a drop in recruitment. The earliest autumn migrant Least Sandpipers appear at about the latitude of Sable Island by early July (Bent 1927), so evidence of the first gatherings of pre-migratory adults from Sable Island and of early migrants from farther north probably showed up in my counts at that time. This interpretation is supported by data on the relative abundance of banded and unbanded adults. From 3 July to 2 August 1976, the following percentages of adults were banded (in 5-day periods): 56, 40, 40, 18, 9, 13, and 2, respectively. Thus the resident pool of adults started to be diluted in the first half of July, and this continued at least until my counts ended. Fledglings increased in numbers over the same period, while numbers of "nonparental" adults (i.e., adults neither obviously attending broods nor exhibiting parental distress at my presence) declined (Fig. 4). The sudden increase in numbers of fledglings and nonparental adults in the last 5-day period was probably due to an influx of migrating birds. In late summer, fledglings gradually increased in relative abundance due to the migratory departure of postbreeding adults and the increased number of birds fledging.

Males of monogamous species of scolopacids tend to assume a greater role in incubation as it progresses, and almost always tend to hatch the young longer than do females (Miller 1977). Females are consequently freed of parental duties earlier than are males and generally migrate south earlier (Miller 1977). I investigated the relationships of sex, reproductive success, and date of "freedom" from reproductive duties (e.g., through loss of an unreplaced clutch or fledging of a brood) to the time to migratory departure. I estimated the time to migratory departure as the number of days between "freedom" and the date upon which a bird was last identified. Estimates of this postbreeding interval (PBI) were affected little by the amount of time remaining to me in each year's field season, since very few PBIs were longer than half the time remaining to me (Fig. 5).

Overall, successful breeders departed sooner after "freedom" than did unsuccessful ones (3 vs. 7–10 days), and their PBI was not affected by date of freedom (Table 2; Fig. 5, inset). In contrast, unsuccessful breeders of both sexes departed sooner after "freedom" late in the season. Females which bred successfully left earlier than did successful males, as expected, and unsuccessful breeders, regardless of sex, departed earlier than did successful breeders (Fig. 5, inset; Table 2; Sutton 1961). To test if males and females differed in their PBI (all else being equal), I examined the relationship of PBIs of successful and unsuccessful breeders to date of freedom. Analysis of covariance of data for unsuccessful breeders

disclosed a statistically insignificant difference between the slopes of the regression lines for males and females ($F_r = 1.89$, adjusted $df = 1, 51$, $0.10 < P < 0.25$). However, my strong impression was that unsuccessful males remained on Sable Island longer than did unsuccessful females, when loss of nest or brood occurred early in the season. Only one of these males resumed display flights and "territorial" behavior; the others left their nesting areas altogether and gathered in areas frequented by premigrants.

Least Sandpipers on Sable Island typically occurred in small loose flocks. These held as many as eight birds up to 19 May (this and following dates refer to both years of study), but then declined in size and, until the period 19–23 June, none contained more than four birds (Fig. 6A). Flock size then started to increase, but never exceeded about 20 birds in either year. Flocking tendencies of adults without broods followed the same trend: few were in flocks (defined as groups of at least three birds) between 20 May and 18 June, but by mid-July roughly 60% were in flocks (Fig. 6A). In mid-May about 30% of adults were in pairs (defined as groups of two birds, regardless of whether or not they were paired for reproductive purposes), and about 50% were alone (Fig. 6, B and C). Most males present then were without mates and were spaced out on their mating territories. Following this period there was first a rise and then a decline in the percentage of adults alone and in pairs, for two main reasons: mated adults spent much time together before they started full incubation (Miller 1979a), but during incubation usually fed alone. The increase in the percentage of nonparental adults in flocks after late June was accompanied by a drop in the percentage in pairs and alone.

During the nesting season adults fed throughout the pond system and did not gather in particular areas. In both years, postbreeders tended to feed on the sandy westernmost ponds and on one small cranberry-girded pond in the eastern part of the study area; in both locations flocking was pronounced. Older fledglings behaved similarly. Late-breeding birds off their nests feeding were commonly in flocks, and birds still with broods late in the summer occasionally joined flocks that flew nearby.

I examined data on flock composition for the period when fledglings occurred in groups. This period was late in the summer in both years (some time later than the first appearance of fledglings), and hence excluded mated adults. Data on groups of two, three, or four birds are summarized in Fig. 7; I could not determine the complete age composition of many large flocks. Pairs tended to be composed of either both adults or both fledglings, when observed data are compared with those expected on the basis of random assortment (Fig. 7A). The same tendency was apparent, though weaker, for trios (Fig. 7B). The small sample sizes for quartets

precluded statistical testing, but trends were similar to those for pairs and trios (Fig. 7C). There were no obvious habitat differences between flocks of different age composition.

Returning birds, estimates of adult mortality, and breeding cycle

In 1975 I banded 57 adults and could also regularly identify a partially albino male. Of these, 26 (17/26 males, 9/24 females) returned to Sable Island and nested there in 1976. Males generally arrived back earlier than females (medians differed by about 7 days; by median test with Yates's correction, $G_{adj} = 2.79$, $df = 1$, $0.05 < P < 0.10$).

None of the 27 returning birds that I identified (26 adults plus 1 yearling) had lost any of their bands, and I identified virtually all birds by late May. Furthermore, in several surveys of other breeding areas on the island in 1976 I saw no banded birds. However, early in 1975 I may have banded some migrants, for none of the nine birds caught in mist nets from 20 to 27 May was resighted that year (one female returned and bred in 1976), and one bird that I netted on 6 June 1975 also was not resighted. Subtracting 9 birds from the total yields 49 as an estimate of the number of resident adults known in 1975. Excluding from consideration a male injured in handling that year, the return rate of adults was 26/48, or about 54%. Separate estimates for adult males and females were 65% and 38%, respectively. These figures reflected overwinter survival only if all surviving birds returned to Sable Island and were identified. I have no data on emigration by breeding birds between years, but my data on returns of males to particular mating territories support much published information on strong nesting-site fidelity in most species of scolopacids (Miller 1977), so emigration by breeders was probably not great.

In 1975 clutches were completed over 29 days, from 28 May to 25 June, and in 1976 they were completed over 33 days, from 23 May to 24 June (Fig. 8). The briefest interval between loss and replacement of complete clutches was 7 days, and the earliest replacement clutches appeared about midway through the nesting season in both years.

Early breeding is facilitated by remating with the previous mate in many migratory species of birds, and early breeding is generally more successful than late breeding. In this study, eight males that I banded in 1975 took new mates in 1976, and seven of them nested later in 1976 than in 1975 (one-tailed cumulative binomial $P = 0.035$; here and in what follows I have subtracted 5 days from 1976 dates because of later nesting that year

than in 1975). Three females that took new mates in 1976 also nested later than they had in 1975. Three pairs that reformed in 1976 nested no later than when they had in 1975. The female in one reformed pair seemed very weak for several days after her 1976 arrival, and the pair nested about a week later in 1976 than in 1975.

The cumulative frequencies of pairs completing clutches by a given date are summarized in Fig. 8. Data on pairs known to contain at least one bird that was banded in 1975 are distinguished from other pairs. The two data sets did not differ significantly (by median test).

Data on breeding success of pairs that completed clutches in the first and second halves of the nesting season are summarized in Table 3. Early clutches had a greater hatching and fledging success than did late clutches. However, none of the differences was statistically significant. The same result was obtained when success of the first half of clutches was compared with success of the second half. Data on exact dates of clutch completion and on reproductive success of 43 clutches are shown as plots of cumulative frequencies in Fig. 9. Several trends are apparent: (i) the curve for clutches that fledged young follows the curve for clutches that hatched quite closely until 35%, 60%, then 80% of the way through the nesting season, at which times they increasingly diverge; (ii) the curve for the percentage of clutches laid, that hatched, is high until 35% of the nesting season is over, after which it drops slowly; and (iii) the curve for the percentage of clutches that fledged young builds up to a peak at about the same time, then slowly drops. There are therefore several suggestions that reproductive success, variously estimated, was highest for clutches completed in about the first third of the nesting period. Of 13 clutches completed in this period, 84.1% hatched and 81.0% hatched and fledged at least one chick. This compares with 30 clutches completed in the last two-thirds of the nesting season, of which 60.5% hatched and fledged at least one chick. It is not statistically legitimate to compare these figures a posteriori, since they were chosen on the basis of differences apparent in Fig. 9.

Egg laying and incubation

I could not usually estimate times of egg laying and intervals between the laying of successive eggs precisely. To estimate intervals, I assumed that eggs were laid midway between nest checks. For example, if a nest held one egg at 0500, two eggs at 0900, two eggs at 0700 the next day, then three eggs at 1300, I estimated the time of laying of the second egg as 0700, that of the third egg as 1000 of the next day, and the interval between

FIG. 3. Examples of the kind and amount of nesting material used. The two upper nests consisted mainly of bayberry leaves. The nest in the lower left consisted almost entirely of short stiff segments of rushes, and that in the lower right was made mostly of grass.



