



Sandpipers from a painting by John Crosby. From left to right: Semipalmated Sandpiper, *Ereunetes pusillus*, adult in fall plumage; an immature Western Sandpiper, *E. mauri*; and an immature Least Sandpiper, *Erolia minutilla*.



BREEDING BEHAVIOR OF THE SANDERLING IN THE CANADIAN HIGH ARCTIC

DAVID F. PARMELEE

All photographs and black-and-white drawings by the author

The Sanderling (*Crocethia alba*) nests abundantly in the Arctic if we judge by the migration each spring and fall. Yet, despite this, I have found few species more elusive on their breeding ground and none that have intrigued me more. George Miksch Sutton and I failed to find Sanderlings on Baffin Island in 1953; S. D. MacDonald and I recorded only a few on Ellesmere Island and not one on Axel Heiberg Island in 1955. On southeastern Victoria Island and on Jenny Lind Island in Queen Maud Gulf, in 1960, 1962, and 1966, the members of our expedition could not find enough Sanderlings for a detailed study, and there was little consolation in knowing that our few notes were more than were being gathered elsewhere. The fact remained that, until 1968, practically nothing was known of the species' breeding in Canada.

I welcomed the opportunity to join S. D. MacDonald, from 20 May to 13 August 1968 and 7 to 29 June 1969, on the expeditions of the Canadian National Museum of Natural Sciences to Bathurst Island in the Queen Elizabeth Islands, just south of the 76th parallel (Figure 1). Bathurst Island with its distinct location and terrain promised a good Sanderling population, and this proved to be the case though the birds were more thinly scattered than anticipated. Nevertheless, I was able to concentrate on various aspects of the Sanderling's behavior—courtship and mating, pair-bond relationship, and the role of the sexes in the care of the eggs and young.

Information on the Sanderling's breeding, prior to 1968, stems largely from studies in Greenland and Spitsbergen, and most of these, Bannerman (1960) pointed out, date back to Manniche (1910). Though Manniche's work was outstanding for his time and distinctive in being the first useful study of the species, a careful scrutiny reveals many ambiguities, gaps, and flaws. The present study extends our knowledge of this shorebird and will, hopefully, stimulate further research.

Study Areas and Methods

We established our base camp eight miles inland on a prominent, finger-like ridge about halfway between Goodslir and Bracebridge Inlets (Figure 2). The camp ridge, as we called it, extended westward as part of a system of low, barren ridges that continued along the north shore of Bracebridge Inlet (Figure 3). Broad valleys with innumerable marshy ponds and lakes stretched between the two inlets. Goodslir River, the largest stream, flowed from high ground in the northwest to the base of camp ridge, and thence to Goodslir Inlet by a long, meandering route that over the years had left behind many gravel terraces. The varied terrain appeared ideal for Sanderlings.

Originally, in 1968, I planned to select a study area, preferably near camp, where a dozen or more pairs of Sanderlings bred. Not finding such a concentration, I settled on two principal areas—one west of camp and one beyond the stream northeast of camp. The latter, overrun by predators and inaccessible from 9 to 15 July when the stream crested, was an unwise choice.

Because the Sanderling pairs were so thinly scattered over the study areas that we had to cover much ground in checking nests, and because we lost three nests to predators in quick succession, we changed our plan again. Selecting a nest (Nest 2) within half a mile of camp, we erected a blind and kept it under constant surveillance. Thus we protected the nest from predators and, at the same time, collected unparalleled data on a single nest.

We began observation at 15:00 hours on 5 July and continued our surveillance, without a break, until 23:17 on 19 July—after all the young had hatched. Inasmuch as we had observed this nest periodically since 21 June, when it had one egg, the successful hatching of all four eggs had special significance.

We divided the 24 hours of continuous daylight into four, six-hour shifts: MacDonald took the first, 00:00 to 06:00; Cy G. Hampson the second, 06:00 to 12:00; Philip S. Taylor the third, 12:00 to 18:00; and I the fourth, 18:00 to 24:00. Such a division allowed each person time for other studies and gave me the opportunity to check other Sanderling nests and compare them with Nest 2. During critical periods at other nests David R. Gray took over for me at the blind.

The continuous observation at Nest 2 had many advantages. One advantage, perhaps not obvious, was that the incubating bird quickly accepted our presence and behaved as if we did not exist, even when we relieved each other at the blind. Although our coming and going had little visible effect on the bird, it nevertheless quickly responded to all mammals and other birds that approached the nest.

Manniche (1910) observed that once the incubating Sanderling is conditioned to human activities, it soon becomes indifferent to them and sometimes incredibly fearless. This behavior, seen many times in certain tundra sandpipers, appears to be markedly characteristic of the Sanderling, for indeed the incubating birds, with few exceptions, soon became fearless once we found their nest. Our continued presence appeared to steadily increase the fearlessness of the incubating bird at Nest 2. It was so accustomed to us by the time the young hatched that it regularly flew off on routine feeding trips when we knelt beside its young, even when we handled them in plain view. With such fearlessness I feel that our presence influenced or biased the behavior of the bird very little, if at all.

There is no easy way to find a Sanderling nest unless one stumbles upon it accidentally. We observed 11 nests on the Bathurst Island breeding ground in 1968 and three in 1969. We found 12 of these by watching birds that behaved as if they had recently left eggs and only two by systematically dragging ropes over bluffs and ridges. The surest method, it would now seem, would be to watch the feeding areas closely from 06:00 to 18:00 when the incubating birds most often fly from the nest to the feeding ground.

We trapped incubating Sanderlings at the nest in a Myers' trap (1966). The birds appeared not to be overly concerned with the trap and most of them we caught quickly. When the trap partially obstructed their view, certain individuals momentarily lost their ability to locate the nest, and, consequently, ran about looking for it in a disoriented manner. This problem we remedied by allowing the bird to go to the nest with the trap set some little distance away and then gradually moving it closer. Once the bird saw the nest within the trap, it did not hesitate to run across wire and net to its eggs.

We banded the Sanderlings with standard numbered bands provided by the Canadian Wildlife Service, and marked adults with several brightly colored dyes rubbed on various feathers. We found fast drying water-resistant dyes (Dixon Redimark, Joseph Dixon Crucible Company, Jersey City, New Jersey), applied with felt-tip markers, highly satisfactory. In 1968 we banded and color-marked eight adults at eight nests; none of these birds deserted. A ninth adult we caught and marked near its young some distance from the nest. Since only one member, either sex, of the pair incubated and brooded, we caught and marked only one adult for a given nest or brood. How one can catch both members of a pair on the nesting ground prior to incu-



Figure 1. Map of Northwest Territories showing Bathurst Island, the site of this study.

bation is a problem we failed to solve. Young birds were simply banded: 19 of known age on the left leg exclusively; 15 of uncertain age on the right leg.

In 1969, the only birds banded were four siblings at a nest west of camp by Taylor. Gray, Taylor, and F. Pierre Lamothe continued general observations on Sanderlings after I left Bathurst Island on 29 June.

Sexing live Sanderlings is a major problem. The males of paired birds generally are considerably brighter than females with the rusty color of the head, neck, and upper pectoral regions more intense and extensive as a rule, a condition not so obvious in dry skins. Most paired birds showed this dimorphism clearly when side by side, but we noted exceptions — some bright females and some very gray males. When seen singly we had difficulty in determining the sex of these odd birds and had to rely on behavioral characteristics and certain call notes, which even now we do not fully understand. Although we were fairly certain of the sex of the incubating individuals at most of the nests that we watched for some time, we were not always dead certain. We claim no fool-proof method for determining the sex of Sanderlings in the field but merely call attention to the problem.

Few authors attempt to describe differences in the breeding plumage of the sexes, either ignoring the problem or describing the sexes as similar. Palmer's description (1967) is about as good as there is. The female differs from the male in having paler rusty on the head and anterior underparts; some have white throats and hardly any rusty on breast. We noted that some fairly

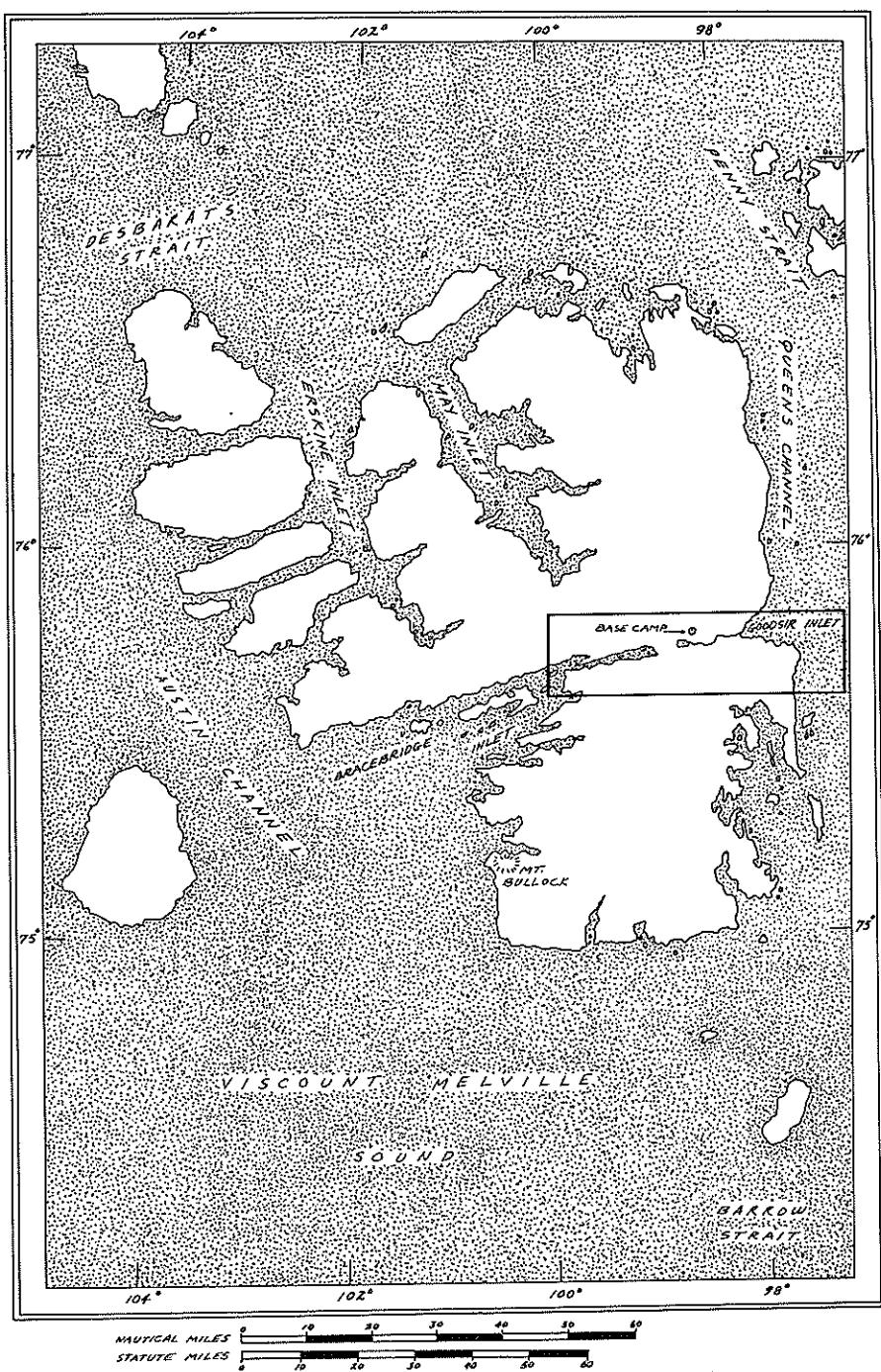


Figure 2. Bathurst Island, showing the location of the base camp. The rectangular area is shown in greater detail in Figure 3.

