Parental behavior in the Least Sandpiper (*Calidris minutilla*)

EDWARD H. MILLER

Vertebrate Zoology Division, British Columbia Provincial Museum, Victoria, B.C., Canada V8V 1X4[1]

and

Biology Department, University of Victoria, Victoria, B.C., Canada V8W 2Y2

Received November 2, 1984

MILLER, E. H. 1985. Parental behavior in the Least Sandpiper (*Calidris minutilla*). Can. J. Zool. **63**: 1593–1601.

Breeding Least Sandpipers were studied in Nova Scotia (1975–1976), Manitoba (1978), Yukon Territory (1979), and British Columbia (1982–1984). The most detailed study was on Sable Island, Nova Scotia, which is near the southern limit of the breeding range. The nesting period there was relatively long, and the species was strictly monogamous. Males tended to incubate during daylight hours and females, at night. There was a weak (insignificant) trend for males to increase their role in incubation as it progressed. Shortly after hatching, broods moved to undefended foraging areas, where they tended to remain throughout the period of parental attendance. Chicks could fly strongly by 14–16 days of age but were attended by parents for longer: females attended broods for 0–22 days (average 6) after hatching and males for 14–27 (average 20). After their parents left, chicks slowly drifted away from where they had been reared. Diversionary behavior of incubating birds, and of parents attending young chicks, was similar in all study areas. "Alarm" behavior and vocalizations of parents were also very similar in all localities and included four types of calls during brooding and undisturbed attendance and two types when disturbed by humans.

MILLER, E. H. 1985. Parental behavior in the Least Sandpiper (*Calidris minutilla*). Can. J. Zool. **63**: 1593–1601.

La reproduction a fait l'objet d'une étude chez diverses populations du bécasseau minuscule: en Nouvelle-Ecosse (1975–1976), au Manitoba (1978), dans le Yukon (1979) et en Colombie-Britannique (1982–1984). C'est dans l'Ile Sable, Nouvelle-Ecosse, à la limite sud du territoire de reproduction, qu'a été entreprise l'étude la plus détaillée. La période de nidification à cet endroit est relativement longue et l'espèce y est strictement monogame. Les mâles ont tendance à couver durant le jour et les femelles, la nuit. Les mâles ont aussi tendance (bien qu'elle ne soit pas significative) à augmenter leur participation à l'incubation à mesure qu'elle progresse. Les portées se déplacent vers des aires de recherche de nourriture non défendues peu après l'éclosion et tendent à y rester durant toute la période de protection parentale. Les oisillons peuvent voler très bien au bout de 14–16 jours, mais les parents continuent de s'en occuper encore: les femelles donnent des soins à leurs portées pour une période de 0–22 jours (en moyenne 6 jours) après l'éclosion, et les mâles pour une période de 14–27 jours (moyenne 20 jours). Après le départ des parents, les oisillons s'éloignent petit à petit de l'endroit où ils ont été élevés. Les comportements de diversion utilisés par les parents couveurs et par les parents avec des petits sont semblables dans toutes les régions d'étude. Les comportements "d'alerte" et les chants sont aussi très semblables chez les parents de tous les endroits: on y retrouve quatre types d'appels au cours de l'incubation et au cours des soins aux petits, et deux types lorsque les oiseaux sont dérangés par une présence humaine.

[Traduit par le journal]

Introduction

Shorebirds have provided significant insights into the evolution of avian parental behavior and mating systems (reviews by Erckmann 1983; Oring 1982; Oring and Lank 1984; Pitelka et al. 1974; Walters 1980, 1982, 1984; Winkler and Walters 1983). Within the Scolopacidae (sandpipers and their kin) parental roles vary greatly across species: parents may incubate and care for a separate clutch and brood each; parental responsibilities may be shared for a single clutch and brood; either the male or female may take sole responsibility, depending on the kind of mating system; or parents may split single broods and each care for one to several chicks (this remains poorly documented). Adequate documentation of the characteristics and adaptive radiation of parental behavior in Scolopacidae demands field studies using individually marked birds, and I present the results of such a study here.

The Least Sandpiper (*Calidris minutilla*) is a member of the Calidridini (24 species), a group whose breeding range encompasses arctic and subarctic areas (nomenclature follows Gochfeld et al. 1984). This species is endemic to North America, where it breeds from Alaska to Newfoundland and south as far as Nova Scotia (Sable Island, Cape Sable Island, parts of the mainland) and Massachusetts (Anderson 1980;

Godfrey 1966; McLaren 1981). It is monogamous throughout this range, but its breeding cycle is longer on Sable Island (and presumably in other southern parts of the range) than elsewhere (Miller 1983a). The purposes of this paper are to describe the relative participation of males and females in incubation and brood rearing, plus general features of brood movements and fledging, and diversionary and "alarm" behavior of parents. Other information about the breeding cycle, male display behavior, and eggs is available elsewhere (Miller 1979a, 1979b, 1983a, 1983b, 1984).

Methods

Fieldwork was carried out on Sable Island, N.S., from May through July 1975 and May through August 1976. I located 62 nests and banded 210 birds, consisting of 122 chicks and fledglings and 88 adults (40 males, 42 females, and 6 of unknown sex). Most birds were caught with a simple drop trap while they incubated. Sex was judged mainly from culmen length (usually greater in females) but was sometimes known from prior behavioral observations or corroborated by subsequent ones (e.g., courtship, display flights, and aggressive chases by males).

I checked nests regularly (usually at least once daily) but not randomly. Most off-nest sightings of birds referred to below were made during daily walks along a fixed route; sightings of birds judged to be off their nests because of my presence were excluded. I tried to locate broods daily, and this was facilitated by the conspicuous "alarm" behavior of parent birds.
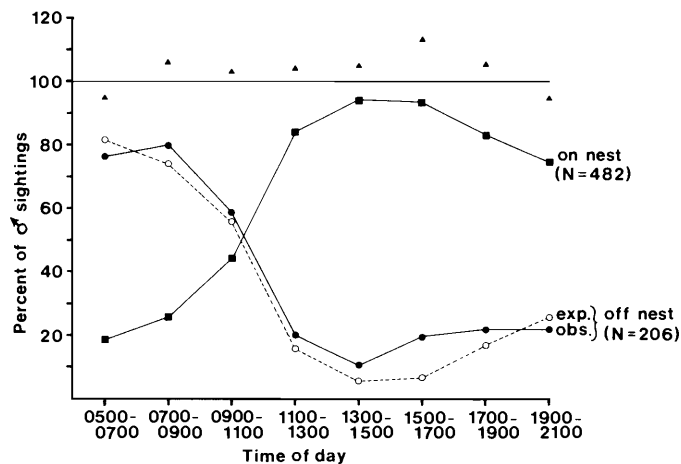
---

[1]Address for all correspondence.