TABLE 2. Relationship of sex and reproductive success to the length of time spent on Sable Island after breeding. Criteria of reproductive success and definition of the postbreeding interval (PBI) are discussed in the text

| | Sex | Mean PBI, days | Regression equation | r^2 | F_s | df | P |
|-----------------------|--------|----------------|--------------------------|-------|-------|------|--------------------|
| Unsuccessful breeders | Male | 10.0 | $PBI = 23.8 - 0.703DATE$ | 0.55 | 32.79 | 1,27 | $P < 0.001$ |
| | Female | 6.9 | $PBI = 14.1 - 0.356DATE$ | 0.24 | 7.65 | 1,24 | $0.01 < P < 0.025$ |
| Successful breeders | Male | 2.9 | $PBI = 6.8 - 0.102DATE$ | 0.04 | 0.49 | 1,13 | $0.25 < P < 0.5$ |
| | Female | 2.8 | $PBI = -0.3 + 0.117DATE$ | 0.03 | 0.41 | 1,14 | $0.5 < P < 0.75$ |

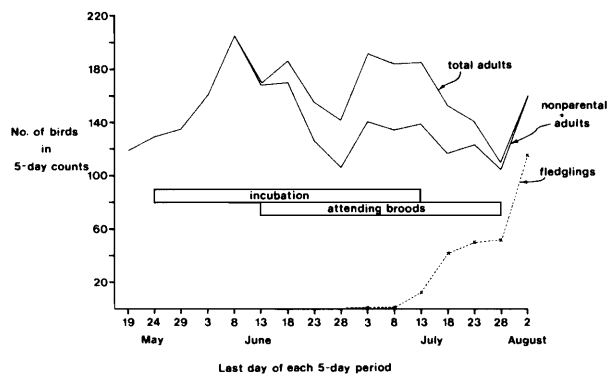


FIG. 4. Seasonal trends in the numbers of adults and fledglings counted. The figures plotted are the totals of five daily counts and refer to 1976 data only. The difference between the "adult" curves reflects the fraction of adults exhibiting parental behavior or distress (see text). The approximate periods spanned by incubation and brood attendance are represented by horizontal bars.

them as 27 h. The mean of 17 such estimates is 29.6 h or 1.23 days. The first two eggs in one replacement clutch were laid at least 62 h apart. In another clutch, two eggs were laid no more than 24 h apart. Jehl (1973) reported a normal laying interval of 24 h for Least Sandpipers in northern Manitoba, and suggested that one interval of 72 h was due to food shortage.

To analyze data on the relationship of egg-laying activity to time of day, I divided the 24-h day into an overnight period (2100 to 0500), plus eight daytime 2-h periods from 0500 to 2100. The probability that laying of an egg occurred in any of these time periods was computed as in the following example of an egg laid between 0900 and 1130. The egg could have been laid in the 120 min of daytime period 3 (0900 to 1100) or in the 30 min of daytime period 4 (1100 to 1400) spanned by the interval of 150 min between nest checks. Assign weights correspondingly, to estimate the "frequency" of egg-laying, f^* , as $f^*(0900-1100) = 120/150 = 0.8$; $f^*(1100-1400) = 30/150 = 0.2$. For eggs laid between 2100 and 0500, f^* -values were divided by 4 to make

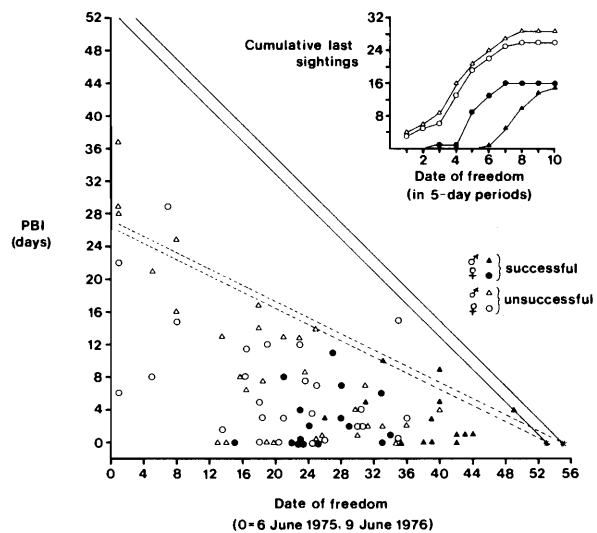


FIG. 5. Relationship of postbreeding interval (PBI) to "date of freedom" from parental duties. The solid lines represent the total time remaining to me in each field season. Very few PBIs were longer than half the time remaining (these "half-time" broken lines are also shown). Criteria for breeding success were the following: for males, the raising to fledging of at least one chick; and for females, the survival of at least one chick to the time when maternal care ended (after which survival of her chicks presumably had no effect on a female's departure date).

them comparable to daytime values. The f^* -values for each period of time were then summed to provide estimates of egg-laying activity. These are plotted in Fig. 10.

Egg-laying activity was much higher in the morning than in the afternoon and evening. The datum for night may be misleading since it represents four 2-h periods; maxima or minima that occurred at night would probably be obscured by this treatment.

Least Sandpipers incubated one-egg clutches about 27% of the time, and increased their attendance progressively over the laying sequence to about 99% for definitive clutches (Table 4). Incubation periods for complete clutches were estimated from the laying of the last egg to the hatching of the last fertile egg. They lasted

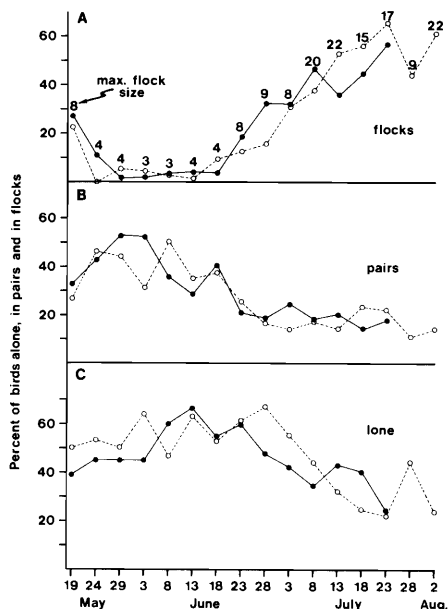


FIG. 6. Seasonal trends in the percent of adults seen alone, in flocks, and in pairs. The maximal flock size seen in each 5-day period is indicated in the upper part of the diagram. A flock contains three or more birds; a pair simply refers to two birds and need not be a mated pair.

20.1, 20.8, and 20.8 days for first clutches, and 20.1 and 20.4 days for replacement clutches (overall mean = 20.4 days). The estimates may be as much as several hours in error, but no incubation period could have been less than about $19\frac{1}{2}$ days or more than about $21\frac{1}{2}$ days.

Of the 62 clutches found in this study seven were lost because of human interference, one was trampled by a horse, 25 disappeared and were presumably taken by gulls, and the remainder hatched. These data are summarized in Table 5.

Losses to man were of various kinds; a few examples follow. I cracked an egg of one full clutch when measuring it but replaced it in the nest. Ants were swarming on the broken egg at my nest check the next day and the unbroken eggs were cold; the parents did not return. In another case, on 2 successive days I surprised one male incubating a full clutch, and he cracked three eggs as he flushed hurriedly from his nest. I saw him fly off with the first cracked egg in his beak, and drop it about 15 m away. Presumably he also removed the other two cracked eggs because on the 3rd day one lone egg lay cold in the nest. He and his mate re-nested nearby. Some birds were extremely sensitive to disturbance by man: one pair deserted their four-egg clutch after I discovered it. Others were less so; for example, I accidentally crushed three of four eggs in one nest early in incubation, but the parents continued to incubate the lone remaining egg (I removed all traces of the three

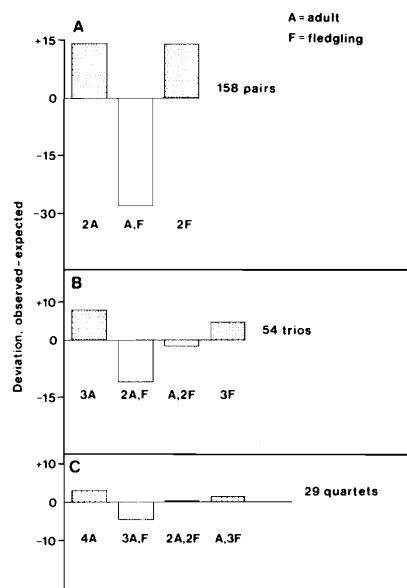


FIG. 7. Assortment into small pre-migratory flocks by age. The stippled bars represent positive deviations of observed from expected frequencies; the open bars represent negative deviations. Flock composition is indicated below each bar: 2A = 2 adults, A,F = 1 adult plus 1 fledgling, and so on. G -tests of the goodness-of-fit of the observed to the expected (= random) values were performed for pairs and trios (the hypothesis is intrinsic to the data, so one degree of freedom is lost): for pairs, $G = 36.2$, $df = 1$, $P < 0.001$; for trios (figures for A,2F and 3F were combined), $G = 11.4$, $df = 1$, $P < 0.001$. Data for quartets were not tested because of the small sample size.

broken eggs), which hatched and eventually produced a fledgling.

I did not witness clutch predation, but attribute all of it to Herring Gulls (*Larus argentatus*), mainly because there are no resident mammalian, reptilian, or other avian predators on Sable Island except for occasional domestic dogs and cats. Also, gulls commonly cruised low over the vegetation around the ponds and over the juniper-crowberry heath, while scanning vegetation below them. Gulls took all eggs from clutches they discovered except twice, when they left two intact eggs in one nest and one intact egg containing a 16-day-old embryo in the other nest. The parents deserted both nests.

Clutches were discovered at different stages of incubation, by which times they had experienced differential mortality. The data on loss of nests shown in Table 5 therefore cannot be used to estimate the real incidence of nest loss (Mayfield 1961; Ricklefs 1969). To make such estimates I assumed that I found incomplete clutches midway between the laying of successive eggs. For example, I located six one-egg

TABLE 3. Relationship of hatching and fledging success to the date of clutch completion

| | Part of nesting season in which clutches were completed ^a | | <i>P</i> of difference ^c |
|-----------------------------------|--|-------------|-------------------------------------|
| | First half | Second half | |
| (A) No. of clutches completed | 20 | 29(23) | — |
| (B) No. of clutches which hatched | 13 | 16(12) | — |
| (C) No. of clutches which fledged | 10 | 9(7) | — |
| % (B/A) | 65.0 | 55.2(52.2) | >0.2(>0.2) |
| % (C/A) | 50.0 | 31.0(30.4) | >0.1(>0.2) |
| % (C/B) | 76.9 | 56.2(58.3) | >0.2(>0.1) |

^aFor 1975, the first and second halves were 15 and 14 days long, respectively. For 1976, the first and second halves were 17 and 16 days long, respectively.

