

BREEDING CYCLE AND BEHAVIOR OF THE SEMIPALMATED SANDPIPER AT BARROW, ALASKA

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ABSTRACT.—Pair formation of *Calidris pusilla* near Barrow, Alaska occurs 3–6 days after the territory is established. The pair is then engaged in nest scraping displays during 2–3 days, in which 10–12 scrapes are made by the male and examined by the female. Eventually 2–3 scrapes are lined by the female, and in one of these the first egg is laid 4–6 days after pairing. During the egg-laying period further lining is performed by the female and partial incubation takes place by both sexes. Continuous incubation commences 8 h prior to laying of the 4th egg. Male and female alternate in incubation: in the first 2 days a turn lasts 3–5 h, and the duration gradually increases up to 13–14 h during the 2nd week. Long incubation turns reduce the number of approaches to the nest and may therefore reduce the chances of it being discovered by predators. The incubating bird is intermittently engaged in egg-rolling and in camouflaging the nest by bending adjacent grass blades over its back, and is constantly alert. The off-duty bird may feed 2–3 km away from the nest. The eggs hatch after 20 days of incubation, all within 1 day. Females desert the family 2–8 days after hatching: they desert late if hatching is early, and early if hatching is late in the season. After female departure the family moves from the nesting territory, typically in a high-centered polygonal area, to establish a home range as far as 2–3 km away, often in a low-centered polygonal area. During the first 6–8 days after hatching, the male prepares each evening a scrape for night brooding. After fledging, the male and young join wandering flocks. *Received 24 January 1978, accepted 11 October, 1978.*

THE four common breeding calidridine species of Barrow, Alaska, *Calidris alpina*, *C. pusilla*, *C. melanotos*, and *C. bairdii*, constitute a significant component of the tundra ecosystem, feeding on arthropods and being preyed upon by birds and mammals. They also function as a link between the terrestrial and aquatic trophic webs. The breeding biology of *C. alpina* and *C. melanotos* at Barrow was studied by Holmes (1966) and Pitelka (1959), respectively, but the other two species remained relatively unknown.

The Semipalmated Sandpiper (*C. pusilla*) the smallest and often the commonest of the four species, has a Nearctic breeding distribution (Pitelka et al. 1974) and winters in southern United States and in Central and South America (McNeil 1969, Ashmole 1970, Baker and Baker 1973). The time-energy budget of this species was studied at Barrow in 1973 (Ashkenazie and Safriel 1979), and the bioenergetic implications are to be incorporated in an integrated synthesis of the structure and function of the tundra ecosystem at Barrow (see Brown and West 1970). A knowledge of the breeding cycle and the behavioral repertoire of this sandpiper, as well as of the phenology of the population during 1973, is essential for evaluating the significance of its time-energy budget. This paper describes the reproductive cycle as observed during 1973, and supplements the description with some additional observations made by Safriel during several previous years.

STUDY AREA AND METHODS

The tundra at Barrow (72°21'N 156°40'W) is a plain with an intricate network of rivers, streams, lakes, and ponds covering about 50–75% of the surface (Hussey and Michelson 1966). The remaining

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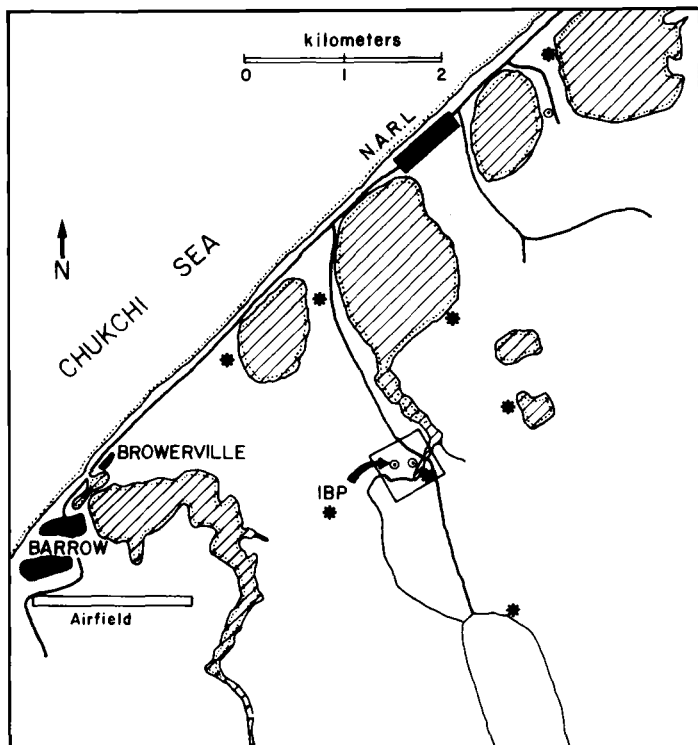