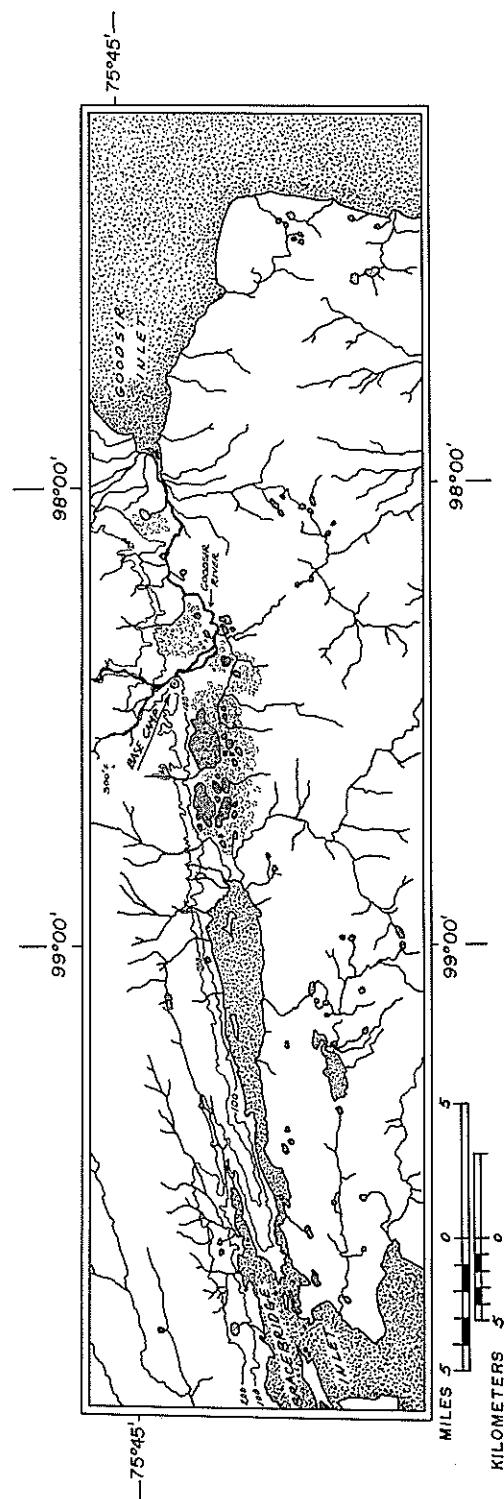


Figure 3. The base camp region (rectangular area in Figure 2) shown in greater detail. The area between the two inlets is dotted with valleys, lakes, and marshy ponds.

area is shown

bright males also have whitish throats. Interestingly enough, Pedersen (1942) described the summer bird as having "two distinctly different appearances — one red-brown, the other one grey." Referring to the color of the neck and back, he stated that both forms "occur in equal numbers everywhere in its area of distribution." He did not say that the dimorphism was sexual, nor did he imply it.

There is a slight sexual dimorphism in size. Females average larger, a condition especially noticeable in wing measurements. According to Manning *et al.* (1956), bills of females average longer. Because of an apparent overlap in bill lengths, one can separate probably only 80 to 90 per cent of the birds on this character alone.

Breeding Distribution in Canada

The Sanderling, a monotypic species, breeds principally in the high Arctic. Although it has a circumarctic distribution, it does not breed continuously around the polar region. Its better known breeding grounds include northern Greenland (Hall and Peary Lands), northeast Greenland south to Scoresby Sound, and Spitsbergen. The extent of its breeding in the Soviet Union is little known, though Gladkov (Bannerman, 1960) reported nesting grounds on the Taimyr Peninsula, Svernaya Zemlya, New Siberian Islands, and at the mouth of the Lena River. It is a rare breeder along the arctic coast of Alaska, and, despite the abundance of the species and the numerous expeditions into the arctic islands, its breeding range in Canada is ill defined.

Roderick R. MacFarlane discovered the first authentic nest of the Sanderling on the mainland of Canada, in the Franklin Bay area east of Fort Anderson, on 29 June 1863, although a Sanderling egg, purporting to be a Purple Sandpiper's, apparently had been collected by Sabine as early as 1823. MacFarlane (1908) considered the Sanderling a rare breeder in the Franklin Bay area where a nesting has not since been reported.

The status of the Sanderling elsewhere along the mainland coast is equally uncertain. Low (1906) reported "Skins and eggs from Fullerton" (Cape Fullerton, northwest Hudson Bay), but the record is vague. On Southampton Island nearby, the species probably breeds at least sparingly — a belief based on reports by Eskimos and juvenile specimens with much natal down (Sutton, 1932). Presumably, Sanderlings breed at least sparingly north and west of Southampton on Melville and Boothia Peninsulas. However, Macpherson and Manning (1959) did not even record the species as a rare breeder on Adelaide Peninsula.

The great numbers of Sanderlings that come south from the Canadian breeding grounds almost certainly originate on the arctic islands, but even there they are not uniformly distributed. Sanderlings appear to be practically absent from huge Baffin Island though no one has explored Brodeur Peninsula for them especially. Records for Bylot Island northeast of there are scarce: Tuck and Lemieux (1959) believed that at least "two pairs" bred on the northwest coast where a "female with a well-developed brood patch" was collected on 20 July 1957 and Drury (1961) reported, for the south coast, only one bird performing a "distraction display."

Farther west, on the southern part of King William Island, the species very likely breeds at least sparingly, as it does on Jenny Lind Island and probably in southern Victoria Island (Parmelee *et al.*, 1967). A major breeding ground is Prince of Wales Island where a large population summered in 1958 (Manning and Macpherson, 1961). Probably Sanderlings breed commonly elsewhere in the central islands (northern King William, Somerset, northern Victoria, Stefansson), but we have no direct evidence. Banks Island in the far western part of the archipelago is certainly a major breeding ground (Manning *et al.*, 1956).

In the northernmost islands of the archipelago, the Queen Elizabeth Islands, the species is decidedly scarce in the mountainous eastern section. For Ellesmere Island, Sanderling records, including some of nests, date back to 1878, but none suggests that the species ever approaches even modest densities. Sanderlings appear to be equally uncommon on rugged Axel Heiberg Island. According to David J. T. Hussell (pers. commun.), they breed sparingly in northeastern Devon Island.

In the extreme northwest, on Prince Patrick Island, Sanderlings bred commonly at Mould Bay in 1949 and only four were observed in 1952 (MacDonald, 1954). Although data on the yearly fluctuations in numbers of nesting Sanderlings are scarce, doubtless these fluctuations occur.

A probable major breeding ground east of Prince Patrick Island is Melville Island where Sanderlings were common at Winter Harbour years ago (Hennessey, 1910), but that island remains mostly unexplored ornithologically.

The Sanderling's status on Bathurst Island heretofore was almost unknown. Harington (1961) recorded the species twice on the tundra between Goodsir and Bracebridge Inlets in 1961, one bird on 29 June and two on 1 July. However, we believe that this area, and probably the vast lake areas in southern parts of the island, may be an excellent breeding ground for Sanderlings in some years.

The barren stretches of northern Bathurst appear to be poorer nesting grounds, and some of the islands northward even less suitable, if the Isachsen area of Ellef Ringnes Island is any indication; MacDonald (1959) did not record the species there at all. The density of Sanderlings may be low east of Bathurst on Cornwallis Island as well; Urban (1957) failed to record one there though I and others have since seen a few at Resolute Bay. Grinnell Peninsula in western Devon Island conceivably is more favorable.

Since MacFarlane's discovery in 1863, there have been few nests reported from arctic Canada. Feilden (1877) reported a nest with two eggs at 82 N Lat. on the north coast of Ellesmere Island on 24 June 1876; Parmelee and MacDonald (1960), one with four eggs, two pipped, at 80 N Lat. near Slidre Fiord in west-central Ellesmere Island on 12 July 1955; Parmelee *et al.* (1967), one with four fresh eggs at 68 N Lat. on Jenny Lind Island on 24 June 1966. With observations of broods almost as scarce, it is no wonder that little is known of the Sanderling's breeding.

Breeding Density

We have few estimates of the population densities of Sanderlings on the nesting grounds. Manning *et al.* (1956), by converting the number of Sanderlings recorded per hour in a given area to an estimated standard number per square mile (multiplier technique), concluded that an adult population of 65,000 birds summered on Banks Island in 1952. Although pairs nested throughout the 24,600-square-mile area, the principal nesting ground was on the western side. The same authors thought that only the Semipalmated Sandpiper (*Ereunetes pusillus*), with an estimated population of 70,000 birds, was more abundant than the Sanderling. They found the other sandpiper species much less abundant: White-rumped Sandpiper (*Erolia fuscicollis*) and Baird's Sandpiper (*Erolia bairdi*), 25,000 birds each; Pectoral Sandpiper (*Erolia melanotos*), 14,000 birds; and Buff-breasted Sandpiper (*Tryngites subruficollis*), 2,000 birds. They gave no figures for the largest number of Sanderlings per square mile for any one area.

On Prince of Wales Island and its small adjacent islands, 12,500 square miles, Manning and Macpherson (1961) estimated the Sanderling population at the beginning of the 1958 nesting season to be 70,000 birds — a population more than twice as dense as that of Banks Island in 1952. Numbers of Sanderlings varied from place to place, ranging in density from 3.5 to 35.0 birds per square mile, and was greatest in the Inner Browne Bay area on the east side of the island, but low in the "rather barren, lakeless, inland country."

Manning and Macpherson considered the Sanderling the most abundant sandpiper on Prince of Wales Island, placing Baird's Sandpiper second (40,000 birds) and the White-rumped Sandpiper third (15,000 birds). This is the only reference putting the Sanderling first in order of abundance on any Canadian breeding ground.

In 1968 the Sanderling was by far the most abundant sandpiper in our study area on Bathurst Island, the Knot (*Calidris canutus*) being only a third to half as abundant and other sandpipers much less. Nevertheless, we hesitate to list the Sanderling as a truly abundant species on Bathurst Island that year, because the pairs were thinly scattered — less so than other shorebirds, however. In 1969 the Sanderling was decidedly uncommon, even less common than Knots.

At Bathurst we visited various areas in the broad, lake-dotted valley between GoodSir and Bracebridge Inlets and concentrated on Sanderlings in two. The first area was a strip of ridges and marsh, roughly a mile wide, that extended six miles west from camp toward Bracebridge Inlet. For the most part the ridges lay in straight lines paralleling the marsh that formed the north shores of the two largest lakes in the valley. Within this six-square-mile area we found five Sanderling nests, five broods (unmarked) of small downy young, and two broods of larger young which may or may not have hatched there. Ten pairs, and possibly 12 or more, bred in this area in 1968.