^bThe figures outside the parentheses refer to initial plus repeat nestings; those within parentheses refer to initial nestings only.

^cBy Fisher's exact test; the one-tailed values shown reflect only the cumulative *P* reached in the first few steps of computation.

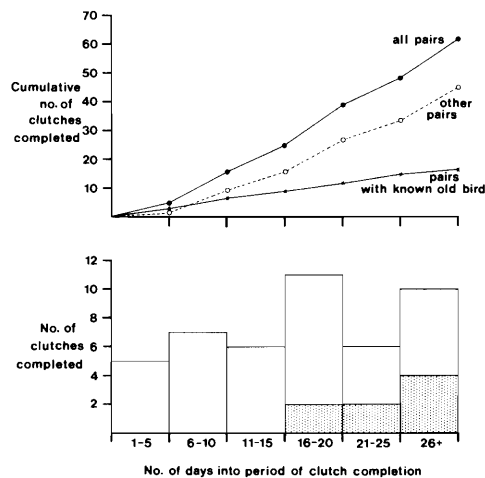


FIG. 8. Frequency histogram (below) of the number of clutches completed per 5-day period. The stippled portions of the histogram represent known replacement clutches. In the upper part of the diagram are shown cumulative plots of the number of clutches completed by the end of each 5-day period; data were added for some clutches according to the date they were located. For example, if a complete clutch was located on the 7th day of the period in which clutches were completed, and it was predated before it hatched, then it was considered to have been completed by day 10. Cumulative plots are also shown for pairs that were known to contain at least one old bird (i.e., banded in 1975) and other pairs.

clutches of which two (33.3%) were predated before the laying of the second egg. Assume that 33.3% were also predated prior to my finding the nests, thus depleting an initial number of nine to six, then to four. This reduction (5/9) in the number of one-egg clutches, divided by the

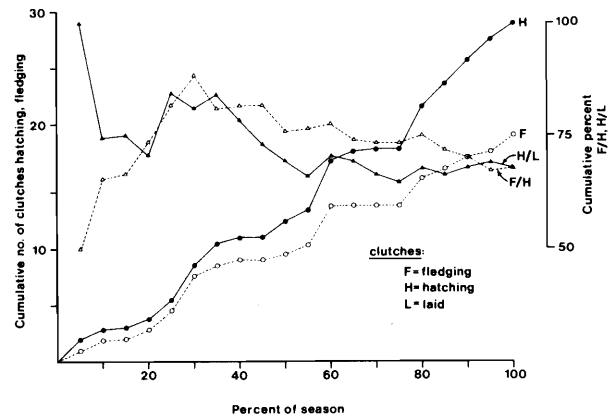


FIG. 9. Relationship of reproductive success to date of clutch completion. To make the 1975 and 1976 seasons comparable, I divided the total period in which clutches were completed in each year into 5% blocks and summed the 2 years' data. For example, clutches that were completed in the first 5% of the clutch-completion periods had 100% hatching success (H/L) and 50% fledging success (F/H; the early values fluctuate because of the few clutches completed, e.g., only two were completed in the first 5% block: see the line joining the cumulative number of clutches hatching).

average laying interval between eggs of 1.23 days, yields a mortality rate per nest-day of 0.45, for one-egg clutches. Estimates of mortality rates were computed in a similar manner for clutches that contained two or three eggs when found, and these estimates were combined with data on clutches found earlier in egg-laying and surviving up to those stages. For definitive clutches, the data in Table 6 represent only nests that were found prior to clutch completion, and that survived until then.

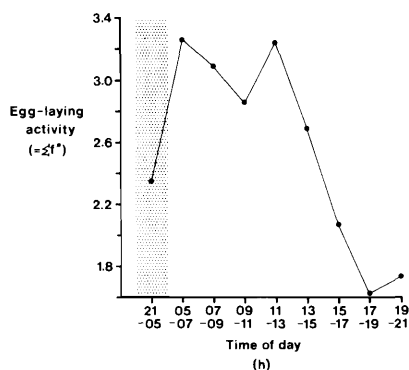


FIG. 10. Relationship of egg-laying activity (see text for explanation) to time of day. "Night" is shown by stippling. All points, including that for night, refer to egg-laying activity per 2-h interval.

TABLE 4. Incubation attendance of clutches at various stages of completion. Cell entries show the number of times that adults were seen on their nests, over the number of times that their nests were checked

| | Clutch size | | | |
|-----------------|-------------|-------|-------|-----------------|
| | 1 | 2 | 3 | 4 or definitive |
| 1975 | 1/13 | 5/18 | 16/30 | 258/262 |
| 1976 | 5/9 | 14/29 | 21/31 | 347/351 |
| N | 22 | 47 | 61 | 613 |
| % of attendance | 27.3 | 40.4 | 60.7 | 98.7 |

Mortality rate declined steadily from one- to four-egg clutches, and did not change during incubation of definitive clutches. If survival of a nest through early stages of egg laying is positively correlated with survival at later stages, then estimates of mortality rate past the one egg-stage would be increasingly biased downward (see Green 1977). However, the trends apparent in Table 6 are unaltered if data from surviving clutches are excluded. The estimate of 0.12 for the two-egg stage increases slightly to 0.17, and that for the three-egg stage (0.07) drops to zero. Mayfield (1961; see his paper for more details) suggested estimating rate of nest loss by the expression, (no. of nests lost/no. of nest-days of observation). Using this expression for my data yields an estimate of mortality rate of 0.045 per nest-day for definitive clutches.

Eggs that survived to hatching had high fertility, and most of the chicks that hatched left the nest alive (Table 6). Three of the five chicks contributing to the figure on loss of chicks before leaving the nest were in a single brood taken by a gull. The other two chicks were in separate broods and died of unknown causes. Mortality of chicks after leaving the nest is discussed in the next section.

Hatching and prefledging mortality

The amount of time spent on the nest by hatchlings depended upon the time of day when the clutch finished hatching, and upon the number of chicks hatching. Nests in which hatching was completed in the late afternoon and evening were usually not abandoned until early or mid-morning of the next day. This is normal for scolopacids (Hale 1980). The first chicks to hatch thus usually abandoned the nest when about 20–30 h old, at which time the youngest were sometimes only a few hours old. Broods remained in or near the nest for a considerable period of time even when weather, age of chicks, and time of day seemed propitious for leaving. For example, the chick from the single egg in one nest hatched at 0830 one day and was still being brooded in the nest cup at 0740 of the next day; this chick was healthy and eventually fledged. During the time when chicks remained at the nest one parent brooded constantly (both members of intact pairs shared the duty), and the chicks spent their time being brooded in the nest cup or exploring its immediate vicinity for several minutes, then returning to be brooded. The oldest chicks stayed out longest (sometimes more than 20 min), especially in fine weather. These sorties were highly contagious, and generally the two or three oldest chicks left the nest at about the same time, though they wandered about and returned to be brooded individually. At such times the parent remained on any remaining egg or chick in the nest cup, and sometimes even remained on an empty nest cup, until the wandering chicks returned. When the chicks were fairly old, the simultaneous absence of two or more of them from the nest seemed to trigger the parent to start the exodus from the nest. It rose, walked up to 0.5 m from the nest and called to the chicks. Chicks off the nest and any remaining in the nest cup then quickly approached the calling adult which brooded them briefly. Sometimes the adult brooded for so long that a chick would eventually wriggle out from underneath it and start exploring locally; this invariably set the adult into another sequence of walking away a short distance, calling the young together again, and so on. More typically the adult brooded perfunctorily then immediately moved off itself and started the sequence again. When broods left the nest it was often apparent which chicks had been longest and which most briefly out of the shell simply because of their locomotory facility, and this was confirmed by their identities based on their color bands, which were placed on chicks immediately upon hatching for those nests under observation. Once an adult started to lead the brood from the nest but the youngest chick could not climb out of the nest cup, so the parent returned and kept the brood centered there for several more hours.

Mortality of chicks between the time of leaving the nest and fledging was readily estimated, since I knew

TABLE 5. Summary of data on the incidence and causes of loss of nests and on the number of nests hatching

| Year(s) | No. lost to man ^a | | No. trampled by horses | No. taken by gulls | Total nests hatched | No. of nests |
|---------|------------------------------|-----------|---------------------------|-----------------------|------------------------|--------------|
| | Direct | Desertion | | | | |
| 1975 | 2 | 2 | 1 | 14 | 11 | 30 |
| 1976 | 2 | 1 | 0 | 11 | 18 | 32 |
| Both | 4 | 3 | 1 | 25 | 29 | 62 |

^aExamples are given in the text.

TABLE 6. Estimates of mortality rates of clutches, eggs, and chicks^a

| Year(s) | Mortality rate per nest-day for nests of clutch size: | | | | | % of eggs hatching ^d | Chick mortality on nest (%) | Chick mortality in interval, leaving nest to fledging (%) |
|---------|--|--------------|--------------|----------------|-----------------|------------------------------------|--------------------------------------|--|
| | | | | 4 ^b | | | | |
| | 1 | 2 | 3 | I ^c | II ^c | | | |
| 1975 | — | — | — | — | — | 95.5 (44) | 0 (42) | 55.9 (38) |
| 1976 | — | — | — | — | — | 90.5 (63) | 8.8 (57) | 62.5 (71) |
| Both | 0.45 (6) | 0.12 (13) | 0.07 (15) | 0.04 (14) | 0.04 (8) | 92.6 ^e (107) | 5.1 ^e (99) | 60.2 ^e (109) |
| | | | | 0.03 (13) | | | | |

^aMethods of computation are described in the text. Sample sizes are given in parentheses.