Fig. 1. The study area. \odot —site of nest whose owners were under detailed surveillance; *—site of a territory whose owners were under less detailed surveillance; IBP—International Biological Program Intensive Site.

landscape is made up of several habitats arranged in a mosaic of polygon centers, rims, and troughs. The daylight is continuous between 10 May and 2 August. Based on records of 46 successive years (1921–1967), daily mean temperatures above freezing prevail as of 11 June (MacLean and Pitelka 1971) by which time thaw is normally well underway. Thawing starts on polygon tops and eventually all troughs, ponds, and lakes become snow- and ice-free. The mean annual precipitation during the 46 years was 118 mm, the wettest months being July and August (Brown 1968).

Our study was conducted from 1 June, when only a small portion of the population was present, to 4 August 1973, by which time most birds left our study areas. Compared with the 46-year record, the average daily air temperatures in 1973 were below normal during the study period, except for a few warm days at the beginning of June and at the end of July.

Observations on color-banded individuals were recorded on a portable cassette tape-recorder during continual watches of the birds through a 20 \times telescope or 8 \times 30 binoculars. In 1973, 20 different birds were followed, of which 3 pairs were under close surveillance (Fig. 1), and altogether 500 h of observations were recorded (Ashkenazie and Safriel 1979). Incubating birds were followed using time-lapse photography (Minolta Autopack 8D6 super-8 movie camera equipped with an intervalometer-P time-lapse device). Additional observations of the same population were made during the 1968–1972 breeding seasons (Safriel 1971).

RESULTS

Arrival.—The birds arrived in two distinct waves: the first at the end of May and the beginning of June, the second during the second half of June. Consequently, there were two laying peaks in the 1973 season, around 10–11 June, and 20–22 June. The first clutch was started on 3 June, the last one on 29 June. There is some

variation in arrival time between years, which is weather dependent (Holmes 1966, Safriel in prep., Schamel pers. comm.). First arrivals usually appeared during late May, when about 90% of the area is snow-covered, but a significant arrival of breeding birds during mid- and late June was less common.

It is not known how long the birds spend on their way, what their strategy of fuelling is, and in what physical state they arrive at Barrow. A flow of northbound *C. pusilla* has been detected in New Jersey between 10 May and 7 June, with an average peak around 20 May (Urner and Storer 1949); further north, in Anaktuvak, Alaska, the detected passage lasted only 9 days (Irving 1972).

The birds arrived at Barrow in flocks of 5–10 individuals of unknown sex. In *C. alpina*, males arrive first and females later, and only when thaw is late do the birds arrive mated (Holmes 1966). Nearly simultaneous with the arrival of the first *C. pusilla* flocks, banded males were observed on established territories, and in these territories females were not seen for some time.

The territorial male prior to pair formation.—Males established territories right after their arrival and the process was probably accelerated when males returned to their last year's territory; there is some evidence that *C. pusilla* are site-tenacious when their previous breedings in that site were successful (Norton, Ailes, and Curatolo MS, Safriel 1971). The male spent most of the time within the boundaries of his territory, and his activities were frequently interrupted by territorial display flights or by aggressive encounters with other males. These activities intensified as the number of established territories increased. Pair formation occurred 3–6 days after the territory was established, when a female alighting in the territory was accepted. We observed two cases of females alighting in territories of unmated males. In one case the female had fed in the territory for a short time while being observed by the male, and later it was chased off by him. In the second case the female was accepted. Thus, females seem to be attracted to territories, but once there they may be selected by the males.

Pre-laying period of the pair.—Four to 6 days elapsed between pair formation and laying of the first egg. During that period the frequency of territorial display flights was reduced, and such flights occurred mainly during fixed hours of the day or when small flocks flew over the territory. Rarely the female joined the male in chasing off flocks.

The female determined the greater part of the activity pattern of the male, through choosing their common feeding and resting sites and times. Whatever the female did, she was followed by the male, who performed the same activity, but interrupted it by chases and spells of alertness, elicited by other males or by predators.