Sanderlings were scattered all along the six-mile strip during the arrival period and for some days following. With the onset of nesting, some of the pairs concentrated in certain areas. Four of the five nests were within an area five to six miles west of camp; three of the four nests were within a half mile of one another; and two were only 352 paces apart. In another concentration, just west of camp, at least four pairs (one nest, three broods) resided in a one-square-mile area, and two only 520 paces apart.

The second study area was roughly four square miles of variable terrain — ridges, alluvial plains, marshy ponds — extending north, east, and southeast of camp. Here we found five nests and two broods of fairly old young. These too were concentrated with three nests within a one-square-mile area, and two only 520 paces apart.

The three to four pairs per square mile was the greatest concentration of nesting Sanderlings recorded by us on Bathurst Island. Considering that predators probably destroyed the eggs

of some pairs before we found them, that we certainly did not find every brood, and that the late thaw may have kept some pairs from nesting, I believe that the resident population probably did not exceed six to eight pairs per square mile in the choicest areas on the Bathurst breeding ground in 1968. The density in 1969 was much less, perhaps only one to two pairs per square mile.

Although Manning and Macpherson (1961) did not locate nests or broods, they did estimate the adult population on Prince of Wales Island at the onset of nesting. If their figures are taken at face value, it appears that upwards of 17 pairs of Sanderlings may occupy a one-mile-square nesting ground, a reasonable figure considering the proximity of some nests on Bathurst Island. Manniche (1910) gave no data on population densities for the Greenland breeding ground, but one can surmise that Sanderlings are numerous there at times. Although he found only 11 nests during 1907-1908, he observed some 50 broods — itself highly indicative of a dense population. Such a breeding ground has not yet been found in Canada, unless it is on Prince of Wales Island.

Arrival on Breeding Ground

Arrival dates for the Sanderling on the Canadian breeding ground are scarce, practically none for the eastern Arctic, and little more for the western Arctic. Hennessey (1910) reported that Sanderlings arrived at Winter Harbour, Melville Island, on 1 June 1909 but gave no details. On Banks Island (Manning *et al.*, 1956) Sanderlings arrived at De Salis Bay in 1952 no earlier than 8 June. In 1953 the same authors saw a flock of 24 birds at Cape Kellett on 30 May and 100 birds during a four-hour walk there the following day. Presumably both sexes were present. Macpherson and Manning (1959) noted migrating Sanderlings during 14-16 June 1957 on Adelaide Peninsula where the species is not known to breed. Parmelee *et al.* (1967) saw no migrating Sanderlings in spring along the southeastern coast of Victoria Island but witnessed the arrival of the birds on Jenny Lind Island nearby. There, on 7 June 1966, they saw what appeared to be the first Sanderlings—a flock of 13 of both sexes—at a marshy pond two miles inland and on the following days noted widely scattered pairs, invariably a bright male and a dull female.

The arrival is better known for Greenland. According to Salomonsen (1950-1951), the spring migration takes place extremely rapidly, there being no spring records for southeast Greenland and none south of Disko Bay on the west coast. The birds arrive on the breeding grounds in late May and early June. At first the Sanderlings move about in "flocks of 8-12 individuals, frequenting the sea-shore and the few spots free of snow." After a "couple of days they are paired" and move inland to the breeding places. Pedersen (1930) recorded the arrival near Scoresby Sound, respectively, on 26 May 1928 and 2 June 1929; the birds immediately proceeded to the interior of the fiord where during the first days they went about in groups; after 8 June they "paired off" and two days later left the coast for the inland breeding ground. Manniche (1910) made the point that the Sanderlings arrived at Stormkap "singly or in couples," respectively, on 2 June 1907 and 28 May 1908, though he believed that "pairing began towards the middle of June." He further stated that the Sanderlings at Stormkap in the first days after their arrival resorted to snow free areas in the marshes and on the surrounding stony plains in company with other waders and large flocks of Snow Buntings. According to his experience, the "old birds would never resort to the salt water shore."

The first Sanderlings, seen on Bathurst Island in 1968, were well inland. Two birds of undetermined sex flew by me some five miles east of the head of Bracebridge Inlet on 3 June. The same day Hampson watched a mixed flock

ood, and that the population prob-
on the Bathurst e to two pairs per

they did estimate : figures are taken a one-mile-square 1 Bathurst Island. eding ground, but und only 11 nests dense population. e of Wales Island.

ng ground are or the western t Winter Har- Banks Island 952 no earlier t Cape Kellett following day. g (1959) noted insula where no migrating island but wit- tere, on 7 June k of 13 of both ng days noted ale.

o Salomonsen ly, there being sko Bay on the May and early individuals, fre- 'couple of days edersen (1930) May 1928 and or of the fiord r 8 June they eding ground. d at Stormkap y 1908, though .” He further r their arrival ng stony plains ngs. According ater shore.” re well inland. of the head of a mixed flock



A male Sanderling, *Crocethia alba*, in breeding plumage.
Painted in June 1969 on Bathurst Island by George Miksch Sutton.

of eight birds, four bright and four pale, that had alighted near camp. We saw none the following day, but by 5 June single males were displaying in widely separated places, and the male and female of one pair that flew and fed together behaved as if they were mated. We saw no Sanderlings immediately along the ice-locked shores of Bracebridge Inlet where there was little melt water on 5 June.

The Sanderlings continued to arrive inland. A mixed flock of 10 birds flew along a ridge three miles west of camp on 7 June. We saw the last flock, seven birds of both sexes, feeding on muddy ground, where the thaw was most evident, a mile north of camp on 9 June. No other species accompanied these flocks although the Sanderlings in the flocks, both single and paired birds, shared the feeding areas with other species. Pairs increased daily after 5 June until, by 11 June, the Sanderling was the most abundant wader on the tundra between Goodsir and Bracebridge Inlets—a distinction it held for the remainder of the season.

Paired birds were inseparable. When one of the pair flew, the other quickly followed. On the ground the bright male walked with a jerky gait and chattered loudly on occasion while the female, usually much duller and always somewhat agitated, followed and regularly uttered a sharp, one-syllable note in our presence.

Because of the considerable individual variation in the plumage of these birds, we were reasonably certain that we saw the same pairs time and again in special areas where they walked about and fed. The female of the pair that frequented our camp, for example, was excessively pale. Although certain pairs left their special loafing and feeding areas for long periods, they nevertheless returned often enough to hold our attention. So attached were they to the special slopes and ridge tops that we spent much time in those places searching for nests. Not until later did we discover that these birds nest in different areas and usually mate in still others (see Precopulatory Scrapes below).

In 1969, Sanderlings arrived on Bathurst Island somewhat later. The first that we recorded inland flew along the frozen valley northeast of camp on 6 June, and a mixed flock of six birds visited camp on 8 June. Except for one pale individual on a ridge two miles west of camp on 10 June, we did not see the species anywhere during 9–11 June. The bulk of the Sanderlings appeared between 12–15 June when we saw singles, pairs, and a few mixed flocks of five to 10 birds each. Thereafter, we noted only thinly scattered singles, pairs, and triplets.

Both sexes arrive together on the inland breeding ground in small flocks of probably from two to 13 or more birds. Some of these birds seem to be paired on arrival although we have no proof of this. It also appears that most Sanderlings go about in pairs soon after the flocks break up. Single, unmated Sanderlings, seemingly a small minority, occur both early and late in the season. Whether these birds arrive alone is uncertain. Many of these points need further study.

Territory

The territory of the Sanderling is basically a plot of level or sloping, wet or dry, ground over which the male performs flight displays in advertising for

a mate, and which, until he pairs with a female, he defends vigorously against other males of his kind. We did not determine the precise limits of any one territory. It seemed to include an area approximately equal to that covered by the male when performing flight displays—an area with a radius of roughly 200 yards. The territories were so widely scattered on the Bathurst Island breeding ground that we were never aware of two or more of them close enough to be a source of constant fighting, though conceivably this does happen.

The problem is further complicated by unmated males which appear to be relatively few in number, but which do most, if not all, of the performing and defending. These males do not defend their territories at all times. They appear on them sporadically for indefinite periods. Several different males may use certain favored areas, each in turn, no two displaying or defending at once. Such was the case a quarter-mile from our camp on a well-defined slope frequented by both Sanderlings and members of our expedition. In 1968, a very bright male displayed there as early as 13 June; another exceedingly dull male displayed there on 9 July, our latest date for flight-displaying though we heard flight-singing until 13 July. At least four different males performed on the slope at various times that year.

We may question the size and use of the territory, but not its defense. A male, when present, defends his chosen ground to the limit—a fact appreciated by Manniche (1910) who stated that the male also defended it against other species. We noted defense against Sanderlings only. The defending male quickly flew to a strange Sanderling entering his ground. If it were a lone male, he chased it hard. If it were a lone female, he courted. The male also investigated all pairs, and the confrontation that followed often ended in a swift flight chase by the trio. Sometimes both members of a mated pair turned on the single male and attacked it viciously with body-to-body contact.

The conspicuous flight chases by three or four birds is a phenomenon common not only to Sanderlings but to many other shorebirds as well. Presumably both sexes take part but this is not well documented. Our observations on the Sanderlings, the sexes of which can usually be separated during breeding time, may shed some light. Such chases often started with a confrontation between a single defending male and a mated pair. MacDonald's observation in 1968 is of special interest: At 00:05 hours on 18 June a performing male flew down and landed within five feet of a mated pair. The paired male immediately raised his scapulars, lowered his head, and rushed at the single male which erected his feathers and charged, but then turned and ran. The female, meanwhile, left the ground and flew close to the single male which leaped into the air after her. The mated male followed him and the trio flew off in a typical erratic flight. Eventually they broke up while flying. The female flew down to the ground, her mate glided in behind on V-set wings, and the defending male continued flight-displaying. He was still displaying when MacDonald left at 03:30.

Paired birds walking about in undefended areas usually ignored one another. Occasionally a confrontation between pairs terminated in a flight chase when one of the females jumped out in front of the others and flew off. Invariably the males and sometimes the remaining female followed her. So it

appears that the female may initiate a flight chase which may or may not concern territorial defense.

Flight Display

In 1968, we first noted Sanderling flight displays less than half a mile from the head of Bracebridge Inlet on 5 June — within two days of the species' arrival and one of few pleasantly mild days that month. Flying up from wetish spots and moving low for short distances above the gentle snowy slopes, two widely separated males rose on rapidly vibrating wings and sang lustily. Dropping down to exposed turf, they soon performed again. Another male flew and sang above low-lying ridges, partly free of snow, three miles east of the inlet, and we were certain that courting activities would soon be common in many places.

The weather turned for the worse on days following. Flight-displaying, like the thaw, never did rush forward on a broad front in the Goodsir-Bracebridge area. Although Sanderlings were more persistent in displaying during inclement weather than other shorebirds, including Knots, their display activities were highly sporadic and usually brief. Sanderlings displayed vigorously during calms or low winds even though the air was frigid and the ground beneath them mostly snow covered. High winds seemed to inhibit their displaying more than any other physical factor yet were not the only factor influencing flight display.

From the beginning the males did not perform flight displays before females. Almost invariably a displaying male flew or hovered above an area where we could not find a female. According to Manniche (1910), flight-displaying (called "pairing display" by him) can take place without the presence of a female. This indicates that flight display of the Sanderling, like its territory, functions primarily in advertising for a mate. If this is true, the display probably falls off sharply or ceases with the establishment of a pair-bond. Although we observed many pairs on the ground for long periods, we never saw a male suddenly leave his mate and perform. Since most pair-bonds form early, only unmated males are left to perform and they may at times be so scarce, especially during those years when the population is low, that one may not notice any flight-displaying.