^bThis category includes all definitive clutches, including those with less than four eggs.

^cI, first half of incubation (days 1–10); II, second half of incubation (days 11+).

^dIn clutches that hatched normally.

^eWeighted mean values.

which chicks should have fledged by my departure date, and because fledglings were tame (hence easily approached and identified) and seen repeatedly. Prefledging mortality was high in both years, averaging about 60% (Table 6). I excluded from these estimates one brood whose father died midway through incubation and whose mother alone incubated and led the brood from the nest; one of the brood died on the nest, and the others died a few days later. Also excluded are records for two nests that hatched late in 1976 (12 and 28 July) and from which the broods were led by females. The males apparently deserted in both cases, and the broods were either deserted by the females or predated within a day or two of leaving the nest. The figures in Table 6 thus refer to broods that were tended normally by males. It was impossible to determine the cause of brood loss except in the cases mentioned. It was also difficult to assess when broods were lost, but this generally seemed to happen within the first week of leaving the nest. Parents that lost broods usually remained for several days where they had been tending them and showed reduced alarm at my presence.

Data on the relationship of the number of chicks in a brood leaving the nest, to the number fledging, are summarized in Table 7. Of 98 chicks leaving their nests in broods of three or four chicks, 33 survived to fledging, and of these 23 survived with two or three siblings. Twelve of the 27 broods were lost completely, from 12 others some chicks fledged, and from 3 broods all chicks fledged. If a chick's survival to fledging is independent of that of his siblings, then surviving chicks should be distributed randomly across broods leaving the nest. If survival of siblings is correlated then broods should tend to survive or be lost as units. To test the hypothesis of random survival of chicks across broods I computed expected (Poisson) distributions separately for three- and four-chick broods, summed the observed and expected frequencies for these two brood sizes, then lumped classes for the number of chicks that fledged as 0, 1 or 2, and 3 or 4. These have cell sizes of 12, 8 and 8, respectively. The resulting *G*-statistic was highly significant ($G = 10.7$, $df = 2$, $P < 0.005$), indicating strong departure from a random distribution of surviving chicks among broods.

TABLE 7. Relationship of the number of chicks in each brood leaving the nest to the number sighted as fledglings

| No. of chicks leaving nest | No. of chicks fledging from brood | | | | | Row totals |
|----------------------------|-----------------------------------|---|---|---|---|------------|
| | 0 | 1 | 2 | 3 | 4 | |
| 1 | 0 | 1 | — | — | — | 1 |
| 2 | 0 | 0 | 0 | — | — | 0 |
| 3 | 6 | 3 | 0 | 1 | — | 10 |
| 4 | 6 | 3 | 2 | 4 | 2 | 17 |
| Column totals | 12 | 7 | 2 | 5 | 2 | |

Trends in chick production can now be summarized, based on preceding discussion and on data in tables 5–7. About 93% of fully incubated eggs hatched, 95% of hatched chicks left the nest, and 40% of chicks leaving the nest fledged. Hence 35% (the product of the preceding values) of fully incubated eggs produced fledglings. Since 62% of clutches that reached definitive size ultimately hatched, then clutches reaching definitive size produced an average of 2.1 chicks leaving the nest and 0.9 fledglings. Conversely, each egg in a completed clutch had a probability of 0.23 of producing a fledged chick (= 0.9/3.9).

Discussion

I will focus discussion on features of habitat and breeding cycle which are of ecological or evolutionary interest because of geographic variation over the nesting range, or because Least Sandpipers differ from other, more northern Calidridini.

Habitat

Elsewhere in its breeding range, the Least Sandpiper typically nests in bog, muskeg, or sedge meadow, and sometimes in drier upland sites near mudflats or tidal or standing water (Jehl and Smith 1970; Moore 1912; Philipp 1925; Todd 1963; Townsend 1927; Yarbrough 1970). Its habitat on Sable Island is therefore broadly similar, except for those nests situated in dry sparsely vegetated areas (e.g., Fig. 3). Such conservatism is due partly to the need to nest in habitat which provides crypticity or concealment from visually hunting predators, and because nests must be near richer, moister habitats where broods can be taken and raised after hatching; these factors are fairly uniform throughout the breeding range. On Sable Island there were a few exceptions to both, since some nests were placed in unusually open habitats, and some broods were raised in dry areas away from the ponds (Miller 1977). Even so, general features of nesting and brood-rearing habitat are very similar throughout this species' range.

Characteristics of nesting material used by calidridines vary locally because of available materials, and because of additions made throughout incubation (e.g., Ashkenazie and Safriel 1979a). Geographic variation must be correspondingly even greater, but it is unexplored. There is some evidence for geographic uniformity in favored materials, however: the use of dead leaves of bayberry has also been noted by Macoun and Macoun (1909), Moore (1912), and Philipp (1925).

The apparent conservatism in this species' nesting habitat and nesting materials may just reflect inadequately detailed descriptions (see Skeel 1976, 1983). Future work on the species should include reference to those factors which are likely to exhibit significant ecological variation, including the wettability and thermal properties of nesting material (e.g., Kull 1977; Purdue 1976), nest microclimate (e.g., Rahn et al. 1977), nest microhabitat as related to different kinds of predators (e.g., mammalian vs. avian), and to local environmental extremes (e.g., flooding). Such factors could also be addressed at the interspecific level, for major habitat differences exist even among locally sympatric species of Calidridini.

The breeding season

The beginning of the breeding season

Arrival date and the start of breeding in Scolopacidae are adapted to average conditions on the breeding grounds, a generalization which also applies to Least Sandpipers (Holmes 1966a). It is crucial for high-latitude species to be able to respond facultatively to proximate factors, as well, and to breed as early as possible, because of the brief nesting season (Soikkeli 1967). But it is probably more critical for nesting to be timed so that chicks hatch when there is a plentiful supply of their major food, surface-active adult insects (Holmes 1966a, 1966b, 1966c; Holmes and Pitelka 1968; Hurd and Pitelka cited by MacLean and Pitelka 1971, p. 37; MacLean 1975; MacLean and Pitelka 1971; Nettleship 1973, 1974; Ratcliffe 1976); at high latitudes this period is determined mainly by when melting of snow occurs (Holmes 1970; MacLean 1975). Proximate cues which stimulate breeding activity therefore should be closely correlated, causally or temporally, or both, with events such as snow melt which strongly influence early spring activity in life cycles of prey species of chicks. (Byrkjedal (1980) suggests that nesting when snow is present also increases susceptibility to nest predation.)

Numerous observations point to delayed breeding by northern shorebirds in years with late snow cover (e.g., Bengtson 1970; Green et al. 1977; Holmes 1966a, 1971b, 1972; MacLean 1969; Parr 1980; Pitelka 1959). Conversely, early breeding typically occurs in warm

springs, even at lower latitudes (Bianki 1977; Hildén and Vuolanto 1972; Kistchinski 1973; Lind 1961; Miller and Miller 1948; Pitelka 1959; Soikkeli 1967; this study). This relationship may not just reflect a general response, but may reflect the ability of females to acquire resources needed for egg production (see Högstedt 1974). Jehl (1973) noted that the breeding season of Stilt Sandpipers (*Calidris himantopus*) is prolonged in late springs, possibly because of persistent standing water delaying the emergence of insects and preventing many females from quickly producing eggs. He also noted an unusually long interval between the laying of two successive eggs in a Least Sandpiper nest in such a spring. Oring and Lank (1982) reported delayed egg-laying in Spotted Sandpipers in springs of low food abundance (see also Maxson and Oring 1980). The importance of food resources to laying females is evident from Skeel's (1976) observations on Whimbrels (*Numenius phaeopus*): eggs were significantly longer and broader in an early than in a late spring.

A simple functional explanation for the onset of breeding, such as one based on food availability for females, is insufficient. For example, males of most species arrive on the nesting grounds before females, and typically begin advertisement displays late in late springs (Miller 1977; Pitelka 1959); this activity may be proximately influenced by food availability too, but may also by itself be an important factor in the onset of nesting (Soikkeli 1967). Such complications notwithstanding, the most parsimonious explanation for year-to-year and geographic variation in the onset of breeding is one based on a causal relationship (like food availability), rather than a correlational one. The latter would require unique sets of programmed and facultative responses for different seasons or different places (like Sable Island vs. more northern breeding grounds of Least Sandpipers). This seems unlikely, because of the remarkable uniformity in characteristics of early breeding activity both within and among shorebird species.

Length of the nesting period

The period of clutch completion or hatching is about a month long for many calidridine populations (Bengtson 1975a, 1975b; Holmes 1966a, 1971b, 1972; Norton 1973; Norton et al. 1975; Pitelka 1959; Väisänen 1977), but is often even briefer (12 days to 3 weeks) in the high arctic (Drury 1961; Kistchinski 1975; Kokhanov 1973; Parmelee et al. 1968). Altitude must exert a comparable effect (see Byrkjedal 1978). The hatching period for Least Sandpipers in northern Manitoba is about 14–17 days (Jehl 1970), about half as long as in my study. Data do not exist for other nesting locations, but they are also likely to be less extreme than at Sable Island.