One or 2 days after pair formation the birds started to engage in nest site presentation or nest scraping display, known also to occur in several variations among other calidridine species (Holmes and Pitelka 1964, Bengston 1970, Holmes 1973, Pitelka et al. 1974). In *C. pusilla* we found performance of this display restricted to 2–3 days. The following description of the display is based on observations of one pair. The male selected sites with dense cover of grass where a scrape was formed by pressing the grass with the breast while rotating the body. The female stood nearby and watched. When the scrape was prepared, the male perched on its edges and attained a posture in which it leaned forward, with the wings bearing upon the edges of the scrape, and extended its neck forward. The female approached the male from behind, and entered the cup by pressing itself under the male's belly. She examined the cup for a few seconds, made a complete turn within the cup while it

was being thatched by the male, and then emerged from the point of penetration. The male then rose from the cup edges, stepped away to stand by the scrape, and started preening. After a while the male lured the female to another site, where another scrape was formed and the same ritual repeated. Having prepared 10–12 scrapes, the male ceased to make new ones, but led the female to scrapes previously prepared for her examination. By that time the female tended to spend more time checking 2–3 particular scrapes. At that stage the male seemed impatient to wait for the female until she emerged from the scrapes she examined, and ran between scrapes without waiting for the female to follow. The female too, started checking scrapes at her own initiative, unaccompanied by the male. She might check any scrape in the area, not necessarily those made by her mate, and on one occasion a female was observed checking a scrape prepared by a neighboring *C. bairdii*. Those 2–3 scrapes favored by the female were lined by her with lichens and grass shoots. This lining activity was performed ritually, through the “sideway building” display (Tinbergen 1959, Holmes and Pitelka 1964, Harrison 1967), in which the female sat within the cup, picked lining items from the vicinity of the cup and threw them backwards over her back. The picked items slid down from both sides of the bird’s back and settled on the cup’s surface. At the stage that lining was being constantly added to the favored scrapes, copulations occurred.

The pair during egg-laying period.—The egg-laying period lasted 4 days, with one egg laid per day. We obtained observations on four pairs. An actual laying of a first egg was observed once. This female was still checking two different scrapes 1 h before laying occurred, but then started persistently to visit just one of them, lining it with vegetation at each visit. The visits were then prolonged, the last one taking 20 min, at the end of which a faint vocalization was heard from the nest and slight movement inside the cup was detected. At that point the male, who during that time had been standing near the nest, approached the cup very slowly. The female then emerged and both flew off. The cup contained a warm, pale-pink egg. Within an hour the egg cooled off and attained the strong violet pigmentation typical of this species.

We also observed females several times during the moment of laying of successive eggs, which occurred in the mornings, evenings or at night. Because the period between two successive layings is shorter than 24 h (Norton 1973), every egg within a single clutch is laid at a different time of the day.

When the first egg was laid, the cup was only sparsely lined and the bottom was moist. After the second egg was laid the amount of lining increased and the cup was dry. The lining thickened throughout the laying period, being continually added to by the female when performing the “sideway building” display. Partial incubation occurred before the clutch was complete. In 1973 incubation started on the first day of laying with incubation spells of 10–15 min totalling to about 2 h per day, performed mainly by the male. The duration of incubation during the laying period increased with time, and altogether eggs were incubated by the male 14% of the total period, whereas females incubated for 4% of the time. The female incubated just before or after an egg was laid, the male incubating during short spells several times throughout the day. Continuous incubation commenced about 8 h prior to the laying of the fourth egg. By this time incubation was shared between male and female, and the shifts occurred every 3 h. Compared with other calidridine species breeding at Barrow (Norton 1972, 1973), incubation prior to clutch completion is most extensive in *C. pusilla*.