Of the relatively few Sanderlings we saw on the Jenny Lind Island breeding ground in 1966, all formed pair-bonds before or soon after arrival. It may be significant that we saw no flight display there that year, and that we recorded flight-displaying only twice, 19 and 21 June, on Bathurst Island in 1969 when the population was low.

Manniche (1910) briefly described the flight display of the Sanderling, stating that the male uttered a snarling or slight neighing sound, mounted to a height of some two meters from the ground on strongly vibrating wings and continued his flight for a short distance at this height, most frequently in a straight line but sometimes in small circles.

We noted the display a number of times on Bathurst Island in 1968. In flight, the forward part of the male's body is more or less parallel to the ground, the tail is level with the body, or down turned, and usually somewhat

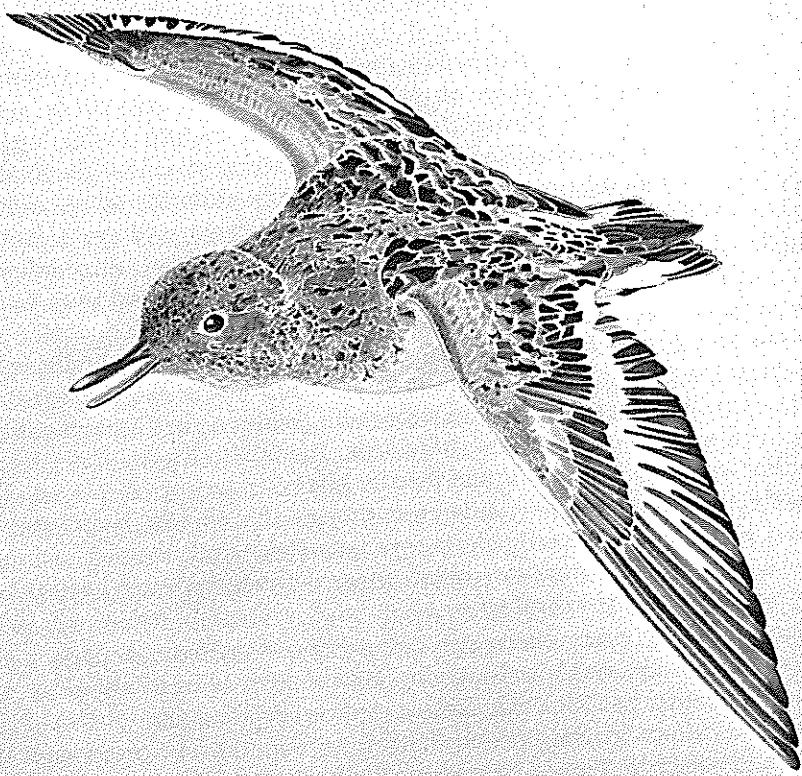


Figure 4. While performing its flight-display, the male Sanderling moves its wings up and down through a 45-degree arc at such great speed that they literally vibrate. The rapid wing-beats are not continuous but in bursts, and each burst is followed at irregular intervals by a brief pause during which the wings remain perfectly immobile. The white of the wing, which is still clearly visible during rapid wing-beats, is shown in detail in this drawing which I made directly from the spread wing of a mounted specimen.

spread; and the head is drawn back presenting at times a hunched appearance—also typical of the displaying bird on the ground. The head and bill are pointed straight ahead or turned down slightly; both move frequently from side to side as the bird surveys the ground below. The wings, held straight out from the sides of the body, move up and down, through a 45-degree arc, at such great speed that they literally vibrate, although the prominent white wing-bars are still clearly visible (Figure 4). The rapid wing-beats are not continuous but in bursts, and each burst is followed at irregular intervals by a brief pause during which the wings remain perfectly immobile, fully extended, and parallel to the ground. The rapid wing-beats through the narrow arc, followed by the brief pauses, produce a most peculiar flight.

The ascent from the ground may be rapid or slow, as may be the forward flight above ground and the descent. The bird descends either abruptly or slowly in a long arc, sometimes with wings extended and held far out, resulting in a glide. On occasion the bird descends to a foot or two above ground and flies for many yards before touching down. Many times a bird about to land suddenly picks up momentum and continues displaying. It may repeat this performance several times before landing.

Manniche (1910) did not mention hovering by displaying Sanderlings, and I find no reference to it. It is true that the male often performs a complete flight-song without hovering; in other words, the bird moves forward continuously. But frequently a displaying male stops in midair and hovers in one spot, during which a series of rapid wing-beats are followed by brief pauses, as when the bird moves forward. The hovering at times is very conspicuous, and we once timed a hover that lasted fully two minutes. On the other hand, the entire flight display, from take-off to touch-down, may take as little as 30 seconds or even less.

The height of the display flights is said to be very low—only “two meters” (Manniche, 1910), only “as much as 15 ft.” (Witherby *et al.*, 1940), and only “2–3 metres” (Salomonsen, 1950–1951). We saw Sanderling males performing commonly from 15 to 30 feet above ground and occasionally 60 feet or more. Even these high flights, however, do not approach the high flights of certain shorebirds. Compared to the Knot, Stilt Sandpiper (*Micropalama himantopus*), and Hudsonian Godwit (*Limosa haemastica*), the Sanderling is essentially a low-altitude performer.

The flight display of the Sanderling has been described simply as one that covers a “short distance,” meaning a small area of ground. Once again, compared with those of the Knot, Stilt Sandpiper, and Hudsonian Godwit, the statement is valid. We measured the distance from point of take-off to point of touch-down several times and estimated the distance a good number of times, finding that most displays fell within a radius of 200 yards. Occasionally males covered a much greater distance, and sometimes flew out of sight. Displaying birds flew in a “straight line” or “small circles,” as described by Manniche (1910); also, erratically with no clear-cut direction at times.

The song of the flight display is highly complex, so difficult to describe in terms of phonetics that I hesitate to try lest I add to the confusion of the various renditions given it by others. However, I can say that the song was loud and distinct, given by performing males above ground, and occasionally by performing males on the ground immediately preceding flight display. To all of us the notes seemed so frog-like that I refer to it as the frog song. Like the rapid wing-beats during display, the song was delivered in bursts, though we could not be sure that the wing-beat and song were synchronized. The frog song was frequently, yet not invariably, followed by chattering notes during the descent immediately before the flight terminated. The chattering notes, equally difficult to describe, were of a familiar type given by non-performing birds. We taped both calls under adverse conditions.

We believe that female Sanderlings performed flight displays, heretofore unreported in the literature, at least a few times on the Bathurst breeding

gs up and down
1 wing-beats are
by a brief pause
ch is still clearly
directly from the

ched appear-
d and bill are
equently from
ld straight out
degree arc, at
ominant white
-beats are not
ar intervals by
obile, fully ex-
igh the narrow
ht.

ground in 1968, but we did not collect a displaying female for positive identification. However, I saw such a display on 18 June the following year. The pale bird of a pair, that I had been watching for over an hour, suddenly left the ground on rapidly vibrating wings, ascended to a height of 30 feet, descended 10 feet, ascended again, and finally glided down to a muddy slope where it was immediately joined by the much brighter mate which gave every indication of being a male. The flight was like that of a male, except that I heard no vocalizations of any sort, and the bird did not hover. The peculiar mating behavior (described below), following the flight, indicated that the pale bird was almost certainly a female and not merely a pale male involved in the phenomenon of reversed copulation. What the adaptive function of such a display could be is puzzling, unless it is one of a number of devices employed by the female in strengthening the pair-bond which in Sanderlings appears to be weak. Possibly the female display reduces hostility between the sexes, or simply advertises the nesting ground.

Ground Display

Manniche (1910) evidently saw pairing take place on the breeding ground in northeast Greenland. He described the male as frequently sitting on "... top of a solitary large stone, his dorsal feathers blown out, his tail spread and his wings half let down, producing his curious subdued pairing tones." He further stated that the male ". . . soon returns to the female, which always keeps mute, and then he tries by slow affected, almost creeping movements to induce her to pairing, until at last the act of pairing takes place; when effected both birds rush away in rapid flight to return soon after to the nesting place." Manniche's meaning of the term "pairing" is not clear. Salomonsen (1950-1951) interpreted the findings of Manniche and others to mean that, following flight-displaying, the male displayed to the female either from a protruding boulder or rock or by running on the ground, and that copulation followed. These authors give the impression that copulation, not merely the establishment of the pair-bond, follows displaying immediately. Whether display by the male alone initiates copulation is questionable. In observing precopulatory behavior (see below) many times, we concluded that females, not males, initiate successful copulation.

We were not certain that any of the ground displays (never on a rock), observed on Bathurst Island, were steps leading to establishment of a pair-bond. Some appeared to be. The first occurred on 7 June when a bright male ran with a dull female near the top of a wind-swept ridge. With head drawn far back against shoulders, bill straight ahead, feathers erected, tail slightly depressed, and wings drooping with primaries partly spread, he closely followed the female until the run terminated in a flight.

Some ground displays were dramatic. On 26 June a single bright male with his head so withdrawn and feathers so puffed out that he appeared ludicrous ran up a muddy slope to a pale female. Uttering notes almost inaudible in the wind he extended both of his wings fully and arched them down near the tips, causing the somewhat spread primaries to drag on the mud and wet turf. He spread his tail and turned it downward. Viewed from the back, the

ve identi-
The pale
y left the
descended
ere it was
ndication
heard no
ar mating
pale bird
ed in the
of such a
employed
appears to
e sexes, or

ing ground
; on "... top
spread and
tones." He
hich always
ovements to
hen effected
sting place."
nsen (1950-
at, following
t protruding
on followed.
he establish-
er display by
g precopula-
es, not males,

r on a rock),
ent of a pair-
a bright male
n head drawn
l, tail slightly
he closely fol-

e bright male
appeared ludi-
nost inaudible
em down near
e mud and wet
a the back, the

white of the tail was nearly continuous with the white of the wing-bars, and we wondered whether this bold display of white ever functions as a releaser. In this case, it did not.

Because we never witnessed copulation following displays of this type, we felt that the birds were not truly paired. Nearly all copulatory activity among the Sanderlings occurred in areas quite apart from the areas where the birds nested though single males occasionally performed flight displays over or near such areas. Invariably, the female initiated copulation by displaying in special nest scrapes that we called precopulatory scrapes.

Precopulatory Scrapes

Although a few Bathurst Island Sanderlings may have had eggs as early as 16 June in 1968, the pairs we watched did not lay before 20 June. That day, on a flat stony terrace just up from a slushy stream bed, a pale Sanderling ran toward us scolding. Flying off once, it quickly returned and scolded again. We backed off and watched this bird, which we believed to be a female, but it did not go to a nest.

The following day a bright male was with a pale female, likely the one seen earlier, in precisely the same place. With head withdrawn and feathers fluffed out, he immediately voiced protest. Then both birds put up such a fuss as to make us feel certain that one of several neatly lined scrapes found there had to be the nest. The pair especially favored one scrape, a rather deep cup freshly lined with dry willow leaves and lichens and surrounded by *Dryas*. We called it Nest 1 and erected a blind nearby.