The length of the nesting season also varies from year to year. For example, long nesting seasons often follow an early start to breeding (Green et al. 1977; Holmes

1966a, 1971b, 1972; Norton et al. 1975; Skeel 1976; Soikkeli 1967). The opportunity to renest may be an important advantage to nesting early (Soikkeli 1967), an idea supported by data on the high frequency of renesting late in long nesting seasons (Holmes 1966a, 1971b, 1972; Skeel 1976; Soikkeli 1967). Renesting by Least Sandpipers on Sable Island occurred in both years of this study and is probably usually possible considering the long growing season there. Sable Island's mild climate and long growing season contrast with situations throughout much of the nesting range of calidridines (see McKay et al. 1970). This has not resulted in a departure from a conservative single-clutch, monogamous breeding system, however, unlike the Dunlin (*Calidris alpina*; Holmes 1966a; Soikkeli 1966, 1967; see Hildén 1975; Jenni 1974; Pitelka et al. 1974).

Comprehensive analysis of climatic factors influencing nesting phenology, and the seasonal events most important to fitness, must await long-term data on climatic variation and extremes from different regions (Myers and Pitelka 1979; e.g., see Pulliainen 1978).

The end of the breeding season

Fledgling Least Sandpipers migrate south from Sable Island later than do adults. This agrees with the widespread trend in scolopacids for adults to precede fledglings along autumn migration routes (Paulson 1983). Adult female Least Sandpipers leave Sable Island earlier than do males mainly because they are freed from reproductive duties earlier. However, even among unsuccessful breeders females may tend to leave slightly sooner than males, if reproduction fails early enough, imparting a sexual difference in timing of departure in addition to that resulting from sex differences in parental roles. It is widely recognized that in most species of scolopacids males stay with their broods longer than do females and therefore females tend to migrate south earlier (Jehl 1963, 1973; Kistchinski and Flint 1973; McNeil and Cadieux 1972; Page 1974a, 1974b; Page et al. 1972; Soikkeli 1967, and many others). As in my study, Soikkeli (1967) documented that male Dunlin migrated south much sooner after the end of parental care than did females (1 day as compared with 10 days).

The factors of age (i.e., adult or juvenile), sex, and reproductive success impart late summer characteristics to the breeding cycle of Least Sandpipers that are very similar to those of related species. This species' small size and relatively brief breeding cycle permit earlier southward migration than in large species (Nisbet 1957; Page and Bradstreet 1968), though the migration schedule presumably varies latitudinally because of latitudinal effects on the breeding season (Paulson 1983).

Few workers have commented upon assortment into flocks according to age for other than ecological reasons

(e.g., Connors et al. 1979). However, Holmes (1972) noted the occurrence of fledgling flocks of Western Sandpipers (*Calidris mauri*) at a time when fledglings and adults have similar diets; Hagar (1966) commented upon juvenile Hudsonian Godwits (*Limosa haemastica*) forming their own flocks on tidal flats where adults are also gathered, and Boyd (1962) mentioned the same phenomenon in Dunlin. Bianki (1977) suggested that sibling Ruddy Turnstones (*Arenaria interpres*) flock and migrate together (but see Parmelee and MacDonald 1960). The adaptive significance of such segregation seems apparent, for juveniles and adults migrate at different times, but why males, females, and fledglings migrate at different times has received little comment (see Myers 1981b). One view is that the early departure of one sex relaxes pressure on the food supply of chicks (Holmes 1966a, 1971a; Page 1974a; Pitelka 1959; Pitelka et al. 1974). However, chicks and parents do not remain together on the nesting area after hatching, but typically move elsewhere to feed, and continued posthatching movements occur in some species (e.g., Jenni et al. 1982). Furthermore, diets of chicks and of adults are often strikingly different. It therefore seems unlikely that the early departure by one parent could materially increase its offspring's food supply (Soikkeli 1967). The "quick-getaway" strategy represents more properly a case of leaving to capitalize on favorable situations elsewhere, than a case of avoidance of unfavorable feeding conditions" (Norton 1973, p. 36; Schneider and Harrington 1981), and early rearrival on the wintering grounds may also be particularly important to those species which hold winter territories (Morton 1976; Myers 1981a). The distance between nesting and wintering grounds may be related to how long females of monogamous scolopacids attend their broods, at least across species (Ashkenazie and Safriel 1979b; Myers 1981a). A sensitive test of the hypothesis that duration of parental attendance is influenced by migration distance would involve comparisons between conspecific populations. For example, Least Sandpipers on Sable Island winter in the Caribbean and northern South America (one bird banded in this study was recovered from Surinam; Burton and McNeil 1975; McNeil 1970, 1972; McNeil and Burton 1973, 1977), and females should therefore remain with their broods longer than should females from populations with longer migration distances (e.g., Labrador, northern Manitoba). At present, such data are unavailable.

Egg laying and incubation

Egg-laying activity of Least Sandpipers is highest in the early morning (Philipp (1925) also mentions an egg of a Least Sandpiper being laid early in the morning). Scattered information for other calidridines agrees with this trend (Leonovich 1973; Norton 1972; Parmelee

1970; Parmelee et al. 1968). However, Holmes (1972, p. 476) stressed that egg laying in Western Sandpipers occurs "at no particular time of day," and Ashkenazie and Safriel (1979a) made a similar comment for Semipalmated Sandpipers (*Calidris pusilla*). There is therefore some suggestion that calidridines tend to lay eggs in the morning, but this is not invariant and is not true of scolopacids in general (Lind 1961; Nethersole-Thompson 1951).

My estimate of an egg-laying interval for Least Sandpipers is 1.23 days, which agrees well with estimates for scolopacids of similar size (1–2 days for 11 species; Grosskopf 1958; Hildén and Vuolanto 1972; Hobson 1972; Holmes 1972; Jehl 1973; Kagarise 1979; Nettleship 1974; Parmelee 1970; Parmelee et al. 1968; Parmelee et al. 1967; but see Ashkenazie and Safriel 1979a). The widely separated populations of Dunlin studied in the Old and New World show rather similar egg-laying intervals, despite their ecological differences (Nethersole-Thompson and Nethersole-Thompson 1979; Norton 1970; Soikkeli 1967). Taken together, these data point to remarkably little variation in egg-laying intervals among populations of similarly sized species (Hale 1980). The small differences that have been reported may reflect availability of calcium to laying females, as suggested by MacLean (1974) (see also Burton 1979; Byrkjedal 1975; Maxson and Oring 1980; Portenko 1972; West and Norton 1975). The reason for this conservatism may lie in the importance of relatively synchronous hatching, so that even if foraging conditions are poor, laying females will keep the egg-laying interval constant by using their own fat reserves in egg production (MacLean 1969; see Nethersole-Thompson 1973). However, it must be stressed that there is considerable variation in egg-laying intervals within populations, the ecological, genetical, and physiological significance of which is unknown.

Scolopacids typically do not start full incubation until the clutch is complete (Graul 1971; Holmes 1966a; Jehl 1973; Kuzyakin 1959; Lind 1961; Norton 1970, 1972; Parmelee 1970; Skeel 1976; Soikkeli 1967). Few authors have estimated the amount of time actually spent on incomplete and complete clutches. I saw adult Least Sandpipers on their incomplete one-, two-, and three-egg clutches in about 27, 40, and 61% of my nest checks. Lind (1961) listed comparable figures for Black-tailed Godwits of 43, 66, and 82% (egg-laying behavior included), and Norton (1972) measured an increased attendance at nests of Dunlin, Baird's Sandpipers (*Calidris bairdii*), and Semipalmated Sandpipers as successive eggs were laid. For the latter species, Ashkenazie and Safriel (1979a) estimated 18% attendance averaged over the laying period. Kondratiev (1977) summarized data for 14 species of Charadriiformes, which attended their incomplete clutches 2–55% of the time. Jehl (1973) hinted at an increase for Stilt Sandpipers. It is not

certain that attendance of incomplete clutches is true incubation, however. Adults may sit on incomplete clutches without incubating them, especially in cold weather (Norton 1970). This has also been discussed by Kondratiev (1977), Lind (1961), Nethersole-Thompson (1951, 1973), and Thomas (1969). Norton (1972, p. 174) argued that "desultory incubation during the laying stage, followed by rapid buildup of continuous incubation, represents a 'compromise' between the danger of allowing eggs to freeze and the danger of inducing too much development in first-aid eggs" (see also Kondratiev 1977; Norton 1970). However, eggs are in fact quite resistant to chilling and to injury by freezing (Norton 1973; West and Norton 1975). The main force moulding incubation schedules may therefore be the need to maintain rapid embryonic development (see also Hussell and Page 1976).

Finally, it should be mentioned that incomplete late clutches may be attended more than early ones; Kondratiev (1977) measured 14% attendance of incomplete Dunlin clutches early one season, and 54% of late clutches. This may be partly attributable to the predominance of late breeding by young birds with different incubatory behavior, or to the increased value of rapid hatching even at the risk of it being asynchronous.

Essentially complete coverage is typical for definitive clutches in monogamous calidridines. Dunlin and Baird's Sandpipers incubate full clutches 97.6 and 96.5% of the time, respectively (Norton 1972). These estimates compare with a figure of 96.6% for Sanderlings (*Calidris alba*) in Greenland, using data of Pienkowski and Green (1976; I excluded four absences of the male that were attributable to human disturbance) and with my estimate of 98.7% for Least Sandpipers on Sable Island. Rubinstein (1973) reported essentially constant coverage of full clutches of five other species in which sexes share incubation, and Kondratiev (1977) gave a range of 84–99% for 14 species, including some with single-sex incubation.

The estimated incubation period on Sable Island is nearly identical to that reported for northern Manitoba, where it averages 20½ days (range, 19½–23; Jehl and Hussell 1966; Jehl and Smith 1970).