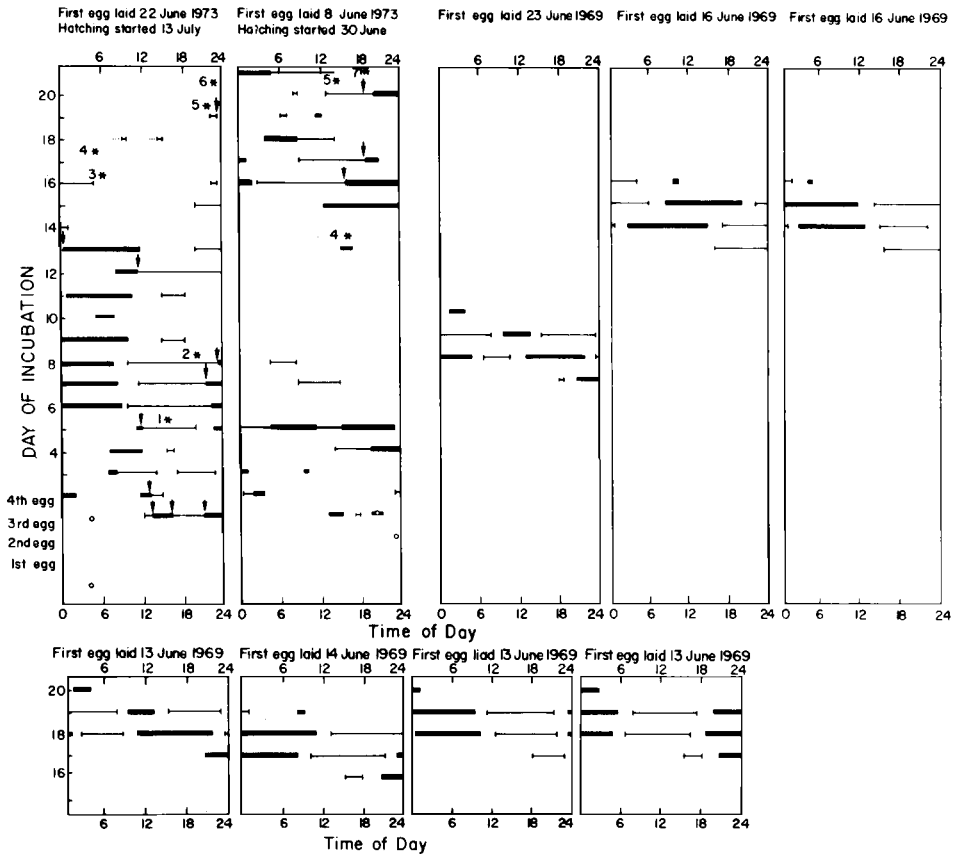


Fig. 2. Incubation schedule in nine nests of *Calidris pusilla* near Barrow. The two nests in 1973 were under continuous surveillance by us and/or by a time-lapse movie camera. The seven 1969 nests were checked every 2 h during 4 successive days. In all nests birds were individually marked. Thick lines, female incubated; thin lines, male incubated; dotted lines, nest observed, but found unincubated; arrows, a shift was actually observed; circles, an egg-laying was actually observed. Key to asterisks: 1* hail storm; 2* female arrived but chased off by male; 3* hail and snow storm; 4* snow storm; 5* eggs chipping; 6* hatchlings preyed upon; 7* first egg hatches; 8* last egg hatches; 9* hatchlings leave the nest.

Other pronounced activities during the egg-laying period were an intensive feeding by the female and protection of the female and nest from predators by the male. The male was aggressive and even chased the female in precopulatory postures, though copulations in that period were not observed.

The pair during incubation period.—The eggs were continually incubated by both male and female throughout the 20 days from the laying of the fourth egg until hatching (Fig. 2). The male and the female alternated in their incubation duties and in the first 2 days each turn lasted 3–5 h. The duration of an incubation turn gradually increased; it lasted 8 h in the fifth and sixth day, and attained a maximum of 13–14 h of continuous incubation per bird during the second week. This duration remained unchanged until about 2 days before hatching.

In *Larus argentatus* the timing of the incubation shift is determined by the bird that is off duty, either male or female (Drent 1970). In *C. pusilla*, however, we