FIG. 1. Relationship of the percent of sightings of individually known males incubating or foraging to time of day. In theory, the curves are complementary and should sum to 100% (horizontal line above). The actual summed values are shown as triangles around this value. Also shown is the expected curve for sightings of males off their nests and foraging; this was obtained by subtracting each "on-nest" figure from 100%. exp., expected; obs., observed.

General observations on the species were also made east of Churchill, Manitoba (May to June 1978), and in the Blackstone River Valley, Ogilvie Mountains, Yukon Territory (May 1979). Fieldwork in British Columbia took place along the Haines Road connecting Haines, Alaska, and Haines Junction, Yukon Territory, June 1982, and May and June 1983, and in the Delkatla Wildlife Sanctuary at Masset, Queen Charlotte Islands, June 1984. The latter location represents a substantial extension of the breeding range for the species; it was discovered nesting there in 1983 by Rev. Peter Hamel. Some tape recordings were made from observation hides near nests around the time of hatching. Others were made during routine activities and observations. Tape recording equipment used on Sable Island was a Uher Stereo Report IC tape recorder, with dynamic microphone (mounted in a Dan Gibson parabola 45 cm in diameter), and Scotch 176 tape, and in British Columbia was a Nagra IS tape recorder, Sennheiser MKH816 "shotgun" microphone with wind sock, and Scotch 208 tape. Sound spectrograms were prepared on a Kay Elemetrics Sona-Graph 7029A.

Results

Incubation rhythms and roles of the sexes

Least Sandpipers gradually increased the percentage of time spent on the nest, from about 27% for one-egg clutches to nearly 100% for definitive (usually four-egg) clutches (Miller 1983a). I estimated the proportions of time spent incubating by paired birds only for definitive clutches. There was a strong diel rhythm in incubation, according to a bird's sex (Fig. 1). Males assumed an increasing role in incubation as the day progressed. They were identified in about 18% of the nest checks in early morning (0500–0700) but in more than 80% of those from 1100 to 1900, by which time a decline was evident (Fig. 1). Data on birds that were known to. have definitive clutches and that were identified off their nests accord well with those on the identity of incubating birds (Fig. 1). To check for biases in the identification of the sex of nonincubating birds, I summed the curves for on- and off-nest sightings. The resulting figures averaged about 105%, slightly above the expected value of 100%, indicating that males off their nests were slightly easier to identify than were females. This agrees with my impression that males were less nervous and more approachable than females. Pairs varied in their times of

TABLE 1. Relationship of incubation attendance by males to stage of incubation

	Days after clutch completion		
	1–10	11+	P^a
% males on nest[b]	58.6	66.6	0.053
N	187	193	
% males off nest[c]	44.9	33.6	0.066
N	74	100	
Sum, %	103.5	100.2	

"One-tailed estimate, for test of the hypothesis that males take a greater role in incubation as it proceeds. P estimates are based on a t-test for the equality of two percentages.

[b]The times of day when I checked nests differed little in the two halves of incubation.

[c]Listed values are the mean corrected percentages, weighted by sample sizes for the years of study. Corrected percentages for each year were obtained by multiplying the figure (percent males in off-nest sightings) by the quotient (number of banded breeding females per number of banded breeding males).

changeover at the nest, but my data are not extensive enough to analyze this variation.

Some authors have suggested that males of monogamous species of scolopacids may increase their share of incubation as it proceeds. Data on Least Sandpipers weakly support this impression: in the first half of incubation males constituted 45% of off-nest sightings and 59% of the sample of incubating birds. These figures compare with 34 and 67%, respectively, in the second half of incubation (Table 1). Since females incubated mainly at night and in the early morning, when I made relatively few nest checks, this trend may have been greatly underestimated. Late in the season a few females apparently stopped incubating altogether a day or so before their clutches hatched and left the males alone in charge of the hatching eggs and brood. Soikkeli (1967) made a similar observation on Dunlin (*Calidris alpina*).

Brood attendance and fledging

Hatching behavior and the exodus of broods from the nest are described elsewhere (Miller 1983a). Most nests were situated at some distance from where broods were reared, a widespread characteristic of shorebirds (Miller 1979a). Some examples of brood movements after hatching and the relationship of nest site to the area where a brood was reared are summarized in Fig. 2. Broods were usually sedentary once they arrived in a favorable area, but some parents moved their broods a few times. One pair started to lead their brood overland from one pond to another because I was observing them. When I moved to the new area, they led the brood back to the original pond and remained there until fledging. Brood-rearing areas (BRAs) were not defended by parents, but foreign adults very close to young chicks were occasionally rushed by a parent. Both parents attended the young in the brood-rearing area; I encountered parents elsewhere very rarely.

The age at which chicks can fly strongly enough to escape from terrestrial predators and the age at which they are abandoned by their parents reflect different components of maturation and fledging. I estimate the age of first strong flight as 14 to 16 days; J. R. Jehl, Jr. (personal communication), made a similar estimate for the species in northern Manitoba. One 14-day-old chick that flew strongly away from me simply crouched when I reapproached it and allowed me to pick it
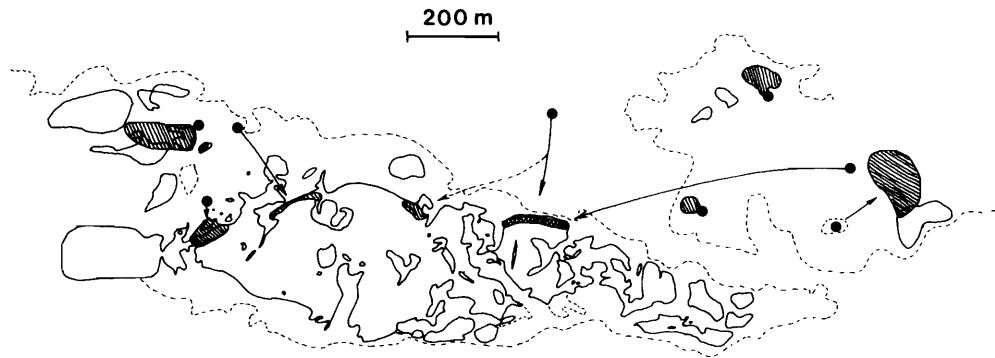
200 m

FIG. 2. Examples of movements of broods from nest sites to brood-rearing areas. The brood from the nest in the central part of the map changed locations after about 5 days, as shown. The three broods in the right part of the map were raised in dry areas; of these the brood closest to the right only moved to the pond margin, as indicated, in the last few days before their father left them. Solid lines are outlines of ponds and islands; broken lines delimit areas of consolidated vegetation (see Miller 1983a). Distance marker, 200 m.

up. One brood was abandoned on the 14th day after hatching, but none earlier; this occurred late in one summer (23 July). Females almost always abandoned the brood first (6 vs. 20 days, on average (Table 2)). One male left before his mate, but he stayed 14 days. Chicks were brooded by both parents for at least several days after leaving the nest. The main parental duties were to brood, to warn of danger (primarily potential predators), and by parental presence and active leading, to maintain the brood together in an area good for feeding and safe from predators. Parents could alert their chicks by alarm calls even when they did not know exactly where the chicks were. Young chicks crouched when their parents called in alarm and remained crouched even when I picked them up. The crouching response declined with age, and older chicks ran into concealing vegetation and continuously moved away from me. Parental behavior toward the brood changed accordingly. Parents with young chicks flew about the intruder, calling loudly, and relied upon the chicks' crypticity for protection, though occasionally they hovered low over the brood and looked below them (identical behavior has been described for Wilson's Phalarope, *Phalaropus tricolor* (Howe 1972)). When chicks were older and more dispersed, adults tended to follow the intruder around while calling incessantly. In the last few days of brood attendance a different kind of parental behavior appeared, coincident with an increased tendency of chicks to remain in the open when I approached. Now parents sometimes landed beside their chick and flew up quickly at my further approach; this often excited the chick into flight. One concerned male swooped on his near-fledgling several times as I approached and finally almost landed on top of it to prompt it to fly away from me.