We do not understand the relationships among laying rhythms, laying intervals, and incubation schedules, from either a proximate or an ultimate viewpoint. Many of the explanations advanced apply only to local conditions, yet the characteristics they address appear to vary little even across mating systems, habitat types, or species. In this section I have reviewed comparative data which emphasize uniformity in certain features of the Least Sandpiper's nesting biology. Research which ties together information on local variability in such features, with information on constraints to variation at higher levels, is needed to place these observations in proper perspective.

Mortality: causes and rates

Predation and unseasonable weather are probably the two most important causes of nest loss in breeding waders. Both terrestrial and aerial predators take shorebird eggs, and the total effects of predation on nesting success of shorebirds are often substantial (e.g., Oring and Knudson 1972; Ratcliffe 1976; Soikkeli 1967; Williamson 1946; and many others). Jehl (1971) summarized data on 298 nests of 12 species of ground-nesting shorebirds in northern Manitoba. Hatching success (eggs hatched/eggs laid) varied from about 20% to nearly 100% (weighted mean = 79%), and predation accounted for about half of the egg losses. Least Sandpipers on Sable Island have been exposed to predation of eggs and chicks by Herring Gulls only in this century, since the latter species colonized Sable Island (McLaren 1981). Full clutches were predated at a rate of about 3.1% per nest-day, which is more than double the rough estimate of 1.44% computed by Ricklefs (1969) for a variety of shorebird species. Jehl (1971) cautioned that the data used by Ricklefs may have been biased toward years of high productivity and low predation. In agreement with this, Hussell and Page (1976) estimated nest mortality of Black-bellied Plovers in their study at about 2.2% per day.

Estimates of nesting success made in different studies are biased by the stage of the nesting cycle when nests are located. In this study, incomplete one-, two-, and three-egg clutches, and complete clutches, comprised 11.5, 19.2, 7.7, and 61.5%, respectively, of all the clutches I found. Hildén (1975) reported comparable figures of 30.2, 7.7, 6.8, and 55.4% for Temminck's Stint (*Calidris temminckii*). Norton (1973) found most calidridine nests just after clutch completion and just before hatching, while Byrkjedal (1978) found only one incomplete Greater Golden Plover (*Pluvialis apricaria*) clutch. For clutches which were complete when found, and which eventually hatched, it is possible to estimate the stage of the incubation period at which they were discovered. About 70% of definitive clutches of Least Sandpipers were found in the 1st week of incubation, 10% in the 2nd week, and 20% in the 3rd week.

Fertility of Least Sandpiper eggs on Sable Island was about 93%, which is close to an estimate of 94% for the species at Churchill (Jehl 1971) and in agreement with the trend for wader eggs to have high fertility (Bolotnikov et al. 1973; Jehl 1971; Kokhanov 1973; Ratcliffe 1976; Williamson et al. 1966; and many others).

I estimated that about 40% of Least Sandpiper chicks that left the nest eventually fledged. This is about the lowest survivorship reported by Boyd (1962) in his review on mortality in European Charadrii. Mortality of chicks was contagious. This could result from a predator concentrating his search in the area where he

has just located a chick, or because a parent fails to maintain brood integrity and chicks disperse into areas where they are exposed to predation or are too far from parents to attend to warning calls, or both. Such a failing by a parent would also render it difficult for parents and chicks to quickly come together for brooding, with deleterious effects on survival of all chicks. Similarly, all chicks would suffer if their parents brooded irregularly or infrequently, especially in cold wet weather and in the first few days after hatching (see Norton 1973). Safriel (1975) noted that predation of single Semipalmated Sandpiper chicks endangered survival of entire broods, and attributed this to increased searching effort by a predator after it found the first chick.

My data are limited but suggest that Least Sandpipers on Sable Island may not be maintaining themselves in the face of Herring Gull predation. Further information on year-to-year variation in losses to predators and on the influence by investigators on mortality are needed to evaluate this possibility.

Concluding comments

Components of the breeding cycle must vary in their contributions to fitness over the Least Sandpiper's nesting range, and relationships among components must vary correspondingly. For example, if a "quick-getaway" strategy at summer's end is favored, this should be affected by distance to migratory and wintering grounds and should affect the nature of parental attendance. The latter must be affected in turn by a host of biotic and abiotic sources of chick mortality, which vary geographically and ecologically. Thus while it is important to estimate variations in breeding biology, it is equally important to estimate the interactions among components, for these interactions establish constraints within which adaptive (and nonadaptive) optima are reached.

A major difficulty to generalization about the proximate and ultimate causes of shorebird breeding cycles arises from the confusion of levels of explanation, particularly in viewing as "adaptive" those characteristics which vary across species or even genera. For example, phalaropes typically abandon young before they can fly, while Least Sandpipers (and most other calidridines) attend young until well after they can fly strongly (Miller 1977); this difference can be explained most parsimoniously in phylogenetic terms, not adaptive ones. Similar comments apply to general differences in nesting habitat between snipe and dowitchers, on the one hand, and calidridines, on the other; or between Charadriidae and Scolopacidae. This difficulty can be reduced by increased attention to distinctions among proximate and ultimate causes within species, to relationships among fitness compo-

nents within populations, and to linkages between local variations and their impact on individual fitness (see Arnold 1983).

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- ANDERSON, K. S. 1980. Least sandpiper (*Calidris minutilla*) breeding in Massachusetts. *Am. Birds*, **34**: 867.
- ARNOLD, S. J. 1983. Morphology, performance, and fitness. *Am. Zool.* **23**: 347-361.
- ASHKENAZIE, S., and U. N. SAFRIEL. 1979a. Breeding cycle and behavior of the semipalmated sandpiper at Barrow, Alaska. *Auk*, **96**: 56-67.
- . 1979b. Time-energy budget of the semipalmated sandpiper *Calidris pusilla* at Barrow, Alaska. *Ecology*, **60**: 783-799.
- BENGTSON, S.-A. 1970. Breeding behaviour of the purple sandpiper *Calidris maritima* in West Spitsbergen. *Ornis Scand.* **1**: 17-25.
- . 1975a. Observasjoner av hekkebiologien hos fjaerelytt *Calidris maritima* på Svalbard. *Fauna (Oslo)*, **28**: 81-86.
- . 1975b. Timing of the moult of the purple sandpiper in Spitsbergen. *Ibis*, **117**: 100-102.
- BENT, A. C. 1927. Life histories of North American shore birds. Order Limicolae. Part 1. U.S. Government Printing Office, Washington, DC.
- BIANKI, V. V. 1977. Gulls, shorebirds and alcids of Kandalaksha Bay. National Technical Information Service, U.S. Department of Commerce, Springfield, VA. (Translated from Kandalakshii Gosudarstvennyi Zapovednik, Trudy (USSR). 1967).
- BOLOTNIKOV, A. M., A. A. DOBRODEYEVA, and S. S. KALININ. 1973. On the breeding biology of the lapwing in the Kurgan region. *In* Fauna and ecology of waders. Vol. 1. Edited by V. E. Flint. Moscow Society of Naturalists, Moscow. pp. 28-31. (Translation on file with the Canadian Wildlife Service, Ottawa).
- BOYD, H. 1962. Mortality and fertility of European Charadrii. *Ibis*, **104**: 368-387.
- BURGER, J., and B. OLLA. (Editors). 1983. Behavior of marine animals. Vol. 5. Shorebirds. Plenum Publishing Corp., New York.
- BURTON, J., and R. MCNEIL. 1975. Les routes de migration