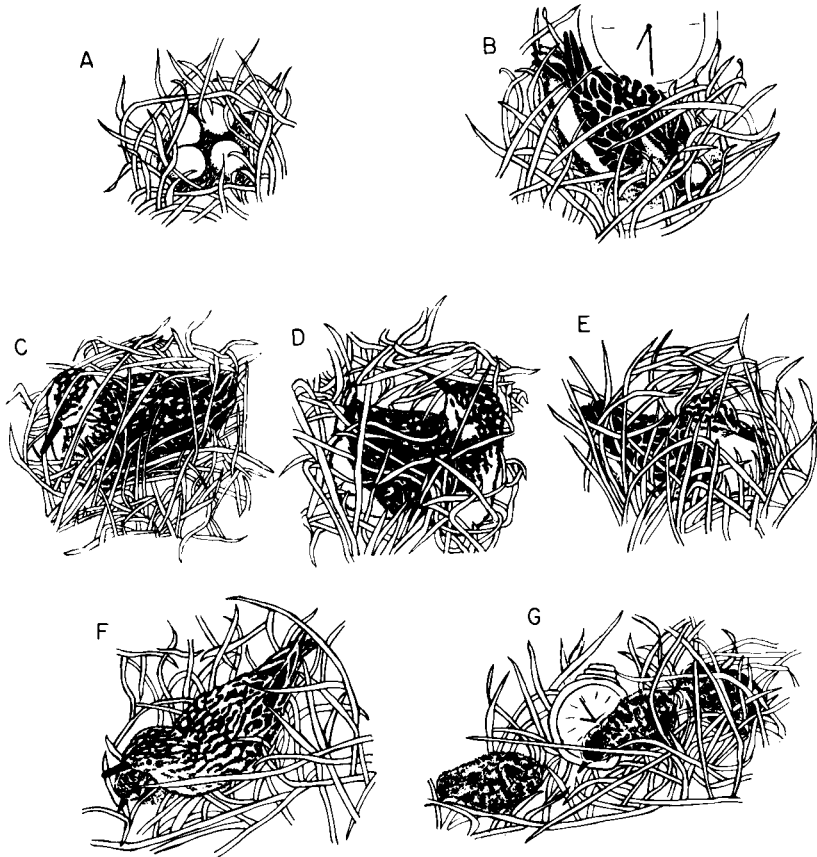


Fig. 3. Behavior of *C. pusilla* at nest (drawn from "8 mm super" film). A. Unattended nest. Note that leaf blades are not fully bent over the cup; B. Arranging the eggs before starting to incubate; C. and D. Bending the blades over the head and back, for camouflage. Note the blades in the bird's bill; E. Alertness while incubating. Note the complete "roof" of blades over the bird; F. Trying to prevent a chick from leaving the cup (while others are still being brooded); G. The moment of nest-desertion. The parent with one chick is leading (not in picture) while the fourth chick is still in cup.

observed four cases in which the female approached the nest earlier than the expected shift and was chased off by the incubating male, later to return on schedule. In two of these cases the female returned 3 h earlier than the scheduled time, on the 5th and on the 8th day of incubation. In all these cases the females involved were recorded first only in the 1973 season and not in the previous years, and hence they were presumably in their first breeding (Safriel 1971) and therefore relatively inexperienced. Also, most of these cases occurred when the weather was bad and when there probably was a temporary food shortage. We do not know why supposedly inexperienced females rather than males sometimes had difficulties in timing their return to incubation duty. It is possible that in *C. pusilla* the feeling of satiation serves as a stimulus for this return. Since males do not lose much weight during the incubation period (Ashkenazie and Safriel 1979), we suggest that by the end of each off-duty period they may be fully satiated. Females, however, lose significant weight in that period, so they may never be fully satiated and hence may not benefit from the timing mechanism suggested for males. They probably time their returns using

less efficient stimuli, and these may require experience in order to be correctly interpreted. There was one case during a snow storm in which the female deserted a nest in the middle of her incubation turn and never returned. After a few hours the male returned and started incubating the cold eggs. His turn lasted 15 h. He then adopted a schedule in which 3 h of incubation were interrupted by off-duty periods of 40–45 min, during which the unincubated eggs did not cool off but remained relatively warm. The eggs hatched 2 days after the female's desertion, but were preyed upon immediately (Fig. 2, column 1). A desertion of the clutch by the female during a snow storm was observed in another nest, too, but in this case, on the 13th day of incubation, the male chased the female back to the nest.

By no means can the incubation turn be regarded as a period of rest. When entering the cup and before crouching upon the eggs, the eggs were moved, rolled, and turned with the aid of bill and breast (Fig. 3B). This activity was repeated several times during the incubation turn and was often associated with a change in the bird's orientation. Immediately after sitting on the eggs, and several times during its incubation duty (usually after a change in its orientation), the bird camouflaged the cup by bending adjacent grass blades over the nest and interweaving them with its bill, thus creating a "roof" over the cup (Fig. 3C, D). When not turning the eggs or maintaining the "roof," the bird was constantly alert, carefully examining the surroundings by head movements (Fig. 3E). At the presence of a flying predator in the vicinity the bird lowered its head and back in a typical crouching posture.