On 22 June at 02:30 hours, Hampson and I watched the pale female settle in Nest 1 with head low and tail almost vertical. She squirmed a little, and the male which had been standing close by ran and thrust his bill down beside her and several times removed bits of lining from the scrape. Then he stood on her back, stepped off, and deliberately eased her out of the scrape with his bill and forehead thrust beneath her belly. Both then ran off side by side with bodies pressed together and rubbing vigorously. Having run some 10 feet, the male lowered his head and pressed his bill forcibly against the breast of the female, immediately stopping her. She stood still and copulation followed.

We thought his mating procedure most unusual and wondered if it was typical. Later on 24 June, at 04:30, we saw a pale female settle low in a scrape about a hundred paces from Nest 1. Her head was hidden from view, but not so her posterior which was elevated high above the scrape and surrounding stones. As before, the male ran up and deliberately eased her out with bill and forehead, though he did not pick at the lining of the scrape and stand on her back this time. Both ran for 10 feet, rubbing sides as they went, the male seemingly rubbing the hardest and running about a half step behind. Once again he stopped her by pressing his lowered bill against her breast. Immediately the female stood still and the male mounted. Later, when the female investigated other scrapes, squatting in one of them, the male, some distance away, did not respond. Eventually they flew off together and disappeared over low-lying hills.

After these two instances we saw remarkably similar behavior among other Sanderling pairs. The sequence of the female squatting in the scrape with rear elevated, the male easing her out with his bill and forehead, the side-to-side-rubbing-run, and the breast-pressing, followed by copulation, all appeared to be basically typical and similar with some variation. Taylor made additional observations at 07:30 on 24 June: When a male first approached a squatting female, he walked around the scrape six times with his shoulders and sides brushing hers; the male positioned himself a full step ahead of the female near the end of the side-to-side-rubbing-run, and by the time the female had stopped running, the male was facing her nearly head-on with forehead as well as bill pressed hard against her breast.

At least four widely scattered pairs used scrapes on the stony stream terraces north of camp for mating purposes. Other pairs used similar precopulatory scrapes on the ridges west of camp. All of the scrapes, including Nest 1, were eggless. We continued to watch them although we soon learned that the Sanderlings using them were nesting elsewhere, seemingly a long way off in some cases. However, we did see precopulatory scrapes and copulatory activity sparingly in a nesting area both years.

Upon closer inspection, the precopulatory scrapes appeared to be old nests, possibly of other species and perhaps used later by Sanderlings. Compared to genuine Sanderling nests, they were often larger and invariably deeper, neater hollows. The active movements of the Sanderling smoothed the scrape and gave it the unmistakable appearance of freshness.

We studied Sanderling precopulatory behavior with renewed interest on the Bathurst breeding ground in 1969, but noted only one behavior that we had not observed the previous year. On several occasions I heard a female, positioned carefully in a scrape, utter low buzzing notes—not unlike the sound of a typewriter carriage in motion — while awaiting the male. The buzzing notes appeared to attract the male and in conjunction with body posture may have functioned as enticing notes. Unfortunately, we did not record them.

That Sanderlings use old scrapes during precopulatory activity there can be no doubt. In 1969 a pair of Sanderlings used a well-defined scrape that I had marked with rocks in 1968. To our knowledge no Sanderlings had used this particular scrape the first year. Conceivably, Sanderlings make precopulatory scrapes when none exist. The Bathurst breeding ground is literally covered with scrapes that probably last for years under desert conditions of the high Arctic. Pedersen (1942) noted that the Sanderlings in Greenland used empty scrapes which he called "playing nests," stating that they were a "self-dug hollow lined with dry *Dryas* and *Salix* leaves." He did not know their function, but speculated that the "birds wanted to throw off possible enemies with these nests by sitting on the empty nest as if brooding and flying away abruptly when the intruder had approached the nest to a distance of a few steps."

Copulation

No one has described copulation in the Sanderling. Manniche (1910) stated that the "act of pairing" was the "completing act" that followed flight and ground displays. Presumably his "act of pairing" meant copulation.

Salomonsen (1950-1951) arrived at the same conclusion. Unfortunately, Manniche was vague on this point and made no attempt to describe the act in detail; conceivably, he never witnessed it.

We watched copulation in the Bathurst Island Sanderlings at least a dozen times during 22-26 June in 1968, and again during 18-25 June in 1969. Invariably, it occurred after a female squatted in a precopulatory scrape or hollow and, usually, after the birds had completed the side-to-side-rubbing-run and breast-pressing. When the female finally stopped running and stood still on straight legs, the male mounted her back. Maintaining his balance by fluttering, he jabbed at her head and frequently pulled her crown and nape feathers with his bill. Copulation occurred when both turned their tails; the actual contact lasted less than five seconds. Near the completion of the act, the female usually ran in small circles, eventually dislodging her mate. Then she ran off with feathers somewhat fluffed or, sometimes, crouched with feathers somewhat disarranged.

The entire act, from the time the male mounted until she dislodged him, was surprisingly long—40 seconds or more. One act, timed by Sutton counting slowly from one to 148, lasted at least two minutes; another, timed by Hampshire with a watch, lasted fully three minutes and 25 seconds. The fact that these birds have such elaborate precopulatory and copulatory behaviors suggests the pair-bond is weak and needs constant reinforcing. The aggressiveness later helps split the pair-bond—which in Sanderlings occurs surprisingly early, before steady incubation takes place (see below).

The female Sanderling appears to take a major role in reinforcing the weak pair-bond. She usually follows the male about and vocalizes the most on the ground. When a strange female appears, she runs with feathers erected and tail spread, squatting with tail up in every depression she reaches in a concerted attempt to entice the male back. Even while she is running along the ground outside a scrape she utters the low, buzzing, typewriter-like notes described above. If her mate flies after a strange female, she follows, whereupon another kind of flight chase ensues that involves three birds.

Nest Sites

Many years ago Manniche (1910) described the nesting habitat of the Sanderling in northeast Greenland as "dry clay-mixed stony plains sparsely covered with *Salix arctica*, *Dryas octopetala*, *Saxifraga oppositifolia* and a few other scattered low growths." He stated that he never found nests on moors or on plains entirely uncovered though, apparently, he found the most nests on "stone-isles" which he described as scattered islands of stone and clay within the extensive moor-and-marsh stretches west of Stormkap. He thought that the distance from, and elevation above, the sea were of little consequence, but that the presence of freshwater lakes or ponds was significant.

Manniche's description probably suffices for many Sanderling nests in the Canadian Arctic archipelago. Most of the 14 nests, seen by us on Bathurst Island, and one each on Ellesmere and Jenny Lind Islands, were on stony, well-drained ridge tops (Figure 5), gentle slopes (Figure 6), or level alluvial plains (Figure 7), each with sparsely scattered willow, *Dryas*, and saxifrage plants —

among
the scrape
head, the
ation, all
n. Taylor
e first ap-
s with his
full step
nd by the
ly head-on

stream ter-
precopula-
ing Nest 1,
ed that the
way off in
ory activity

l to be old
lings. Com-
l invariably
noothed the

l interest on
vior that we
rd a female,
ke the sound
The buzzing
posture may
record them.
ity there can
pe that I had
had used this
precopulatory
rally covered
is of the high
d used empty
re a "self-dug
their function,
nies with these
away abruptly
w steps."

anniche (1910)
followed flight
nt copulation.



Figure 5. Nesting habitat of the Sanderling. One pair nested (number 13) in a clump of purple saxifrage on the fairly well vegetated, but nearly stoneless, ridge in the foreground. The banded male that incubated here in 1969 also attended eggs and young in 1968 at Nest 7, which at the time was two miles northeast in bluff country (upper right corner) beyond the broad, nearly snow-covered valley of the Goodslir River. Following the laying of the fourth egg at Nest 13, the clutch was abandoned for more than five days. The banded male suddenly reappeared and commenced incubating without assistance. The interval from laying to hatching of the fourth egg was surprisingly long—31.6 days.

essentially low-level dry tundra that was firm underfoot except for brief periods following the thaw. We found two nests on frost-heaved polygons with the ground soft and wet, thinly covered with scattered willow, and extensively enclosed by wet tundra and marshy ponds — hardly the expected spot for nesting Sanderlings.

On Bathurst Island in 1968, MacDonald collected plant samples in a typical Sanderling nesting area where probably less than 30 per cent of the ground had plant cover. Of the 21 species, *Saxifraga oppositifolia*, *Salix arctica*, and *Dryas integrifolia* were dominant. Of lesser importance were *Alopecurus alpinus*, *Festuca baffinensis*, *Poa abbreviata*, *Puccinellia angustata*, *Juncus biglumis*, *Luzula nivalis*, *Oxyria digyna*, *Arenaria rubella*, *Cerastium alpinum*, *Stellaria* sp., *Papaver cornwallensis*, *Cardamine bellidifolia*, *Draba Bellii*, *Parrya arctica*, *Saxifraga caespitosa*, *Saxifraga cernua*, and *Saxifraga tenuis*.

Without exception all the Sanderling nests were in exposed situations, open to the sky and, although surrounded by barren, nearly sterile slopes in some cases, were within a few hundred yards of a marshy pond, and within a mile of extensive wet tundra. Most were below 200 feet elevation; one, on a rugged slope at least 500 feet in elevation, was close to marshy spots continuously receiving water from great banks of slowly melting snow.



Figure 6 (above). Gentle slopes with scattered saxifrage, willow, and *Dryas* are readily utilized by nesting Sanderlings. Although the ground shown here is muddy during the period of egg-laying, it soon dries. The gullies close by provide the birds with wet feeding areas for many days. Muskoxen, caribou, and hares (one at middle right) also frequent these slopes. A young hare nearly destroyed a Sanderling's egg when it accidentally stepped on the nest.

Figure 7 (below). Nesting habitat of the Sanderling. Nest 5 (1968) and Nest 14 (1969) were only 110 paces apart in dark patches of purple saxifrage on this flat, stony alluvial plain. Goodsite Inlet lies six miles eastward and beyond the bold, partly snow-covered ridge facing west in the background. King Eiders and Black-bellied Plovers also nested here. Knots preferred the barren ridge tops.



In 1968, we found the first Sanderling nest, with one egg, on 21 June in a snow-free spot of muddy ground where the ridge top all about was wet and covered with patches of soft snow, several of which were inches from the nest. By the time the clutch was complete on 25 June, all snow about the nest and nearly all on the ridge top had disappeared. Deep snow remained for many days in a gully and on steep slopes nearby.

We found other Sanderling nests that year with clutches completed and most of the snow in the nesting areas already melted. After examining each site with reference to lay of land and wetness of ground, and noting that other species, e.g., King Eiders (*Somateria spectabilis*) and Black-bellied Plovers (*Squatarola squatarola*), laid eggs in exposed, muddy spots near melting snow in the same areas, we concluded that most, but not all, of the Sanderling nests probably had been close to soft snow during egg-laying. In 1969 we found the first Sanderling nest, with one egg, on 25 June on a muddy slope where snow was rapidly disappearing.