The age at which I first encountered and identified chicks can be taken as a measure of their behavioral maturity. There was a strong correlation between the duration of parental care and the age of chicks when I first saw them ($r = 0.523$, df $= 27$, $P < 0.01$). This includes records of chicks first identified on or after the last day of attendance by parents. If chick growth and behavior (aside from that involved in active dispersal) affect the duration of parental care, only data for chicks sighted *before* the end of parental care can be used. For such data, there is a significant positive regression of duration of parental care upon age of chick at first sighting ($r = 0.860$, df $= 12$, $P < 0.01$). This suggests that the end of parental care was strongly influenced by chick behavioral maturity, as distinct from chick age as such.

Fledglings gradually moved away from areas where they

TABLE 2. Duration of parental attendance for broods from at which at least one chick fledged. Records of two females (76-X1, 76-X2) whose broods perished after the females had left them in the care of the male are also included

Nest No.	Duration of brood attendance, days			Date of leaving nest
	Males (A)	Females (B)	A − B	
75-01	14	22	−8	18 June
75-03	21	9	+12	20 June
75-05	21	5	+16	24 June
75-11	23	7	+16	26 June
75-14	21	8	+13	27 June
75-18	—	4	—	5 July
75-19	19	3	+16	25 June
75-27	—	0	—	12 July
76-05	27	13	+14	21 June
76-07	18	0	+18	24 June
76-08	19	9	+10	20 June
76-13[a]	18	1	+17	1 July
76-16	19	0	+19	2 July
76-17	21	0	+21	7 July
76-21	20	4	+16	29 June
76-32	14	3	+11	9 July
76-Z	23	—	—	19 June
76-X1	—	7	—	1 July
76-X2	—	7	—	14 June
$\bar{Y}$	19.9	5.7	12.7	
SE	0.86	1.31	2.02	
N	15	18	14	

[a]Renesting.

were reared. This is apparent from Fig. 3, in which sighting records of fledglings are plotted as distances from areas in which they were reared, against fledgling age. Fledglings aged between 17 and 20 days stayed quite close to where they were reared, and only fledglings older than about 4 weeks regularly were found very far from those areas. One exceptionally sedentary fledgling (marked with an asterisk in Fig. 3) stayed where he had been reared until 8 weeks of age at least (sightings by H. Ross, personal communication).

Parents remained in the brood-rearing area until abandoning the brood, but they did not defend the area and only exhibited local defence of space toward conspecifics in the immediate
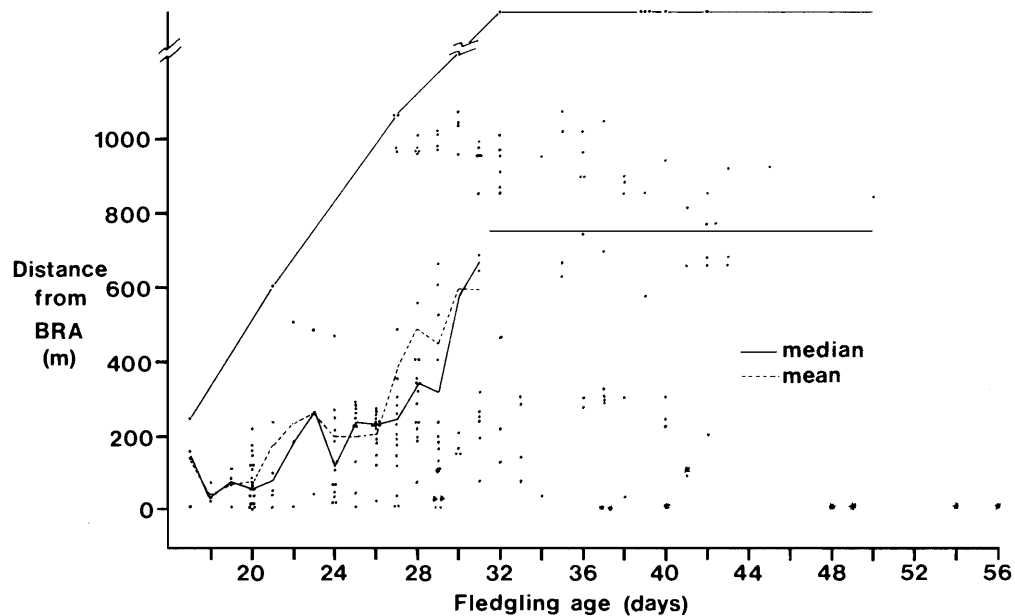
FIG. 3. Movements of chicks away from their brood-rearing areas (BRAs) after being abandoned. The uppermost line joins maximal distances moved at each age. The lower solid lines indicate (*i*), to the left, daily mean distance and (*ii*), to the right, the overall mean distance for fledglings aged 32 days or more. The mean daily distances for birds younger than 32 days are joined by the broken line. The asterisks represent records for one very sedentary bird (see text). Birds seen in their BRAs were assigned a distance of 0; those seen outside them were judged to have moved the distance between where they were seen and the nearest part of their BRA. The six sightings at the top of the diagram were several kilometres from BRAs.

area of chicks, by chasing foreign adults away. Such aggression was weakly developed and variable. Indeed, I saw one foreign adult land by a brood leaving the nest and peck one chick several times while the attending adult looked on; only after a minute or so did the confused parent give chase.

Acoustic signals of parents with chicks on the nest

During hatching and while attending broods on the nest, parents of both sexes vocalized frequently. Four distinct call types were used: (*i*) cluck; (*ii*) compound cluck; (*iii*) trill; and (*iv*) song. Clucking was one of the two commonest call types and varied from single brief, soft elements, emitted irregularly but at fairly brief intervals, to longer, louder ones occurring rhythmically in rapid succession (Figs. 4A–4C; Fig. 17E of Miller 1984). The duration of individual elements varied greatly even within individuals. Clucking typically occurred as parents adjusted themselves on the nest, as they half crouched over the nest, or while chicks were active beneath them. Clucking often merged into sequences of loud compound clucking (Figs. 4D and 4E) which in turn often reverted to clucking, or led into song (Figs. 5B and C1). The behavioral significance of compound clucking is not clear.