When flushed from the nest the incubating bird performed a "broken wing" display followed by the "rodent-run" display (e.g. Brown 1962, Bengston 1970): the bird squattered away from the nest with frequent crouches when the body leaned on one side, one wing flapping and the tail fully spread and depressed toward the ground. *C. pusilla* accompanied this display with a typical vocalization.

When the bird was not flushed but quietly slipped away from the nest, it performed a different display at some distance picking up grass shoots and throwing them away with sharp jerks of the head. Similar behavior is known in gulls (Tinbergen 1959, 1965; Harrison 1967).

When off-duty most of the time was devoted to feeding and preening. When the bird on duty was relieved during the first week of incubation, it first flew to a stream or a pond to bathe and preen and then commenced feeding. During the second week it first fed and only later preened and bathed. Birds of two different nests, in their second week of incubation, were observed (on 28 June) flying immediately from the nest in the polygonal area of the territory to flat plains 2–3 km away from the nest, where they were later discovered feeding in mixed flocks of 70–80 birds with *C. melanotos* and *C. alpina*.

The hatching period.—The following account is based on a time-lapse movie taken at one nest. Two days before hatching the incubation schedule changed, the frequency of changeovers becoming greater and somewhat irregular, and the turns lasting less than 14 h. A change in incubation schedule prior to hatching was also noted in *C. alpina*, *C. melanotos*, and *C. bairdii* (Norton 1973) and in *Larus argentatus* (Drent 1970). This alteration in schedule coincided with the commencement of vocalizations from the eggs that were produced by the embryos' breathing mechanism and became more frequent and stronger as the time of hatching approached. This phenomenon is known in most precocial birds (Gottlieb 1965, 1968; Driver 1967; Gottlieb and Simner 1969; Drent 1970; Orcutt 1974). According to Norton (1973) the alteration coincides with the appearance of holes in the egg shell, 12–48

h prior to hatching, produced by the double egg tooth characteristic of charadriiformes (Jehl 1968) and present in *C. pusilla*. Except for *Arenaria interpres*, in which a female was observed to peck at a hatching egg (Nettleship 1973), it is not known whether parents of *C. pusilla* or other shorebirds assist in the hatching process.

The time from hatching of the first to the last egg was 24 h, but the intervals between hatchings were not identical. The first two chicks to hatch tried to leave the nest a few hours after hatching, but were prevented from doing so by the incubating parent that chased them back to the cup (Fig. 3F). When there were three chicks the parent was unable to manage them all, and the chicks left the cup for feeding tours of a few seconds, then darted back to be brooded by the incubating bird. A few hours after the fourth egg hatched, the nest was deserted (Fig. 3G). In one case a wandering chick lost its way back to the nest; the incubating parent left the cup to brood this chick for a while, then returned to the remaining eggs. In another case the off-duty bird brooded such a chick in the vicinity of the nest.

The pair during young-attending period.—About 16 days elapse between hatching and fledging (Safriel 1971). The following information is based on 10 young-attending families. Females are known to desert the family 2–6 days after hatching (Soikeli pers. comm., Safriel 1971). We found that in 1973 the timing of female desertion was season-dependent; in two cases of very late breeding, one female deserted on the day of hatching, the other 3 days after hatching. In two other families that bred earlier, the females left on the 6th and 8th days after hatching. One observation suggests that the proximate factor for female desertion is rejection by the male. During the sixth day after hatching (12 July) the female spent most of her time feeding away from the family. From time to time she returned to fly over the territory where male and young were feeding, but was chased off by the male and alighted at some distance. Finally she was chased off for a very long distance; from this final chase only the male returned. We observed this male and the brood for another 10 h, during which the female (banded) was not seen, and she was not recorded on subsequent days in the vicinity of the family or at other visited sites.

There are thus two phases in the young-attending period: in the first both parents tend the young, while in the second it is just the male. In the first phase the family usually stayed within the boundaries of the nesting territory. Usually one parent remained with the young and the other fed, preened, and bathed away from the territory. Although we twice observed females to remain continuously for 2 h with young while the male was away, it seemed that even during the first phase the male tended the young more than the female. In the second phase, after the female left, a pronounced exodus usually took place, the family moving to another locality, sometimes as distant as 2–3 km. There it seemed that in some cases a home range was established in which the young stayed until they fledged and their foraging areas were defended against intrusions of other families (Safriel 1971). In other cases we could not establish whether the family stayed within one area until fledging or if they were on a rather continuous move. Whereas the territory in which the young stayed during the first phase was usually in a high-centered polygonal area, during the second phase the families occupied wet plains, along streams, near big ponds or in low-centered polygonal areas. Sometimes young of different broods fed there together, guarded by their parents. Communication between each parent and its own brood was maintained both vocally and visually.