In 1968 the tardy nesting of one Sanderling may have been the result of a stubborn thaw and persistent snow cover. The nest, one of two on polygon ground enclosed by marsh and collected on 11 July along with the attendant bird, contained fresh eggs when other Sanderling eggs were much advanced. The ovary of the female had only four ruptured follicles, indicating that the bird was not renesting. Because the marsh in which this nest was situated had deep snow and ponds nearly frozen shut as late as early July, so far as we knew, no birds of any species nested there. Possibly some shorebirds, like many water-fowl, are so tied by tradition to nesting places that they delay or skip nesting altogether in years when their favored breeding spots fail to open up.

The hypothesis may partly explain why Sanderlings and other shorebirds do not use the many seemingly suitable snow-free areas soon after their arrival. Sanderlings probably did not lay eggs much before 16 June on the Bathurst breeding ground in 1968 although nearly two weeks had passed since their arrival on 3 June. And most birds waited until after 20 June despite the fact that there were extensive low-level dry tundra areas open in early and mid-June. Egg-laying started even later in 1969.

Selection of Nest Site

In 1968 we failed to note a Sanderling selecting a nesting spot, having been repeatedly led astray by the birds' activities at precopulatory scrapes outside of nesting areas. On 25 June 1969 we witnessed the selection of a nest site by a pale female whose bright mate was a bird we had banded at a nest the previous year.

Sutton and Taylor first saw the pair on a slope a mile and a half west of camp. Although we had seen no precopulatory activity, the birds engaged in what appeared to be successful copulation at about 12:00 hours. For the next three hours I followed the birds about the slope, recording activities that were anything but typical of precopulatory behavior.

Without making any attempt to attract the male through vocalizations or body postures, the female settled in depressions or hollows in the turf on six different occasions, each time fluffing out her feathers as though she were

setting on eggs, and usually remained less than a minute. She twirled, tossed bits of material out of the hollow, and, at least once, scratched out material with her foot. Several times the male attempted copulation, indicating that the very presence of a female in a hollow is at times stimulus enough to elicit response. All but perhaps one of his attempts were, however, quickly aborted by the female which simply failed to respond.

At 15:00 hours the female settled in a hollow and remained there for five minutes, leaving only once for a few seconds. She settled down so comfortably within this hollow that I at first believed she had a full complement of eggs; there was not one. Finally, the male ran up and pried her out with his bill. He then attempted a side-to-side-rubbing-run, and even copulation, without success. Several hours later she laid the first egg of a four-egg clutch in this very hollow (Nest 13).

Nests

According to Manniche (1910), the Sanderling in northeast Greenland nests at the edge of, or in, a tuft of *Dryas*. He stated that the bird formed a cup-shaped hollow, not very deep and sparsely lined with withered leaves of *Salix arctica* or other plants growing in the vicinity. He further stated that the situation of the nest, like that of the nesting habitat, was extremely constant. J. H. McNeile (*in Bannerman, 1960*) reported that all nine Sanderling nests, found on Spitsbergen during 1931–1932, were filled with the “brown Arctic willow leaves.”

The nests we found on Bathurst Island were similar, except that six nests were in *Salix*, five in *Saxifraga* (Figures 8 and 9), and only two in *Dryas*. Most were partly filled with dry, withered saxifrage or willow leaves mixed with lichens, chiefly *Thamnolia vermicularis*, bits of moss, and occasionally dry willow twigs and pebbles. Taylor found a nest on 13 July 1969 in a “frost crack” on bare ground near a saxifrage. On Ellesmere Island I saw a nest in *Dryas* which was partly filled with dry willow leaves; on Jenny Lind Island I saw another in a slight depression in a bare spot, partly filled with dry willow leaves and lichens.

Sanderlings enlarge nest hollows even before egg-laying, but whether they ever line or add material to the hollow is questionable. I believe that in some cases Sanderlings simply drop the first egg in a depression, be it ever so slight; and that they enlarge the depression gradually during egg-laying and incubation. I believe also that most, if not all, of the plant material that partly fills the cavity accumulates through accident rather than through any deliberate action on the part of the bird. McNeile (*in Bannerman, 1960*) observed some Sanderling scrapes that were very shallow; one looked as if it might have been an old Purple Sandpiper’s—an observation further suggesting that eggs are simply dropped into depressions without much scrape-building on the part of the Sanderling.

The Bathurst Island nests, especially those situated in willows, were slight, rather crude depressions in which dry leaves accumulated through wind action or some other disturbance. At most of these nests green willow shoots grew through the dry linings of leaves by the time the eggs hatched.



Figure 8. Incubating male Sanderling at Nest 5 in purple saxifrage on the stony alluvial plain six miles west of Goodslir Inlet on 3 July 1968. We trapped and banded this individual (partial Band Number 125101) at this nest which was later destroyed by a predator. The banded bird returned in 1969 and nested close by (see Figure 9). Although we believed that it was a male from the start, the sex was not proven until it was collected at Nest 14 on 28 June 1969. The summer feathers of this bird were so bright that Sutton decided to use the specimen as his model for the Sanderling painting (Plate I).

Nest 2 on Bathurst Island, in a small clump of purple saxifrage, was atypical in that it was filled exclusively with the white lichen that overflowed the saxifrage onto the bare ground beside it. On 21 June the nest contained only one egg partly buried in the loose lichens, leading us to believe at first that the bird had covered its egg. This was not the case.

We found this nest (Nest 2) by watching an adult Sanderling, believed to have been a male, that walked to the saxifrage clump and deliberately poked and tossed lichens and what appeared to be a large chunk of saxifrage into the air. Then it settled down on that very spot and turned several times before running off. This happened some 10 hours after the first egg had been laid. Throughout egg-laying, and right up to the end of incubation, the Sanderling gradually modified and somewhat enlarged the hollow. Even the lichens on the ground immediately adjacent to the saxifrage were removed in time. Taylor, who scattered additional lichens around Nest 2 on 17 July, saw the parent bird remove these lichens within a few hours time. The result of this activity was a neat cup of white lichens that contrasted sharply with the dark saxifrage. Significantly the bird never added any dry leaves to the nest during the long period of observation.

Egg-laying Period

Following discovery of the first egg at Nest 2, at 23:30 hours on 21 June 1968, I checked the site regularly at one- to two-hour intervals. The second egg was laid between 17:00 and 18:30 on 22 June. Up to that time we had not seen any Sanderlings on or near the nest, which appeared undisturbed; lichens still partly covered the single egg.

The two eggs were fully exposed. We covered them with lichens and they remained concealed until at least 21:30 the following day, indicating that no bird had been on the nest for 27 hours. By 22:20 the eggs had been moved and exposed.

The female laid the third egg between 23:15 and 23:25 on 23 June, making the interval between the second and third eggs 29 hours, 35 minutes (± 50 minutes). The pair had made no attempt to cover the three eggs. Still, the Sanderlings did not incubate, though at least one bird visited the nest a few times up to the laying of the fourth egg. Of this we were certain for each time that we covered the eggs, the returning bird uncovered them and moved them as well.

The bird laid the fourth egg between 02:15 and 03:15 on 25 June, making the interval between the third and fourth eggs 27 hours, 25 minutes (± 35 minutes). Steady incubation commenced after completion of the clutch. We did not determine when it actually started.

In 1969 we observed egg-laying at Nest 13, which was empty when first discovered at 15:00 hours on 25 June, and had the first egg by 22:45 that same day. Very likely it had been laid during the period from 21:00 to 22:45, since the second egg appeared sometime from 01:45 to 02:15 on 27 June. The interval between the first and second eggs was at least 27 hours.

We saw laying of the third and fourth eggs in Nest 2 from a blind. The female arrived at the nest at 05:05 hours on 28 June. After fluffing her feathers



Figure 9. Incubating male Sanderling at Nest 14 on 28 June 1969. This same male nested 110 paces away during the previous summer (see Figure 8). Females may enlarge the nest cup before and during egg laying; and at any given nest the one incubating bird, either male or female, may further enlarge the cup. Nothing is added although bits of plants, usually dry leaves and lichens, fall into the cup through the movements of the bird or wind action. The white, wormlike lichens (*Thamnolia vermicularis*) that adorn the saxifrage and surrounding stones are everywhere common on the Bathurst breeding ground.

and changing her position several times, she stood up, stretched, and no doubt laid her third egg at 05:40 when she wobbled noticeably. After that time she turned around frequently, preened, and probed at the vegetation outside the nest cup until we flushed her at 05:58. The interval between the second and third eggs was 27 hours, 40 minutes (± 15 minutes).

On 29 June the female ran into the nest at 07:26 hours and probably laid her fourth egg at 07:48, leaving the nest when flushed at 08:25. As before, there had been much turning, arranging of feathers, and probing outside the nest cup, especially after the egg had been laid. The interval between the third and fourth eggs was close to 26 hours, 28 minutes.

Except for those times when the female went to the nest to lay, neither adult visited the nest, so far as we could determine. Actually we failed to find the birds anywhere within a mile of the nest.

The 26- to 29-hour interval between eggs of a Sanderling clutch, a period heretofore not ascertained precisely, falls close to that of other small to medium-sized tundra sandpipers (Parmelee *et al.*, 1967). A nest found by J. H. McNeile (Dalgety *et al.*, 1931), with one egg on 27 June and four eggs on 30 June, led to the belief that Sanderlings lay daily. His notes (*in Bannerman, 1960*) about finding a nest with four eggs (two were "dead fresh, one was just a day or two set, and the other touched with a slight spot of red") on 12 July 1932 suggest that incubation started before completion of the clutch. We question whether incubation actually starts before completion of the clutch in Sanderlings.

Wholly unexpected at Nest 13, however, was an interval of five days and 16 hours between the completion of the clutch on 29 June (07:48 hours) and start of incubation near midnight of 4 July (23:55 hours). Throughout this time, Gray and Lamothe continually checked the eggs and found them exposed and cold. Both men were convinced that the adults had totally neglected the nest — as indeed they had, a fact confirmed later when Gray, Lamothe, and Taylor computed the incubation period for Nest 13 as 31 days — exceedingly long for a Sanderling.

Eggs

Jourdain's description of Sanderling eggs in Witherby *et al.* (1940) is as good as any in the literature: normally four eggs, but three recorded exceptionally; shape pointed ovate or subpyriform; hardly any gloss; ground color dull greenish olive as a rule, ranging to olive-brown and exceptionally greenish blue; rather sparsely marked with small irregular brown spots and shell-marks, generally heavier at big end and at times all concentrated there, sometimes a few fine blackish spots or streaks. We should stress that the eggs quickly lose much of their green color and turn brownish, especially when blown, as Pedersen (1942) stated. No doubt the fading in preserved specimens has led some writers to believe that the eggs are much less colorful than those of other shorebirds. P. Matthiessen (*in Stout *et al.*, 1967*), for example, called Sanderling eggs "exceedingly dull." Obviously, he had never seen a fresh Sanderling egg.

In the 60 live Sanderling eggs, including 52 on Bathurst Island, that I have seen in Canada, there was great variation, not so much in size and shape as in markings and especially in ground color. To be sure, some eggs were dull greenish with few markings of any kind, but most were handsomely embellished with small spots and various other markings, chiefly around the large end, often forming a distinct wreath, on a ground color ranging from pale dull green to the brightest green imaginable. The ground color of some was brownish green and of one clutch pure olive. The eggs in Nest 2 were the greenest of the more than forty kinds of live wader eggs I have ever seen. All four approached an emerald green and contrasted sharply with the white lichens that lined the nest. The fresh green color that makes the Sanderling's egg outstanding starts to fade the day the egg is laid and continues to fade throughout incubation so that much color is lost by hatching time. Whether fading—possibly correlated with change of season—has cryptic value is uncertain. Blowing the egg apparently speeds the fading, but no one has studied this. The few egg specimens we prepared all faded to some degree. The clutch size in all nests, seen by us in Canada, was four except for one nest found on 13 July 1969. That clutch of two eggs, one with a dented shell, very likely had been reduced through predation.