Trills were temporally distinct bouts of brief elements which were emitted rapidly and rhythmically and which sometimes introduced song (Fig. 5A; Fig. 17E of Miller 1984). They were the other most frequently used kind of call. Trills were uttered as parents sat quietly brooding and also seemed to be used to rally the chicks to be brooded. The latter function was also prominent for at least several days after broods left the nest.

Song is a loud, complex vocalization used by males in agonistic and sexual contexts (Miller 1983b). In the context of brooding, male song was much softer and briefer and had fewer terminal elements (frequency- and amplitude-modulated elements (see Miller 1983b)). Brooding song of females was also soft and was much more variable and simple than that of

males (Figs. 5A–5C). Song was usually uttered by adults that seemed to be very agitated or excited by chick activity, e.g., in response to chicks leaving the nest cup to walk around nearby; at such times the adult sometimes rose and stood at the edge of the nest cup, emitting song or trills. Several adults led their brood away from the nest with trills and occasional song, but brooding song was never heard after that.

Diversionary and "alarm" behavior of parents

Most incubating birds remained on the nest until I was within a few metres, then engaged in distraction displays. Such displays have been described and discussed extensively for the Calidridini and will not be described further here (see Cramp 1983; Gochfeld 1984).

Birds in distraction displays always vocalized. Vocalizations given early in distraction sequences varied greatly in structure and usually included noisy components. Later in a sequence calls became less noisy and more uniform and were uttered more rhythmically. Both sexes engaged in distraction behavior, and it did not show any obvious geographic variation. Distraction behavior could always be evoked from incubating birds between clutch completion to within a few days after hatching. It was uncommon earlier or later but could be evoked in certain circumstances, e.g., by capturing and holding a chick in the hand (J. R. Jehl, Jr. (personal communication), has evoked distraction behavior from males with incomplete clutches, in northern Manitoba). The variability and complex spectral structure of distraction calls preclude their treatment here; I will treat this subject elsewhere.

Occasionally, incubating birds that detected my approach walked away from the nest well before I arrived; some individuals became accustomed to my frequent nest checks and did this routinely. At such times, they flew or walked toward me, watched me silently from a distance, or attended me silently, often mock feeding. Rarely, they uttered "alarm" calls, de-
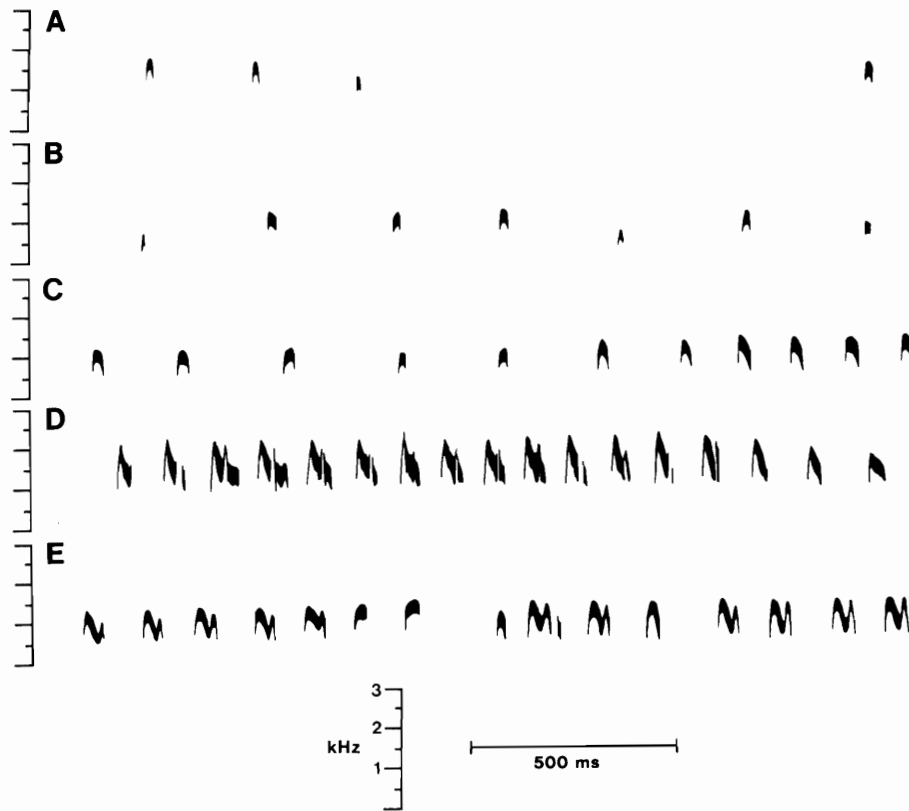
FIG. 4. Clucks and compound clucks. (A, B, C) Sequences of clucking from three different birds. In C, note the transition from the brief fourth and fifth clucks to the more rapid series of louder, longer, higher frequency ones. (D) Sequence of compound clucking. (E) Sequence of compound clucking with a few single clucks. These are ink tracings of the fundamental frequency; analyzing filter bandwidth, 300 Hz.
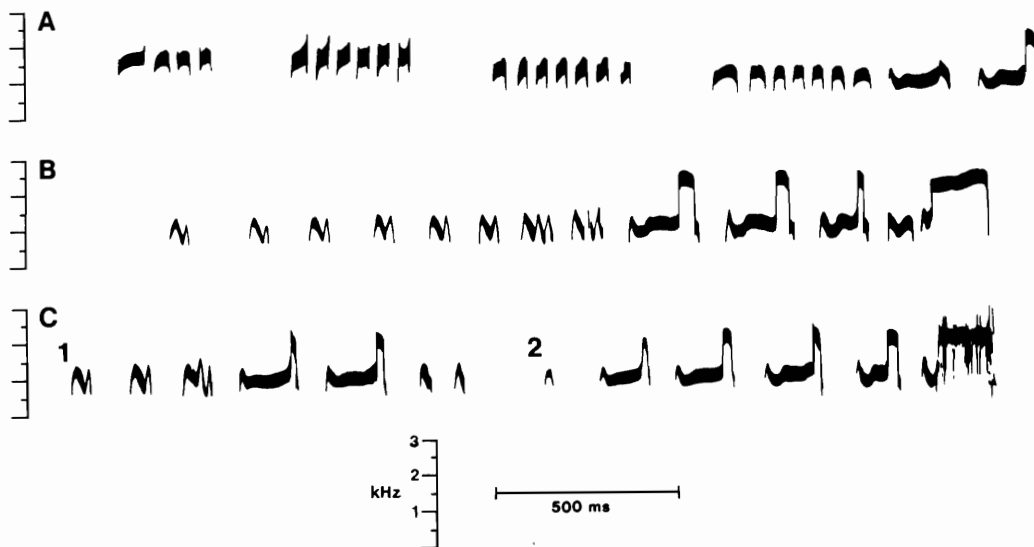

FIG. 5. Brooding trills, compound clucks, and brooding song. (A) Four examples of brooding trills, the first two by the same bird, the fourth leading into brooding song by a female. (B) Compound clucking leading into brooding song (same female as in A). (C1) Compound clucking (partial sequence) leading into brooding song (two elements) then two single clucks (same female as in A). (C2) Single cluck leading into brooding song (same female as in A). These are ink tracings of the fundamental frequency; analyzing filter bandwidth, 300 Hz.

scribed below. Off-duty birds sometimes reacted to their mate's distraction or "alarm" behavior by approaching me and behaving similarly. However, birds typically fed far from their nest sites, so this was unusual except around the time of hatching or after hatching. At other times, off-duty birds detected me in the area of their nest and expressed "alarm" even though their mate remained incubating.