- automne de treize espèces d'oiseaux de rivage nord-américains. *Rev. Geogr. (Montreal)*, **29**: 305–334.
- BURTON, P. 1979. The greenshank's food. In *The greenshanks*. Edited by D. and M. Nethersole-Thompson. A. D. & T. Poyser, Berkhamsted. pp. 174–177.
- BYRKJEDAL, I. 1975. Smagnagerbein som kalsiumkilde ved eggproduksjon hos heilo. *Sterna*, **14**: 197–198.
- 1978. Altitudinal differences in breeding schedules of golden plovers *Pluvialis apricaria* (L.) in south Norway. *Sterna*, **17**: 1–20.
- 1980. Nest predation in relation to snow cover—a possible factor influencing the start of breeding in shorebirds. *Ornis Scand.* **11**: 249–252.
- CONNORS, P. G., J. P. MYERS, and F. A. PITELKA. 1979. Seasonal habitat use by arctic Alaskan shorebirds. *Stud. Avian Biol.* **2**: 101–111.
- DRURY, W. H., JR. 1961. The breeding biology of shorebirds on Bylot Island, Northwest Territories, Canada. *Auk*, **78**: 176–219.
- GOCHFELD, M., J. BURGER, and J. R. JEHL, JR. 1983. The classification of the shorebirds of the world. In *Behavior of marine animals*. Vol. 5. Edited by J. Burger and B. Olla. Plenum Publishing Corp., New York.
- GODFREY, W. E. 1966. The birds of Canada. *Natl. Mus. Can. Bull. No. 203*, Biol. Ser. No. 73.
- GRAUL, W. D. 1971. Observations at a long-billed curlew nest. *Auk*, **88**: 182–184.
- GREEN, G. H., J. J. D. GREENWOOD, and C. S. LLOYD. 1977. The influence of snow conditions on the date of breeding of wading birds in north-east Greenland. *J. Zool.* **183**: 311–328.
- GREEN, R. F. 1977. Do more birds produce fewer young? A comment on Mayfield's measure of nest success. *Wilson Bull.* **89**: 173–175.
- GROSSKOPF, G. 1958. Zur Biologie des Rotschenkels (*Tringa t. totanus*) I. *J. Ornithol.* **99**: 1–17.
- HAGAR, J. A. 1966. Nesting of the Hudsonian godwit in Churchill, Manitoba. *Living Bird*, **5**: 5–43.
- HALE, W. G. 1980. *Waders*. William Collins, Sons & Co. Ltd., London.
- HILDÉN, O. 1975. Breeding system of Temminck's stint *Calidris temminckii*. *Ornis Fenn.* **52**: 117–146.
- HILDÉN, O., and S. VUOLANTO. 1972. Breeding biology of the red-necked phalarope *Phalaropus lobatus* in Finland. *Ornis Fenn.* **49**: 57–85.
- HOBSON, W. 1972. The breeding biology of the knot (*Calidris c. canutus*) with special reference to arctic non-breeding. *Proc. West. Found. Vertebr. Zool.* **2**: 5–26.
- HÖGSTEDT, G. 1974. Length of the pre-laying period in the lapwing, *Vanellus vanellus* (L.) in relation to its food resources. *Ornis Scand.* **5**: 1–4.
- HOLMES, R. T. 1966a. Breeding ecology and annual cycle adaptations of the red-backed sandpiper (*Calidris alpina*) in northern Alaska. *Condor*, **68**: 3–46.
- 1966b. Molt cycle of the red-backed sandpiper (*Calidris alpina*) in western North America. *Auk*, **83**: 517–533.
- 1966c. Feeding ecology of the red-backed sandpiper (*Calidris alpina*) in arctic Alaska. *Ecology*, **47**: 32–45.
- 1970. Differences in population density, territoriality, and food supply of dunlin on arctic and subarctic tundra. *Symp. Br. Ecol. Soc.* **10**: 303–319.
- 1971a. Density, habitat, and the mating system of the western sandpiper (*Calidris mauri*). *Oecologia*, **7**: 191–208.
- 1971b. Latitudinal differences in the breeding and molt schedules of Alaskan red-backed sandpipers. *Condor*, **73**: 93–99.
- 1972. Ecological factors influencing the breeding season schedule of western sandpipers (*Calidris mauri*) in subarctic Alaska. *Am. Midl. Nat.* **87**: 472–491.
- HOLMES, R. T., and F. A. PITELKA. 1968. Food overlap among coexisting sandpipers on northern Alaskan tundra. *Syst. Zool.* **17**: 305–318.
- HUSSELL, D. J. T., and G. W. PAGE. 1976. Observations on the breeding biology of black-bellied plovers on Devon Island, N.W.T., Canada. *Wilson Bull.* **88**: 632–653.
- JEHL, J. R., JR. 1963. An investigation of fall-migrating dowitchers in New Jersey. *Wilson Bull.* **75**: 250–261.
- 1968. The shorebirds of North America. (Book review). *Auk*, **85**: 515–520.
- 1970. Sexual selection for size differences in two species of sandpipers. *Evolution (Lawrence, Kans.)*, **24**: 311–319.
- 1971. Patterns of hatching success in subarctic birds. *Ecology*, **52**: 169–173.
- 1973. Breeding biology and systematic relationships of the stilt sandpiper. *Wilson Bull.* **85**: 115–147.
- JEHL, J. R., JR., and D. J. T. HUSSELL. 1966. Incubation periods of some subarctic birds. *Can. Field-Nat.* **80**: 179–180.
- JEHL, J. R., JR., and B. A. SMITH. 1970. Birds of the Churchill region, Manitoba. *Manit. Mus. Man Nat. Spec. Publ. No. 1*.
- JENNI, D. A. 1974. Evolution of polyandry in birds. *Am. Zool.* **14**: 129–144.
- JENNI, D. A., R. L. REDMOND, and T. K. BICAK. 1982. Behavioral ecology and habitat relationships of long-billed curlew in western Idaho. U.S. Department of the Interior, Bureau of Land Management, Washington, DC. Report under research contract No. YA-152-CT7-54.
- KAGARISE, C. M. 1979. Breeding biology of the Wilson's phalarope in North Dakota. *Bird-Banding*, **50**: 12–22.
- KISTCHINSKI, A. A. 1975. Breeding biology and behaviour of the grey phalarope *Phalaropus fulicarius* in East Siberia. *Ibis*, **117**: 285–301.
- KISTCHINSKI, A. A., and V. E. FLINT. 1973. Materials on the biology of the dowitcher in East Siberian tundras. In *Fauna and ecology of waders*. Vol. 1. Edited by V. E. Flint. Moscow Society of Naturalists, Moscow. pp. 52–55. (Translation on file with Canadian Wildlife Service, Ottawa.)
- KOKHANOV, V. D. 1973. Materials on the biology of the Temminck's stint in Kandalaksha Bay in the White Sea. In *Fauna and ecology of waders*. Vol. 1. Edited by V. E. Flint. Moscow Society of Naturalists, Moscow. pp. 66–71. (Translation on file with the Canadian Wildlife Service, Ottawa.)
- KONDRATIEV, A. J. 1977. Stages of incubation and nest behavior in the Charadriiformes. (In Russian.) *Zool. Zh.* **56**: 1668–1675.

- KULL, R. C., JR. 1977. Color selection of nesting material by killdeer. *Auk*, **94**: 602–604.
- KUZYAKIN, A. P. 1959. The semipalmated sandpiper on the East Chukotsk Peninsula. *Ornitologia*, **2**: 111–114. (Translation on file in Josselyn van Tyne Memorial Library, University of Michigan, Ann Arbor.)
- LEONOVICH, V. V. 1973. The distribution and biology of the long-toed stint. In *Fauna and ecology of waders*. Vol. 1. Edited by V. E. Flint. Moscow Society of Naturalists, Moscow. pp. 70–81. (Translation on file with the Canadian Wildlife Service, Ottawa.)
- LIND, H. 1961. Studies on the behaviour of the black-tailed godwit (*Limosa limosa* (L.)). Munksgaard, Copenhagen.
- MACLEAN, S. F., JR. 1969. Ecological determinants of species diversity of arctic sandpipers near Barrow, Alaska. Ph.D. thesis, University of California, Berkeley, CA.
- 1974. Lemming bones as a source of calcium for arctic sandpipers (*Calidris* spp). *Ibis*, **16**: 552–557.
- 1975. Ecology of tundra invertebrates at Prudhoe Bay, Alaska. In *Ecological investigations of the tundra biome in the Prudhoe Bay region, Alaska*. Biol. Pap. Univ. Alaska Spec. Rep. 2: 115–123.
- MACLEAN, S. F., JR., and F. A. PITELKA. 1971. Seasonal patterns of abundance of tundra arthropods near Barrow. *Arctic*, **24**: 19–40.
- MCKAY, G. A., B. F. FINDLAY, and H. A. THOMPSON. 1970. A climatic perspective of tundra areas. In *Productivity and conservation in northern circumpolar lands*. Int. Union Conserv. Nat. Nat. Resour. Pub. New Ser. No. 16.
- MCLAREN, I. A. 1981. The birds of Sable Island, Nova Scotia. *Proc. N.S. Inst. Sci.* **31**: 1–84.
- MCNEIL, R. 1970. Hivernage et estivage d'oiseaux aquatiques nord-américains dans le nord-est du Venezuela (mue, accumulation de graisse, capacité de vol et routes de migration). *L'Oiseau et la Revue Française d'Ornithologie*, **40**: 185–302.
- 1972. Fat content and flight-range capabilities of some adult spring and fall migrant North American shorebirds in relation to migration routes on the Atlantic coast. *Nat. Can. (Que.)*, **99**: 589–606.
- MCNEIL, R., and J. BURTON. 1973. Dispersal of some southbound migrating North American shorebirds away from the Magdalen Islands, Gulf of St. Lawrence, and Sable Island, Nova Scotia. Preliminary report for 1969, 1970 and 1971. *Caribb. J. Sci.* **13**: 257–278.
- 1977. Southbound migration of shorebirds from the Gulf of St. Lawrence. *Wilson Bull.* **89**: 167–171.
- MCNEIL, R., and F. CADIEUX. 1972. Fat content and flight-range capabilities of some adult spring and fall migrant North American shorebirds in relation to migration routes on the Atlantic coast. *Nat. Can. (Que.)*, **99**: 589–606.
- MACOUN, J., and J. M. MACOUN. 1909. *Catalogue of Canadian birds*. Canada Department of Mines, Geological Survey Branch. Government Printing Bureau, Ottawa.
- MAXSON, S. J., and L. W. ORING. 1980. Breeding season time and energy budgets of the polyandrous spotted sandpiper. *Behaviour*, **74**: 200–263.
- MAYFIELD, H. 1961. Nesting success calculated from exposure. *Wilson Bull.* **73**: 255–261.
- MILLER, E. H. 1977. Breeding biology of the Least Sandpiper, *Calidris minutilla* (Vieill.), on Sable Island, Nova Scotia. Ph.D. thesis, Dalhousie University, Halifax, N.S.
- 1979a. Functions of display flights by males of the least sandpiper, *Calidris minutilla* (Vieill.), on Sable Island, Nova Scotia. *Can. J. Zool.* **57**: 876–893.
- 1979b. Egg size in the least sandpiper (*Calidris minutilla*) on Sable Island, Nova Scotia, Canada. *Ornis Scand.* **10**: 10–16.
- 1983. Structure of display flights in the least sandpiper. *Condor*, **85**: 220–242.
- MILLER, J. R., and J. T. MILLER. 1948. Nesting of the spotted sandpiper at Detroit, Michigan. *Auk*, **65**: 558–567.
- MOORE, R. T. 1912. The least sandpiper during the nesting season in the Magdalen Islands. *Auk*, **29**: 210–223.
- MORTON, E. S. 1976. The adaptive significance of dull coloration in yellow warblers. *Condor*, **78**: 423.
- MYERS, J. P. 1981a. Cross-seasonal interactions in the evolution of sandpiper social systems. *Behav. Ecol. Sociobiol.* **8**: 195–202.
- 1981b. A test of three hypotheses for latitudinal segregation of the sexes in wintering birds. *Can. J. Zool.* **59**: 1527–1534.
- MYERS, J. P., and F. A. PITELKA. 1979. Variations in summer temperature patterns near Barrow, Alaska: analysis and ecological interpretation. *Arct. Alp. Res.* **11**: 131–144.
- NETHERSOLE-THOMPSON, D. 1951. *The greenshank*. William Collins, Sons & Co. Ltd., London.
- 1973. *The dotterel*. William Collins, Sons & Co. Ltd., London.
- NETHERSOLE-THOMPSON, D., and M. NETHERSOLE-THOMPSON. 1979. *Greenshanks*. T. and A. D. Poyser, Berkhamsted.
- NETTLESHIP, D. N. 1973. Breeding ecology of turnstones *Arenaria interpres* at Hazen Camp, Ellesmere Island, N.W.T. *Ibis*, **115**: 202–217.
- 1974. The breeding of the knot *Calidris canutus* at Hazen Camp, Ellesmere Island, N.W.T. *Polarforschung*, **44**: 8–26.
- NISBET, I. C. T. 1957. Wader migration at Cambridge sewage farm. *Bird Study*, **4**: 131–148.
- NORTON, D. W. 1970. Thermal regime of nests and bioenergetics of chick growth in the dunlin (*Calidris alpina*) at Barrow, Alaska. M.S. thesis, University of Alaska, Fairbanks.
- 1972. Incubation schedules of four species of calidridine sandpipers at Barrow, Alaska. *Condor*, **74**: 164–176.
- 1973. Ecological energetics of calidridine sandpipers breeding in northern Alaska. Ph.D. thesis, University of Alaska, Fairbanks.
- NORTON, D. W., I. W. AILES, and J. A. CURATOLO. 1975. Ecological relationships of the inland tundra avifauna near Prudhoe Bay, Alaska. In *Ecological investigations of the tundra biome in the Prudhoe Bay region, Alaska*. Biol. Pap. Univ. Alaska Spec. Rep. 2: 125–133.
- ORING, L. W., and M. L. KNUDSON. 1972. Monogamy and polyandry in the spotted sandpiper. *Living Bird*, **11**: 59–73.
- ORING, L. W., and D. B. LANK. 1982. Sexual selection,