In the first 4–5 days after hatching the chicks were brooded every 3–7 min, for

a period of 3–7 min. Later the frequency of brooding declined, but young were always brooded at night. During the first 6–8 days, each evening the male prepared a shallow scrape for the night brooding. During the first phase the chicks were closely accompanied by a parent and were led to sites probably rich in food for young. All members of the brood then fed together and were brooded together. Later the young tended to disperse and the parent spent more time locating and gathering them, to be brooded solitarily or in pairs rather than all together. Individual variations were detected among members of the same brood in the duration of feeding bouts and brooding frequencies. Young also preened and exercised their wings as of their first day of life. When warned by the parent they crouched in a typical posture.

Males may desert the young just a few days before they fledge (Safriel 1971), but this was not observed in 1973, when males stayed with young on the day of fledging and also for some days later. We also observed flocks in which both young and adults were present. However, in *C. mauri* adults and young form separate flocks (Holmes 1973).

The flocking period.—Around mid-July, when some *C. pusilla* at Barrow still attended young, flocks of this species appeared in the area. Judging from their numbers, most of these birds were not breeders of the Barrow area; Semipalmated Sandpipers as well as other species leave breeding areas in interior Alaska for areas near the coast prior to migratory departure (Myers and Pitelka *in litt.*). Thus, considerable mixing of local populations probably occurred at flocking time, and the birds under our observations undoubtedly joined such flocks.

The size of flocks ranged between 10 and 30 birds, and they were not very coherent; a flock of 11 *C. pusilla* that landed in a pond later split so that only eight birds left the pond in one flock. The flocks were composed of young only, or of adults and young. Because females deserted the family early, it is conceivable that most adults in flocks (especially in late ones) were males. We do not know whether females left solitarily or joined flocks. We also observed mixed flocks of several calidridine species; in one case 5–10 *C. pusilla* were observed in a flock of ca. 100 *C. mauri*.

Individuals in flocks were restless, very sensitive to disturbances, aggressive and vociferous. They frequently changed sites, but preferred pond and river edges. They spent their time feeding, preening, and sleeping. By the end of July no solitary *C. pusilla* were seen near Barrow, and after 4 August no flocks including *C. pusilla* were recorded.

DISCUSSION

The reproductive cycle of *C. pusilla* at Barrow can be schematically summarized by a compartmental flow diagram (Fig. 4). Of all stages in this cycle, incubation deserves special attention. It begins during the laying period, when its timing and duration are crucial. Sandpiper embryos at Barrow are cold-resistant but their cold-sensitivity increases with time (Norton 1972), so eggs should be protected from the outset and hatching success of fertile eggs would be maximal if each of the eggs were constantly incubated from its day of laying. Because the eggs are not laid simultaneously, however, full incubation during the laying period would result in asynchronous hatching, which is highly detrimental to nidifugous young (Soikkeli 1967; Vince 1966a, 1966b, 1968; Norton 1972). Indeed, Norton (1972) found that most