Incubation Period

Since Manniche (1910) stated that the "time of incubation is 23 to 24 times 24 hours" for Sanderlings, numerous references have given the incubation period as 23 to 24 days. Manniche, without giving any information on how he arrived at these figures, further confused the issue by stating that the first nest he found held eggs that already had been incubated for some days. He collected six of 11 nests he found and at least one had heavily incubated eggs. Presumably he did observe one nest with an incomplete clutch, perhaps a clutch he thought to be fresh.

Today, the usually accepted meaning of the incubation period is the time interval between laying and hatching of the last egg of the clutch. In Nest 2, found with only one egg in 1968, we marked each egg of the four-egg clutch and ascertained the period from laying to hatching of the fourth egg, as shown in Table 1. The fourth egg laid hatched first, and the incubation period for this nest was 24 days, six hours, 15 minutes (± 30 minutes).

In 1969 the incubation period of Nest 13 is shown in Table 2. The "official" time for Nest 13 is 31 days, 16 hours, 46 minutes (± 34 minutes), quite a contrast from that of Nest 2.

Although we do not know the minimum time required for incubation, we can say that some Sanderling eggs hatch in less than 25 days. Even the delay of five days and 16 hours, from completion of the clutch to start of incubation, does not fully account for the long period of incubation at Nest 13 because the period from the apparent start of incubation on 4 July (23:55 hours) and hatching on 31 July (00:00–01:07) was more than 27 days! This can only mean that either steady incubation did not actually commence until after 23:55 hours on 4 July, or the development of embryos was in some manner retarded during the period. Perhaps both factors contributed to what appears to be a remarkable variability in the incubation period of this species.

TABLE 1
Duration of Incubation in Sanderling Nest 2

| <i>Egg number</i> | <i>Time laid</i> | <i>Time hatched</i> | <i>Total time in nest</i> | <i>Time from laying of fourth egg</i> | <i>Young number</i> |
|-------------------|------------------------|---------------------|---|---|---------------------|
| 1 | 21 June | 21:41 19 July | | 24 days, 18 hrs., 56 min. (±30 min.) | 4 |
| 2 | 17:00-18:30 22 June | 09:30 19 July | 26 days, 15 hrs., 40 min. (±45 min.) | 24 days, 6 hrs., 45 min. (±30 min.) | 2 |
| 3 | 23:15-23:25 23 June | 16:00 19 July | 25 days 16 hrs., 40 min. (±5 min.) | 24 days, 13 hrs., 15 min. (±30 min.) | 3 |
| 4 | 02:15-03:15 25 June | 09:00 19 July | 24 days, 6 hrs., 15 min. (±30 min.) | 24 days, 6 hrs., 15 min. (±30 min.) | 1 |

TABLE 2
Duration of Incubation in Sanderling Nest 13

| <i>Egg number</i> | <i>Time laid</i> | <i>Time hatched</i> | <i>Total time in nest</i> | <i>Time from laying of fourth egg</i> | <i>Young number</i> |
|-------------------|----------------------------|------------------------|---|--|---------------------|
| 1 | before 22:45 25 June | 08:50-12:15 31 July | at least 35 days, 10 hrs., 5 min. (±103 min.) | 32 days, 2 hrs., 45 min. (±103 min.) | 4 |
| 2 | 01:45-02:15 27 June | 06:00-06:58 31 July | 34 days, 4 hrs., 29 min. (±44 min.) | 31 days, 22 hrs., 41 min. (± 29 min.) | 3 |
| 3 | 05:40 28 June | 01:07-01:10 31 July | 32 days, 19 hrs., 27 min. (± 2 min.) | 31 days, 17 hrs., 21 min. (± 2 min.) | 2 |
| 4 | 07:48 29 June | 00:00-01:07 31 July | 31 days, 16 hrs., 46 min. (±34 min.) | 31 days, 16 hrs., 46 min. (± 34 min.) | 1 |

Role of the Sexes during Incubation and Fledging Periods

The most puzzling aspect of the Sanderling's breeding behavior concerns the role of the sexes in care of eggs and young. On this point authors are argumentative but not lucid. Manniche (1910) thought that females alone incubated eggs and attended young. He presented such a strong case for this viewpoint that he exercised considerable subsequent influence. Bird and Bird (1941), who found upward of a dozen Sanderling nests in Greenland during 1937-1938, did not record any males at nests, though they believed that males may have in some way assisted in the late stages of incubation and the brooding of young (male seen brooding). Of eight birds shot at nests by Pedersen (1942), all were females. Witherby *et al.* (1940) state that male Sanderlings do not possess incubation or brood patches.

Contrary to these views, Feilden (1877) collected a male at a nest as early as 1876, as did Madsen (1925). Manning *et al.* (1956) collected a male with brood patches and another with young. H. Walter (*in Bent*, 1927) believed that both sexes hatched eggs, and G. Kolthoff (*in Loeppenthin*, 1932) thought that both parent birds attended the young. Godfrey (1966) summed up present-day thoughts on the subject, stating that the female definitely incubates and opinions differ regarding assistance of the male.

These statements, plus the fact that only one adult, probably a female, was seen during limited observations at an Ellesmere Island nest and a lone male with distinct brood patches attended young in the same area, led Parmelee and MacDonald (1960) to believe that both sexes incubate, but that one parent, either the male or female, at a given nest deserts at some point in the cycle. We still adhere to this view and present new evidence below.

It appears that one of the pair deserts by the time incubation begins. At Jenny Lind Island, during a nearly 24-hour-long watch at a Sanderling's nest with fresh eggs, only one adult incubated. The bird, a pale female, was shot by Sutton for positive sex identification (Parmelee *et al.*, 1967). At the Bathurst breeding ground on 25 June 1968, I collected a bright male with swollen testes and distinct brood patches at a nest where the eggs were only slightly incubated. On 11 July, I shot a pale female with ruptured follicles and distinct brood patches at a nest with fresh eggs. I looked for the mates of these two birds but did not find them.

Convinced finally that males do incubate, we all set about looking for nests for the purpose of observing incubating birds. In 1968 we succeeded in trapping and color marking the incubating adult at eight nests; two of these birds, banded at Nests 5 and 7, we observed again in 1969 at Nests 13 and 14, respectively. Data concerning the ten nests are presented in Table 3.

In the species of sandpipers in which the sexes share the incubation, it is usually simple to trap both birds of a pair at the nest. Not only did we fail to trap two birds at a Sanderling's nest, we also failed to see two birds at a single nest following egg-laying. We were always on the lookout for both and especially watchful during and immediately following the hatching of young, yet no mate ever appeared during these crucial times at any of the six nests where we observed the hatching. The male or female parent, which alone had incubated the eggs, also raised the brood. We found no exception.

Unfortunately, once the marked adults and broods had left the nest, we lost track of them. We do know, however, that the banded adult from Nest 2 was still the only bird attending when the brood was one week old; and that the banded adult from Nest 12 was the only one attending when its brood was more than two weeks old.

We saw only one adult attending unmarked broods on the Bathurst breeding ground in 1968. On 17 July we banded a pale adult, probably a female, and four downy chicks not long out of the nest. This adult alone attended the brood when we saw them on 18 July and on 25 July. Sightings of unmarked Sanderlings with broods are given in Table 4.

What seemed at first to be an exception to the one-parent-one-brood rule later appeared to be false. A bright individual and a pale individual ran at the edge of a marshy pond where two small young hid on 27 July. Further observation on 28-29 July convinced us that only the bright individual attended the chicks. We never saw the pale bird approach them. Possibly the gray bird had young of its own nearby; or possibly it, like several Knots, was attracted to the area by our disturbance, or perhaps, having lost its own eggs or chicks, it was attracted to the brood — as sometimes happens with White-rumped Sandpipers and some other shorebirds.

How the complex behavior in which the pair-bond suddenly dissolves comes about prior to incubation, and what adaptive value this behavior can possibly have, is a question for which we have no answer at present. The solution to the puzzle may lie in the long period between completion of the clutch by the female and start of incubation by the male, such as the more than five-day period at Nest 13. The nesting period is so short in the arctic summer that the birds must have been doing something constructive during this time. Conceivably they were at another nest, one which the female incubated, allowing the male to return to the first. The idea of sampling predation, as attractive as it may be with some species, does not quite fit the Sanderling, though it cannot be ruled out altogether. Sampling predation implies survival value for a nest site that escapes predation during a period following laying when the eggs are left unattended (see Drent, 1967).*

Behavior of Incubating Adult

The most convincing evidence that one bird alone incubates and cares for the brood came during the day-by-day, round-the-clock observation that started at Nest 2 at 15:00 hours on 5 July 1968 and continued without letup until 23:17 on 19 July — a period of 14 days, eight hours, 17 minutes. The incubating bird, believed from the first to be a male, was trapped and marked at 17:30 on 7 July. Up to that time we had some doubt whether the same bird that flew off periodically returned each time. Following the banding there was no doubt. Only the banded bird incubated and later attended the brood — at least throughout our period of careful observation.

A number of noteworthy observations concerned with incubation came to light during the continuous watch at Nest 2. Inasmuch as one bird alone

*Special note: Each ovary of two nesting Bathurst females, taken by me in 1970 and later examined critically by R. B. Payne, showed clear evidence of ovulation of two clutches in quick succession.

TABLE 3
Sex of Incubating Sanderlings

| <i>Nest number</i> | <i>Probable sex of banded bird</i> | <i>Period of observation following banding</i> | <i>Number of observations of banded bird on nest</i> | <i>Number of observations of an unbanded bird on nest</i> |
|--------------------|------------------------------------|--|--|---|
| 2* | male | 7-19 July** | 379 | 0 |
| 5 | male | 2-4 July | 9 | 0 |
| 6 | ? | 3-4 July | 3 | 0 |
| 7* | male | 16-24 July | 12 | 0 |
| 8* | male | 10-17 July | 19 | 0 |
| 9 | female | 10-21 July | 14 | 0 |
| 11* | female | 13-21 July | 7 | 0 |
| 12* | male | 15-19 July | 4 | 0 |
| 13* | male | 5-31 July | 30+ | 0 |
| 14 | male*** | 28 June | 1 | 0 |

*Hatching period observed.

**Continuous round-the-clock observation.

***Collected at nest with fresh eggs on 28 June. The mate, seen on 22 June, was not found on 28 June.

TABLE 4
Sex of Adult Sanderlings with Broods

| <i>Sex of adult</i> | <i>Number of young</i> | <i>Date</i> |
|---------------------|------------------------|-------------|
| Female* | 3 | 19-20 July |
| Female* | 4 | 27 July |
| Female** | 2 | 28 July |
| Female* | 2 | 30 July |
| Female* | 4 | 31 July |
| Female** | 1 | 3 August |
| Male** | 2 recently fledged | 7 August |
| Male** | 1 nearly fledged | 8 August |

*Probable sex.