In latter stages of incubation and throughout brood attendance, parents approached me and called loudly in flight or on the ground. Two types of "alarm" calls were given, with some intermediate in structure. The first of these (type I) was a loud, brief call with slow rhythmic modulation of the carrier frequency (Fig. 6A; Fig. 8K of Miller 1984). The second (type II) was a trill composed of a series of similar elements, which
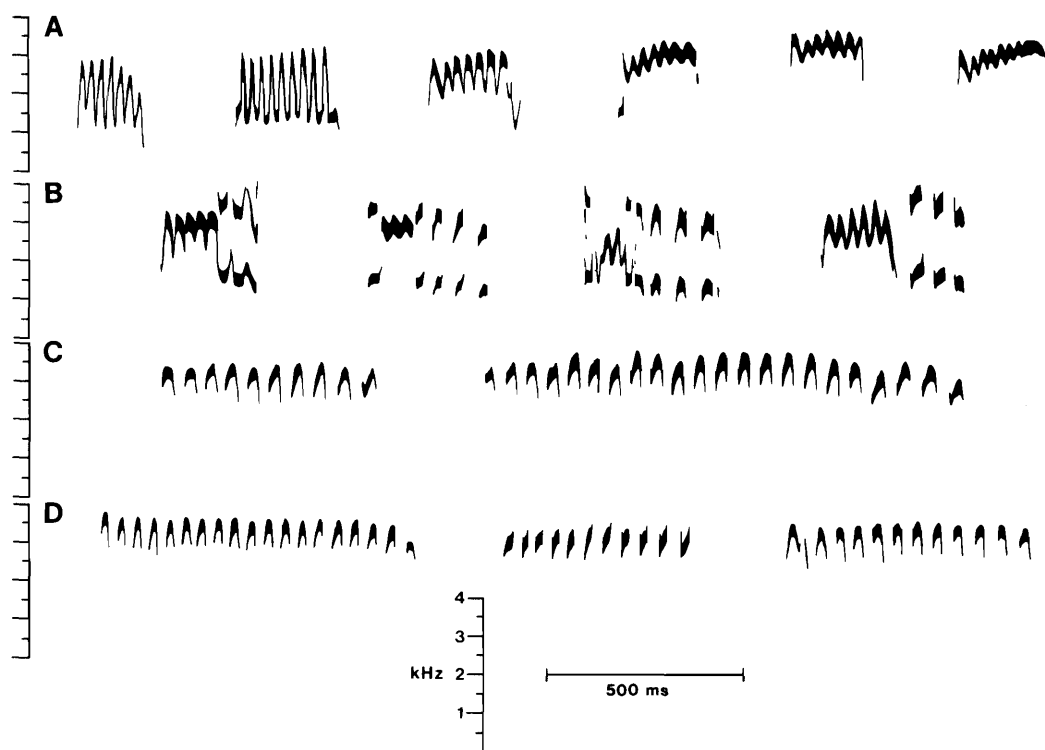
FIG. 6. "Alarm" calls. (A) Six examples of frequency-modulated (type I) calls from different birds. (B) Four examples of calls intermediate between types I and II. (C) Type II calls by a bird in flight and on the ground; the second illustrates the greater duration and more variable frequency that typify ground calls. (D) Three examples of trills (type II calls) from different birds. These are ink tracings. Type I calls have almost all energy in the fundamental frequency, as depicted in A and appropriate parts of B. Type II calls have most energy in the fundamental's first harmonic overtone, and only this is depicted in parts C and D. The type II parts of B also have the fundamental depicted, to show the relationships between the two components. Analyzing filter bandwidth, 300 Hz.

showed sequential grading in duration, amplitude, and frequency (Figs. 6C and 6D; Fig. 8K of Miller 1984). These calls were brief and stereotyped at high intensity, e.g., by a bird flying around me; they were longer and more variable at lower intensity (e.g., by a bird on the ground) (Figs. 6C and 6D). Almost all calls of intermediate structure began with type I then switched to type II (Fig. 6B). Type I calls were indicative of greater "alarm" than type II; thus around the time of hatching, when parents were extremely watchful and responsive, type I calls were commonest. They were also given more often in flight than on the ground and more often in flight toward or around me than in flight away. Individual birds differed in the relative use of the two call types, with some favoring one or the other to an unusual extreme. Even so, such individuals conformed to the general trends just outlined.

I could not distinguish calls uttered in the presence of avian predators (Herring Gulls, Larus argentatus) from those given in my presence, but taped none in the former context. Differences could exist; Walters (1984) noted a difference in alarm calls by Southern Lapwings (Vanellus chilensis) toward reptilian and avian–mammalian predators.

Discussion

Incubation rhythms and roles of the sexes

Female Least Sandpipers on Sable Island incubated from late evening to early morning or midmorning, and males predominated in daytime incubation. This is also true for this species in northern Manitoba (Jehl 1971, 1973; Yarbrough 1970) and for several other monogamous, single-clutched species of cali-

dridines (Jehl 1973; Parmelee et al. 1968; Soikkeli 1967, 1974). Female Western Sandpipers (Calidris mauri) incubate "from late afternoon through mid morning, males during the remainder of the day" (Holmes 1971 p. 203, 1973). For Dunlin in Alaska and Manitoba this general pattern persists weakly if at all (Jehl 1973; Norton 1972), and it is also ill defined for Semipalmated (Calidris pusilla) and Baird's Sandpipers (C. bairdii) on Jenny Lind Island (Parmelee et al. 1968). Drury (1961) seems to imply that one male Baird's Sandpiper incubated more often during the day than did his mate, and Blair (1961 p. 269) reported that accounts of the Little Stint (Calidris minuta) "all stress a preponderance of males amongst the birds found covering the eggs"; this may just reflect a preponderance of daytime collecting (this is hard to reconcile with the species' practice of successive bigamy, however; Cramp 1983). This probably also applies to Austin's (1932) mention that male Least Sandpipers seem to be largely responsible for incubation, and to Flint's (1973) similar conclusion for the Broad-billed Sandpiper (Limicola falcinellus). A detailed study of incubation behavior in Semipalmated Sandpipers in Alaska revealed a variable pattern of shared incubation, with longer stints as incubation progressed (Ashkenazie and Safriel 1979).