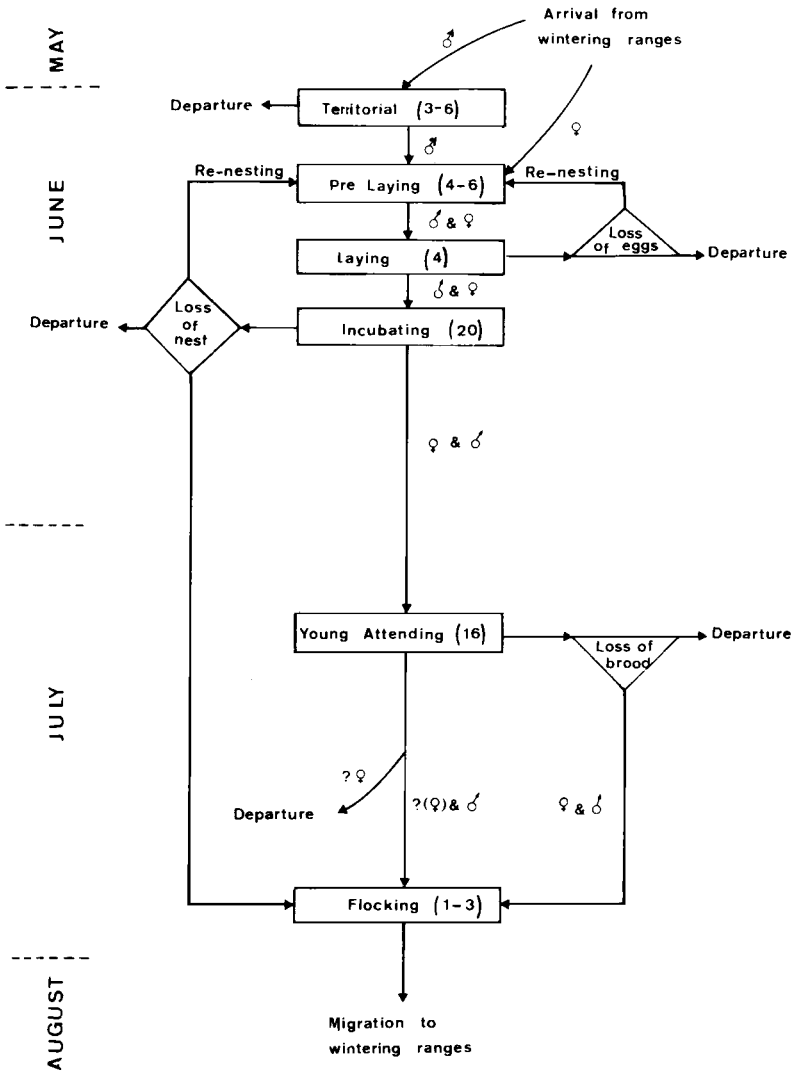


Fig. 4. The phenology of *Calidris pusilla* at Barrow. Rectangles represent reproductive stages, the figures in parentheses stand for the duration of these stages in days. Arrows describe entries and exits from reproductive stages, triangles and rhombus represent events allowing alternative exits. The distances between reproductive stages is scaled to correspond with the time of year (left) in accordance with the behavior of the greater part of the breeding population at Barrow.

cases of mortality among the young occurred during the first 24 h after hatching. We found that when the hatching period was long, the first young to hatch were weakened by hunger and were often lost to predators when they ventured out of the nest to feed. Being then unattended by their parent, they attracted predators by their movements and calls. The last young to hatch were then also at a disadvantage because they were often hastened to leave the nest when still moist and not yet fully recovered from the hatching effort. Alternatively, the parent might desert them when still wet and unattended in the cup while attempting to lure the first young to hatch back to the nest, or while trying to brood them if they were too far away

from the cup. The optimal strategy of incubation during the laying period should thus lead to hatching that is not only maximally successful but is also highly synchronized. In order to achieve this the birds should precisely time incubation spells during the laying period, varying their attentiveness according to the prevailing weather. Because the weather is highly unpredictable, the incubation schedule during the laying period should not be stereotyped, and may also vary between different birds.

The gradual increase in the length of incubation turns with the advancement of the incubation period is also known in *Larus argentatus* (Drent 1970). Long turns reduce the number of changeovers, and hence the time that eggs are exposed. The sensitivity of embryos of *L. argentatus* (Drent 1970) and of *C. pusilla* (Norton 1972) to cold and light increases with age, so increasing the length of incubation turns with the advancement of incubation is likely adaptive (Norton 1972). However, the time during which eggs are exposed when a changeover takes place is very short indeed and may well be insignificant. On the other hand, reducing the number of shifts reduces activity around the nest and decreases the chance that predators may discover the nest while following the relieving bird. As parental investment in the eggs increases with time, an egg loss that occurs late in incubation involves a greater amount of wasted effort than a loss occurring earlier. Also, as incubation progresses the season advances, so that in most cases an early loss of eggs can still be replaced, whereas a late egg loss means a lost breeding season. Thus the increase in length of incubation spells as incubation advances may be advantageous because the stakes are then much higher than earlier. It is probably likewise advantageous to make an effort to reduce the chances of predation when incubation is advanced, even at the cost of severe feeding deficiencies at that time. Indeed, females lose significant weight during incubation (Ashkenazie and Safriel 1979). It therefore seems that 14 h is either the longest on-duty time that a bird can tolerate without feeding, or the consequence of the shortest off-duty time required for replacing feeding deficiencies accumulated during the on-duty period.

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