- arrival times, philopatry and site fidelity in the polyandrous spotted sandpiper. *Behav. Ecol. Sociobiol.* **10**: 185–191.
- PAGE, G. 1974a. Molt of wintering least sandpipers. *Bird-Banding*, **45**: 93–105.
- 1974b. Age, sex, molt and migration of dunlins at Bolinas Lagoon. *Western Birds*, **5**: 1–12.
- PAGE, G., and M. BRADSTREET. 1968. Size and composition of a fall population of least and semipalmated sandpipers at Long Point, Ontario. *Bird-Banding*, **4**: 82–88.
- PAGE, G., B. FEARIS, and R. M. JUREK. 1972. Age and sex composition of western sandpipers on Bolinas Lagoon. *Calif. Birds*, **3**: 79–86.
- PARMELEE, D. F. 1970. Breeding behavior of the sanderling in the Canadian high arctic. *Living Bird*, **9**: 97–146.
- PARMELEE, D. F., D. W. GREINER, and W. D. GRAUL. 1968. Summer schedule and breeding biology of the white-rumped sandpiper in the central Canadian arctic. *Wilson Bull.* **80**: 5–29.
- PARMELEE, D. F., and S. D. MACDONALD. 1960. The birds of west-central Ellesmere Island and adjacent areas. *Bull. Natl. Mus. Can.* No. 169.
- PARMELEE, D. F., H. A. STEPHENS, and R. H. SCHMIDT. 1967. The birds of southeastern Victoria Island and adjacent small islands. *Bull. Natl. Mus. Can.* No. 222.
- PARR, R. 1980. Population study of golden plover *Pluvialis apricaria*, using marked birds. *Ornis Scand.* **11**: 179–189.
- PAULSON, D. R. 1983. Fledging dates and southward migration of juveniles of some *Calidris* sandpipers. *Condor*, **85**: 99–101.
- PHILIPP, P. B. 1925. Notes on some summer birds of the Magdalen Islands. *Can. Field-Nat.* **39**: 75–78.
- PIENKOWSKI, M. W., and G. H. GREEN. 1976. Breeding biology of sanderlings in north-east Greenland. *Br. Birds*, **69**: 165–177.
- PITELKA, F. A. 1959. Numbers, breeding schedule, and territoriality in pectoral sandpipers of northern Alaska. *Condor*, **61**: 233–264.
- PITELKA, F. A., R. T. HOLMES, and S. F. MACLEAN, JR. 1974. Ecology and evolution of social organization in arctic sandpipers. *Am. Zool.* **14**: 185–204.
- PORTENKO, L. A. 1972. Birds of the Chukotskii Peninsula and Wrangel Island. Part 1. Nauka, Leningrad. (Translation on file with the Canadian Wildlife Service, Ottawa.)
- PULLIAINEN, E. 1978. Influence of heavy snowfall in June 1977 on the life of birds in NE Finnish forest Lapland. *Aquilo Ser. Zool.* **18**: 1–14.
- PURDUE, J. R. 1976. Thermal environment of the nest and related parental behavior in snowy plovers *Charadrius alexandrinus*. *Condor*, **78**: 180–185.
- RAHN, H., R. A. ACKERMAN, and C. V. PAGANELLI. 1977. Humidity in the avian nest and egg water loss during incubation. *Physiol. Zool.* **50**: 269–283.
- RATCLIFFE, D. A. 1976. Observations on the breeding of the golden plover in Great Britain. *Bird Study*, **23**: 63–116.
- RICKLEFS, R. E. 1969. An analysis of nesting mortality in birds. *Smithson. Contrib. Zool.* No. 9.
- ROLAND, A. E., and E. C. SMITH. 1969. The flora of Nova Scotia. Parts I and II. *Proc. Trans. N.S. Inst. Sci.* **26**: 3–238 and 277–743.
- RUBINSTEIN, N. A. 1973. Comparative studies on the behavior of certain wader species during the incubation period. *In* *Fauna and ecology of waders*. Vol. 1. Edited by V. E. Flint. Moscow Society of Naturalists, Moscow. pp. 134–137. (Translation on file with the Canadian Wildlife Service, Ottawa.)
- SAFRIEL, U. N. 1975. On the significance of clutch size in nidifugous birds. *Ecology*, **56**: 703–708.
- SCHAMEL, D., and D. TRACY. 1977. Polyandry, replacement clutches, and site tenacity in the red phalarope (*Phalaropus fulicarius*) at Barrow, Alaska. *Bird Banding*, **48**: 314–324.
- SCHNEIDER, D. C., and B. A. HARRINGTON. 1981. Timing of shorebird migration in relation to prey depletion. *Auk*, **98**: 801–811.
- SHEPARD, J. M. 1975. Factors influencing female choice in the lek mating system of the ruff. *Living Bird*, **14**: 87–111.
- SKEEL, M. A. 1976. Nesting strategies and other aspects of the breeding biology of the Whimbrel (*Numenius phaeopus*) at Churchill, Manitoba. M.Sc. thesis, University of Toronto, Toronto.
- 1983. Nesting success, density, philopatry, and nest-site selection of the Whimbrel (*Numenius phaeopus*) in different habitats. *Can. J. Zool.* **61**: 218–225.
- SOIKKELI, M. 1966. On the variation in bill- and wing-length of the Dunlin (*Calidris alpina*) in Europe. *Bird Study*, **13**: 256–269.
- 1967. Breeding cycle and population dynamics in the dunlin (*Calidris alpina*). *Ann. Zool. Fenn.* **4**: 158–198.
- SUTTON, G. M. 1961. American stint or least sandpiper *Calidris minutilla* (Vieillot). Life history. *In* *The birds of the British Isles*. Vol. 9. Edited by D. A. Bannerman. Oliver and Boyd, Edinburgh. pp. 272–279.
- THOMAS, D. G. 1969. Breeding biology of the Australian spur-winged plover. *Emu*, **69**: 81–102.
- TODD, W. E. C. 1963. The birds of the Labrador Peninsula and adjacent areas. A distributional list. University of Toronto Press, Toronto.
- TOWNSEND, C. W. 1927. *Pisobia minutilla* (Vieillot). Least sandpiper. Habits. *In* *Life histories of North American shore birds*. Order Limicolae. Part 1. Edited by A. C. Bent. U.S. Government Printing Office, Washington, DC. pp. 202–209.
- VÄISÄNEN, R. A. 1977. Geographic variation in timing of breeding and egg size in eight European species of waders. *Ann. Zool. Fenn.* **14**: 1–25.
- VAN RHJN, J. G. 1973. Behavioural dimorphism in male ruffs, *Philomachus pugnax* (L.). *Behaviour*, **47**: 153–229.
- WEST, G. C., and D. W. NORTON. 1975. Metabolic adaptations of tundra birds. *In* *Physiological adaptations to the environment*. Edited by F. J. Vernberg. Intext Press, New York. pp. 301–329.
- WILLIAMSON, F. S. L., M. C. THOMPSON, and J. Q. HINES. 1966. Avifaunal investigations. *In* *Environment of the Cape Thompson region, Alaska*. Edited by N. J. Wilimovsky and J. N. Wolfe. U.S. Atomic Energy Commission, Oak Ridge, TN. pp. 437–480.
- WILLIAMSON, K. 1946. Field-notes on the breeding-biology of the whimbrel, *Numenius phaeopus phaeopus* (Linnaeus). *Northwest Nat.* **21**: 167–184.
- YARBROUGH, C. G. 1970. Summer lipid levels of some subarctic birds. *Auk*, **87**: 100–110.