Sharing of incubation by pair members typifies monogamous species of scolopacids which have a single clutch. Male Least Sandpipers may assume a greater share of incubation as it proceeds, a widespread characteristic of scolopacids with a similar mating system (Bird and Bird 1941; Cramp 1983; Holmes 1966, 1971, 1973; Kistchinski and Flint 1973; Labutin 1959; Parmelee and MacDonald 1960). The trend seems to occur widely in shorebirds (Bannerman 1961; Conway and Bell

1968; Cramp 1983; Jayakar and Spurway 1965; Nethersole-Thompson 1951; Spencer 1953). I know of no report suggesting the opposite trend. Males are also reported to be the most solicitous and attentive parent in monogamous single-clutched species of scolopacids (Holmes 1966, 1971, 1972; Parmelee et al. 1968; Parmelee et al. 1967; Pleske 1928; Portenko 1972; Soikkeli 1967) and charadriids (Hall 1964; Holzinger 1975).

Brood attendance and fledging

In agreement with trends just noted, the overwhelming majority of reports on monogamous single-clutched shorebirds indicates that males often attend the chicks without help from their mates or remain in attendance of the brood longer than do their mates (Scolopacidae: Bengtson 1970, 1975; Blair 1961; Cane 1980; Cramp 1983; Holmes 1966, 1973; Jehl 1973; Kistchinski and Flint 1973; Manning 1976; Nethersole-Thompson and Nethersole-Thompson 1979; Parmelee et al. 1967; Parmelee and MacDonald 1960; Safriel 1975; Soikkeli 1967; Yarbrough 1970; Charadriidae: Cramp 1983; Gatter 1971; Hussell and Page 1976; Parmelee et al. 1967; Simmons 1953; Spencer 1953). Sueur (1975) mentions that older chicks of the European Avocet (*Recurvirostra avosetta*) are accompanied by only one parent but does not indicate that parent's sex; this trend is pronounced for late nesters (Adret 1983).

Soikkeli (1967) estimated mean duration of brood attendance by male and female Dunlin in Finland as 19 and 6 days, respectively, which are remarkably close to my figures of 20 and 6 days for Least Sandpipers. Parmelee et al. (1967 p. 222) mention that a female Baird's Sandpiper remained with male and brood for 5 days after hatching; elsewhere (p. 106) they estimate that both parents attend chicks "for at least a week." One female Sanderling stayed with male and brood for about 3 days (Meltofte 1976). There is a weak suggestion in my data that late broods were attended for briefer periods, a trend also noted in Dunlin by Soikkeli (1967) and Little Ringed Plover (*Charadrius dubius*) by Gatter (1971) and Simmons (1953). Despite the few published figures for calidridines, there are some suggestions of species differences in the relative time spent in brood attendance by males and females. For example, female Purple Sandpipers (*Calidris maritima*) are rarely encountered near broods (Bengtson 1970, 1975), and female Semipalmated Sandpipers are said to depart at or shortly after hatching (Ashkenazie and Safriel 1979; MacLean 1969; Safriel 1975). The little-known Baird's Sandpiper may depart from this pattern in some regions or in some years, for Norton (1973) reports that either sex may remain with the young. More data on this subject are badly needed.

In the Scolopacidae it is normal for at least one parent to attend the chicks until they are past the age at which they can make sustained flights. This is true of Dunlin (Soikkeli 1967), Baird's Sandpiper (Parmelee et al. 1967), Red Knot (*Calidris canutus*) (Parmelee and MacDonald 1960), Pectoral Sandpiper (Parmelee et al. 1967), Least Sandpiper (Yarbrough 1970; this study), Semipalmated Sandpiper (Parmelee et al. 1967), Purple Sandpiper (E. H. Miller, personal observation), Greenshank (*Tringa nebularia*) (Nethersole-Thompson and Nethersole-Thompson 1979), European Woodcock (*Scolopax rusticola*) (Shorten 1974), and Ruddy Turnstone (*Arenaria interpres*) (Manniche 1910; Meltofte 1976; Parmelee et al. 1967; Parmelee and MacDonald 1960). Pleske (1928) stresses that Sanderlings deviate from this pattern, for chicks are left unattended as soon as they can fly. On Victoria Island, Parmelee

et al. (1967) observed male Stilt Sandpipers (*Calidris himantopus*) in attendance of large flightless young and fledged juveniles, but farther south, in northern Manitoba, Jehl (1973 p. 131) found that males of that species deserted their chicks after "about two weeks," several days before they could fly. Similarly, male phalaropes abandon their chicks before they can fly (Hildén and Vuolanto 1972; Kistchinski 1975; Mayfield 1978; F. A. Pitelka, personal communication; but see Parmelee et al. 1967).

Biparental care, general comments

There are several situations in which biparental care could be advantageous: (*i*) where temperatures are extreme and chicks require frequent brooding; (*ii*) where predation intensity is high, so that duties of vigilance and responding to predators are shared; or (*iii*) where it is advantageous for chicks to scatter because of food that is scarce or thinly dispersed, or because of high predation pressure.

Brooding of chicks is most important during early life, when chicks are easily and rapidly chilled, and when their energy requirements for growth and maintenance are maximal (Norton 1973; Ricklefs 1974). Brooding may nevertheless continue for a considerable period. Semipalmated Sandpiper chicks are brooded during the coldest part of the day "until a very advanced age" (Safriel 1975 p. 704), and chicks of plovers may be brooded for several weeks (Graul 1975; Little 1967; Wilcox 1959). Such protracted brooding may be more important in maintaining family integrity than in protecting chicks from heat or cold, particularly for species in which parents are active tenders of their chicks (Lenington 1980; Walters 1984).

Parental behavior of high-latitude calidridines is very similar to that of their lower latitude relatives, so temperature and weather extremes have not affected qualitative features of parental behavior of monogamous single-clutched species in any major way. Regardless of latitude, females tend to stay with their mate and brood during the first few days after hatching, when chicks must be brooded most frequently.

The importance of predation as a force affecting the duration of brood attendance by females is difficult to assess (see Jehl 1971). Holmes (1971) suggests that both parents care for the brood in Western Sandpipers because of high predation pressure. However, sources and rates of nest and chick predation vary greatly across shorebird species, many of which exhibit biparental care, so a more general explanation should be sought. Finally, if scattering of chicks is favored, two parents more easily could watch over the area covered by the brood than could a single parent, or they could divide the brood. Brood division in scolopacids has been reported for Common Snipe (*Gallinago gallinago*) (Tuck 1972) and Whimbrels (*Numenius phaeopus*) (Williamson 1946) and may occur in Dunlin (F. A. Pitelka, personal communication), but its incidence and significance are unclear.

In summary, there is a widespread tendency toward biparental incubation and care of brood in shorebirds, with males assuming an increasing role late in the nesting cycle for most or all monogamous species. This includes such characteristics as diel rhythms in sharing of incubation, duration of incubation shifts, and a dominant male role in brood care. Reasons for the lack of adaptive radiation in patterns of parental care and the role of the male as the usual caretaker of the brood are not clear. Research focussing on species or populations with known differences in the presence or quantitative expression of parental behavior should be revealing (Fitzpatrick 1985; Walters 1984).

Diversionary and "alarm" behavior of parents

Responses of shorebird parents and chicks to predators have been reviewed by Cramp (1983), Sordahl (1981), Gochfeld (1984), and Walters (1984). Many such responses exhibit extreme phylogenetic conservatism. For example, gross motor patterns used by Least Sandpipers in distraction occur throughout the Calidridini, as does the habit of adults remaining on the nest until a predator is very close. Comparable comments can be applied to other groups such as curlews (Numeniini), in which incubating birds allow such close approach that they can often be touched before they flush. Distraction and diversionary behavior do not seem to be very finely tuned to local predation pressure. Least Sandpipers on Sable Island have only been exposed to predation by Herring Gulls in this century and have no terrestrial predators there except the occasional domestic cat or dog (McLaren 1981). Even so, their responses to man seem identical with responses in areas like northern Manitoba or northwestern British Columbia, where terrestrial predators abound. Geographic variation in responses of other shorebirds likewise shows no obvious systematic relationship to predation (Miller 1984).

Vocalizations during distraction and the occurrence of two call types in "alarm" occur widely in Calidridini. The former exhibit similar characteristics in species that have been studied, including Sanderling (Fig. III of Cramp 1983); the latter include trills and single frequency-modulated notes in a surprising number of species (Cramp 1983; Miller 1984). The presence of sound signals that are so readily homologized, both by structure and context, suggests that communicative needs in this stage of the breeding cycle are very similar across species. More detailed research on variations and contextual uses of the calls may reveal a finer scale adaptive difference.

Acknowledgements

ADRET, P. 1983. Une étude des comportements parentaux de l'avocette en colonie de reproduction. Organisation spatiale inter- and intra-familiale. Can. J. Zool. 61: 603–615.

ANDERSON, K. S. 1980. Least sandpiper (*Calidris minutilla*) breeding in Massachusetts. Am. Birds, 34: 867.

ASHKENAZIE, S., and U. N. SAFRIEL. 1979. Breeding cycle and behavior of the semipalmated sandpiper at Barrow, Alaska. Auk, 96: 56–67.

AUSTIN, O. L., JR. 1932. The birds of Newfoundland Labrador. Nuttall Ornithological Club, Memoirs, No. 7.

BANNERMAN, D. A. (*Editor*). 1961. The birds of the British Isles. Vol. 10. Scolopacidae (conclusion), Charadriidae, Recurvirostridae, Haematopodidae. Oliver and Boyd, London.

BENGTSON, S.-A. 1970. Breeding behaviour of the purple sandpiper *Calidris maritima* in West Spitsbergen. Ornis Scand. 1: 17–25.

—— 1975. Observasjoner av hekkebiologien hos fjaereplytt *Calidris maritima* på Svalbard. Fauna (Oslo), 28: 81–86.

BIRD, C. G., and E. G. BIRD. 1941. The birds of north-east Greenland. Ibis, 1941: 118–161.

BLAIR, H. M. S. 1961. Little stint. *In* The birds of the British Isles.

Vol. 9. Scolopacidae (part). *Edited by* D. A. Bannerman. Oliver and Boyd, London. pp. 260–272.

CANE, C. 1980. Observations on the behaviour of the purple sandpiper *Calidris maritima* during incubation and hatching. *In* Cambridge Norwegian Expedition 1978 report. *Edited by* J. L. Innes. Cambridge University, Cambridge. pp. 59–66.

CONWAY, W. G., and J. BELL. 1968. Observations on the behavior of Kittlitz's sandplovers at the New York Zoological Park. Living Bird, 7: 57–70.

CRAMP, S. (*Editor*). 1983. Handbook of the birds of Europe, the Middle East, and North Africa. The birds of the western Palearctic. Vol. 3. Waders to gulls. Oxford University Press, Oxford.

DRURY, W. H., JR. 1961. The breeding biology of shorebirds on Bylot Island, Northwest Territories, Canada. Auk, 78: 176–219.

ERCKMANN, W. J. 1983. The evolution of polyandry in shorebirds: an evaluation of hypotheses. *In* Social behavior of female vertebrates. *Edited by* S. K. Wasser. Academic Press, New York. pp. 113–168.

FITZPATRICK, J. W. 1985. Scientific collections and the study of ecological morphology. *In* Museum collections: their roles and future in biological research. *Edited by* E. H. Miller. Occas. Pap. B.C. Prov. Mus. (Victoria), 25. pp. 195–208.

FLINT, V. E. 1973. Data on the biology of the broad-billed sandpiper. *In* Fauna and ecology of waders. Vol. 1. *Edited by* V. E. Flint. Moscow Society of Naturalists, Moscow. pp. 98–100.

GATTER, W. 1971. Aufenthalt und raumliche Bewegungen einer Flussregenpfeifer-Population (*Charadrius dubius*). Anz. Ornithol. Ges. Bayern, 10: 100–106.

GOCHFELD, M. 1984. Antipredator behavior: aggressive and distraction displays of shorebirds. *In* Behavior of marine animals. Vol. 5. Shorebirds: breeding behavior and populations. *Edited by* J. Burger and B. L. Olla. Plenum Press, New York. pp. 289–377.

GOCHFELD, M., J. BURGER, and J. R. JEHL, JR. 1984. The classification of the shorebirds of the world. *In* Behavior of marine animals. Vol. 5. Shorebirds: breeding behavior and populations. *Edited by* J. Burger and B. L. Olla. Plenum Press, New York. pp. 1–15.

GODFREY, W. E. 1966. The birds of Canada. Natl. Mus. Can. Bull. 203.

GRAUL, W. D. 1975. Breeding biology of the mountain plover. Wilson Bull. 87: 6–31.

HALL, K. R. L. 1964. A study of the blacksmith plover *Hoplopterus armatus* in the Cape Town area. II. Behaviour. Ostrich, 35: 3–16.

HILDÉN, O., and S. VUOLANTO. 1972. Breeding biology of the red-necked phalarope *Phalaropus lobatus* in Finland. Ornis Fenn. 49: 57–85.

HOLMES, R. T. 1966. Breeding ecology and annual cycle adaptations of the red-backed sandpiper (*Calidris alpina*) in northern Alaska. Condor, 68: 3–46.

—— 1971. Density, habitat and the mating system of the western sandpiper (*Calidris mauri*). Oecologia, 7: 191–208.

—— 1972. Ecological factors influencing the breeding season schedule of western sandpipers (*Calidris mauri*) in subarctic Alaska. Am. Midl. Nat. 87: 472–491.

—— 1973. Social behaviour of breeding western sandpipers (*Calidris mauri*). Ibis, 115: 107–123.

HOLZINGER, J. 1975. Untersuchungen zum Verhalten des Flussregenpfeifers *Charadrius dubius* bei gestörtem und ungestörtem Brutablauf. Anz. Ornithol. Ges. Bayern, 14: 166–173.

HOWE, M. A. 1972. Pair bond formation and maintenance in Wilson's phalarope, *Phalaropus tricolor*. Ph.D. thesis, University of Minnesota, Minneapolis.

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.

JAYAKAR, S. D., and H. SPURWAY. 1965. The yellow-wattled lapwing, a tropical dry-season nester (*Vanellus malabaricus* (Boddaert), Charadriidae). I. The locality, and the incubatory adaptations. Zool. Jahrb. Abt. Syst. Oekol. Geogr. Tiere, 92: 53–72.

JEHL, J. R., JR. 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.

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.

LABUTIN, YU. V. 1959. The least curlew of the Verkhoyansk region. Ornitologia, 2: 111–114.

LENINGTON, S. 1980. Bi-parental care in killdeer: an adaptive hypothesis. Wilson Bull. 29: 8–20.

LITTLE, J. DE V. 1967. Some aspects of the behaviour of the wattled plover *Afribyx senegallus* (Linnaeus). Ostrich, 38: 259–280.

MACLEAN, S. F., JR. 1969. Ecological determinants of species diversity of arctic sandpipers near Barrow, Alaska. Ph.D. thesis, University of California, Berkeley.

MANNICHE, A. L. V. 1910. The terrestrial mammals and birds of north-east Greenland. Medd. Groenl. 45: 1–200.

MANNING, T. H. 1976. Birds and mammals of the Belcher, Sleeper, Ottawa and King George Islands, and Northwest Territories. Can. Wildl. Serv. Occ. Pap. No. 28.

MAYFIELD, H. F. 1978. Red phalarope breeding on Bathurst Island. Living Bird, 17: 7–39.

MCLAREN, I. A. 1981. The birds of Sable Island, Nova Scotia. Proc. N.S. Inst. Sci. 31: 1–84.

MELTOFTE, H. 1976. Ornithological observations in southern Peary Land, north Greenland, 1973. Medd. Groenl. 205(1).

MILLER, E. H. 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.

—— 1983a. Habitat and breeding cycle of the least sandpiper (*Calidris minutilla*) on Sable Island, Nova Scotia. Can. J. Zool. 61: 2880–2898.

—— 1983b. Structure of display flights in the least sandpiper. Condor, 85: 220–242.

—— 1984. Communication in breeding shorebirds. *In* Behavior of marine animals. Vol. 5. Shorebirds: breeding behavior and populations. Edited by J. Burger and B. L. Olla. Plenum Press, New York. pp. 169–241.

NETHERSOLE-THOMPSON, D. 1951. The greenshank. Collins, London.

NETHERSOLE-THOMPSON, D., and M. NETHERSOLE-THOMPSON. 1979. Greenshanks. T. and A. D. Poyser, Berkhamsted.

NORTON, D. W. 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.

ORING, L. W. 1982. Avian mating systems. *In* Avian biology. Vol. 6. Edited by D. S. Farner, J. R. King, and K. C. Parkes. Academic Press, New York. pp. 1–92.

ORING, L. W., and D. B. LANK. 1984. Breeding area fidelity, natal philopatry, and the social systems of sandpipers. *In* Behavior of marine animals. Vol. 5. Shorebirds: breeding behavior and populations. Edited by J. Burger and B. L. Olla. Plenum Press, New York. pp. 125–147.

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. Natl. Mus. Can. Bull. 169.

PARMELEE, D. F., H. A. STEPHENS, and R. H. SCHMIDT. 1967. The birds of southeastern Victoria Island and adjacent small islands. Natl. Mus. Can. Bull. 222.

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.

PLESKE, T. 1928. Birds of the Eurasian tundra. Boston Soc. Nat. Hist. Mem. 6(3): 1–485.

PORTENKO, L. A. 1972. Birds of the Chukotskii Peninsula and Wrangel Island. Part 1. Nauka, Leningrad.

RICKLEFS, R. E. 1974. Energetics of reproduction in birds. *In* Avian energetics. Edited by R. A. Paynter, Jr. Nuttall Ornithological Club Publ. No. 15. pp. 152–292.

SAFRIEL, U. N. 1975. On the significance of clutch size in nidifugous birds. Ecology, 56: 703–708.

SHORTEN, M. 1974. The European woodcock (*Scolopax rusticola*). A search of the literature since 1940. Game Conservancy Rep. No. 21.

SIMMONS, K. E. L. 1953. Some studies on the little ringed plover. Avic. Mag. 59: 191–207.

SOIKKELI, M. 1967. Breeding cycle and population dynamics in the dunlin (*Calidris alpina*). Ann. Zool. Fenn. 4: 158–198.

—— 1974. Size variation of breeding dunlins in Finland. Bird Study, 21: 151–154.

SORDAHL, T. A. 1981. Predator-mobbing behavior in the shorebirds of North America. Wader Study Group Bull. 31: 41–44.

SPENCER, K. G. 1953. The lapwing in Britain. Some account of its distribution and behaviour, and of its role in dialect, folk-lore, and literature. A. Brown and Sons, London.

SUEUR, F. 1975. Nidification de l'Avocette *Recurvirostra avosetta* en baie de Somme. Alauda, 43: 482–483.

TUCK, L. M. 1972. The snipes: a study of the genus *Capella*. Can. Wildl. Serv. Monogr. Ser. No. 5.

WALTERS, J. R. 1980. The evolution of parental care in lapwings. Ph.D. thesis, University of Chicago, Chicago.

—— 1982. Parental behavior in lapwings (Charadriidae) and its relationships with clutch sizes and mating systems. Evolution (Lawrence, Kans.), 36: 1030–1040.

—— 1984. The evolution of parental behavior and clutch size in shorebirds. *In* Behavior of marine animals. Vol. 5. Shorebirds: breeding behavior and populations. Edited by J. Burger and B. L. Olla. Plenum Press, New York. pp. 243–287.

WILCOX, L. 1959. A twenty year banding study of the piping plover. Auk, 76: 129–152.

WILLIAMSON, K. 1946. Field-notes on the breeding-biology of the whimbrel, *Numenius phaeopus phaeopus* (Linnaeus). Northwest. Nat. 21: 167–184.

WINKLER, D. W., and J. R. WALTERS. 1983. The determination of clutch size in precocial birds. *In* Current ornithology. Vol. 1. Edited by R. F. Johnston. Plenum Press, New York. pp. 33–68.

YARBROUGH, C. G. 1970. Summer lipid levels of some subarctic birds. Auk, 87: 100–110.