**Sex confirmed by collecting.

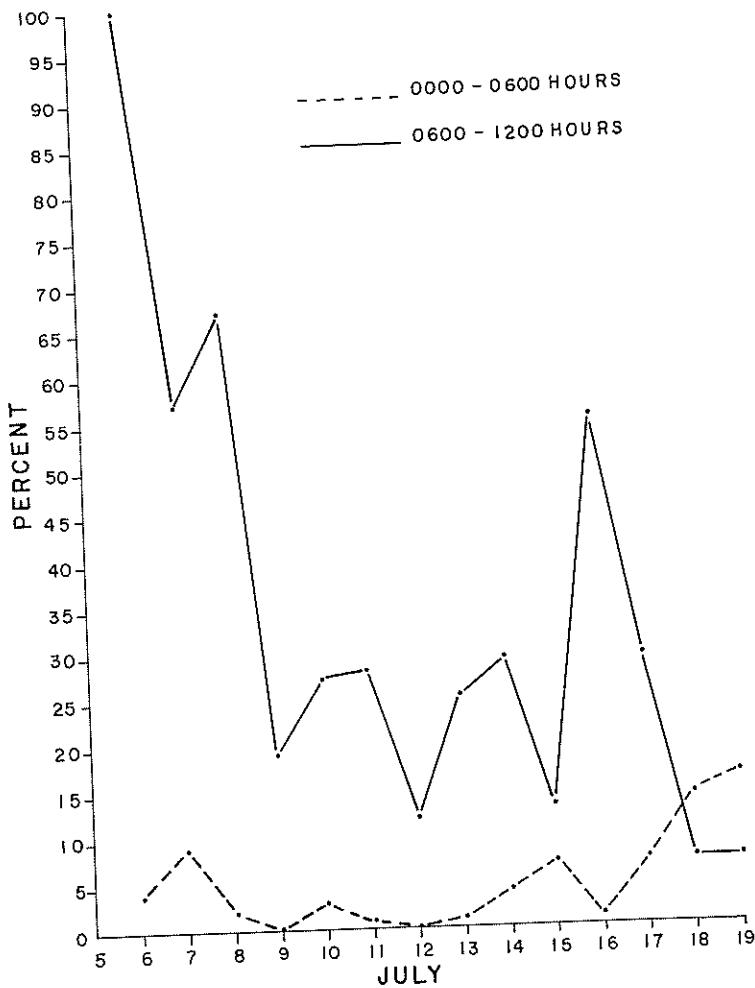


Figure 10. Graph showing the percentage of time that the incubating Sanderling was off Nest 2 during the morning hours of 6-19 July. The broken line indicates the early morning period 00:00-06:00, the solid line, the later period 06:00-12:00. The incubating Sanderling usually remains on the nest during the cool early morning hours (up to 06:00). The inattentive periods rise sharply during the later hours of the morning.

incubated, we especially wanted to know just how much time the bird spent off the nest during any one day and for the entire period. We kept an accurate record of when the parent bird left and when it returned to the nest. Although we occasionally failed to see the bird arrive or depart, the error in these cases was slight, for at no time was an eye off the nest for more than a minute or two. We did not count the times we flushed the incubating adult from the nest for routine egg checks because then the conditioned bird moved away only a few feet and invariably returned to the eggs as soon as we retired.

Figures 10 and 11 show graphically the percentage of time that the incubating Sanderling was away from the nest during 5-19 July.

As seen in Figure 10, the incubating Sanderling remained mostly on the nest during the cool early morning hours (00:00-06:00). The average time away was only 5 per cent; it left the nest 46 times for a total of 237 minutes; and each trip lasted from one to 27 minutes, averaging 5.1 minutes.

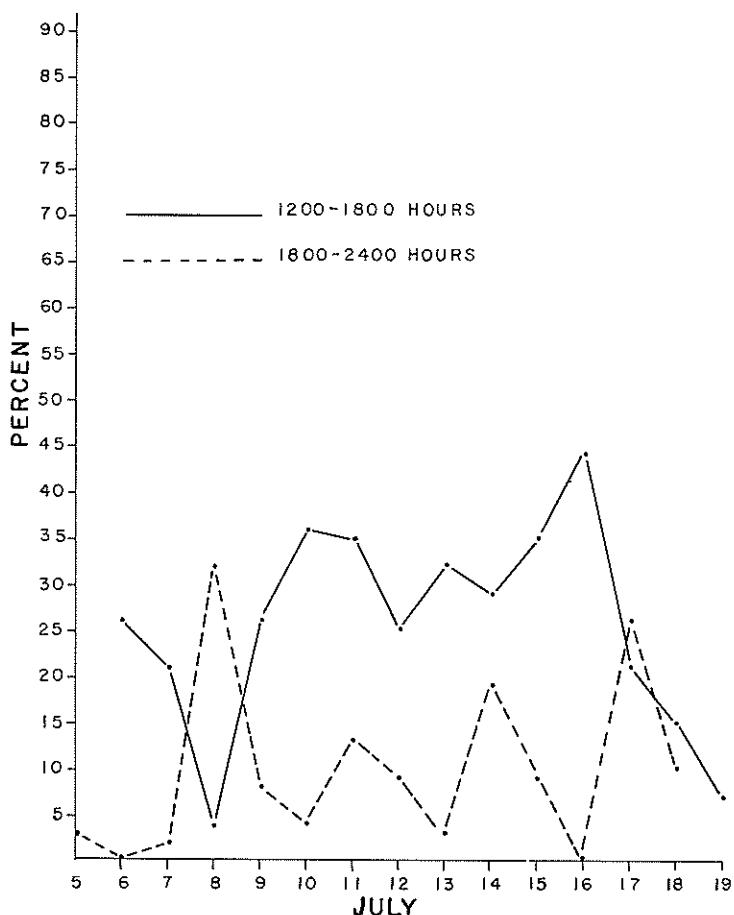


Figure 11. Graph showing the percentage of time that the incubating Sanderling was off Nest 2 during the afternoon hours of 5-19 July. Solid line indicates the afternoon hours 12:00-18:00 for 6-19 July, the broken line, the later period 18:00-24:00 for 5-18 July. Each inattentive period averaged nearly the same number of minutes during both periods (8.5 and 8.2 minutes); but the number of trips off the nest between midday and 18:00 hours was almost three times more than between 18:00 hours and midnight (151 to 58 trips, respectively, during the two-week period).

the bird spent pt an accurate nest. Although : in these cases minute or two. om the nest for way only a few : that the incu- l mostly on the e average time of 237 minutes; ates.

During the late morning hours (06:00-12:00), the Sanderling's time away was from seven to 100 per cent of each six-hour period and averaged 34 per cent for the total time. The bird left the nest 116 times for a total of 1,719 minutes, each trip lasting from one to 360 minutes and averaging 10.1 minutes. The long absences from the nest on 6, 7, 8, and 16 July, shown by the high points on the graph, increased the average time considerably.

Though these high points show that the Sanderling left the nest for unusually long periods, they do not show the longest periods when the times overlapped the observation periods. For example, on 6 July it was off for 454 consecutive minutes, from 05:46 to 13:20; on 7 July, 219 minutes, from 05:33 to 09:12; on 8 July, 223 minutes, from 08:21 to 12:04; on 16 July, 333 minutes, from 09:04 to 14:37. These figures stand out when compared to those for all other times when the bird was never off the nest for more than 20 minutes. See Table 5 for daily timing of periods on and off Nest 2 from 6 to 19 July.

The occasional long absences from the nest are puzzling. In 1966, on Jenny Lind Island, we noted this phenomenon at a Sanderling nest and, also, at the nests of White-rumped Sandpipers where the female alone incubates the eggs. Although these birds generally sit tight during cool or inclement hours, this is not always the rule. Nor do the long absences seem to depend on weather conditions or human disturbances. Whatever the explanation, the embryos within the chilled eggs somehow survive.

As seen in Figure 11, the incubating Sanderling was off the nest from four to 44 per cent (average 25 per cent) of the time during the afternoon hours 12:00 to 18:00 for 6-19 July. It left the nest 151 times for a total of 1,291 minutes, averaging 8.5 minutes per trip. Discounting the long absences in the previous period, the graph indicates that this is an important feeding period.

TABLE 5
Day-by-day, Round-the-clock Timing of Incubation at Sanderling Nest 2

| Date in July | Minutes on nest | Minutes off nest | Number of times off nest | Per cent of time off nest | Minimum number of minutes off nest | Maximum number of minutes off nest | Average number of minutes off nest |
|--------------|-----------------|------------------|--------------------------|---------------------------|------------------------------------|------------------------------------|------------------------------------|
| 6 | 966 | 474 | 4 | 33 | 3 | 454 | 94.8 |
| 7 | 1119 | 321 | 17 | 22 | 1 | 219 | 18.8 |
| 8 | 1061 | 379 | 13 | 26 | 3 | 223 | 29.1 |
| 9 | 1254 | 186 | 27 | 12 | 2 | 13 | 6.8 |
| 10 | 1189 | 251 | 28 | 17 | 1 | 19 | 8.9 |
| 11 | 1159 | 281 | 31 | 19 | 1 | 19 | 9.0 |
| 12 | 1273 | 167 | 20 | 12 | 1 | 14 | 8.3 |
| 13 | 1218 | 222 | 30 | 15 | 1 | 11 | 7.4 |
| 14 | 1170 | 270 | 41 | 12 | 1 | 20 | 6.6 |
| 15 | 1207 | 233 | 35 | 16 | 1 | 16 | 6.7 |
| 16 | 1084 | 356 | 6 | 24 | 1 | 333 | 59.3 |
| 17 | 1141 | 299 | 45 | 21 | 2 | 14 | 6.6 |
| 18 | 1273 | 167 | 35 | 12 | 1 | 8 | 4.8 |
| 19* | 1280 | 160 | 36 | 11 | 1 | 17 | 4.4 |

For the period 6-19 July:

Total time on nest: 16,394 minutes

Total time off nest: 3,766 minutes or 19 per cent

Total number of times off nest: 368

Average time away from nest per trip: 10.2 minutes

Average number of trips per day: 26.2

*Since continual observation at Nest 2 terminated at 23:17 on 19 July, it is only assumed that the bird was on the nest from 23:17 to 24:00 that day.

1966, on
and, also,
ribates the
ent hours,
n weather
e embryos

from four
oon hours
1,291 min-
in the pre-
period.

Nest 2

| n | Average of number of minutes off nest |
|------|---|
| 94.8 | |
| 18.8 | |
| 29.1 | |
| 6.8 | |
| 8.9 | |
| 9.0 | |
| 8.3 | |
| 7.4 | |
| 6.6 | |
| 6.7 | |
| 59.3 | |
| 6.6 | |
| 4.8 | |
| 4.4 | |

ily assumed that

For the cooler hours 18:00–24:00, the incubating Sanderling was off the nest from zero to 32 per cent of the time during 5–18 July, averaging only 9 per cent. The bird left the nest 58 times for a total of 477 minutes, averaging 8.2 minutes per trip.

Data concerning the 24-hour day at Nest 2 for the period 6–19 July are graphed in Figure 12.

The total time (19 per cent) off the nest for the period 6–19 July would be somewhat less if it were not for the few times the bird was away for unusually long spells on 6, 7, 8, 16 July. Nevertheless, 19 per cent is the actual time spent off the nest for a definite period prior to successful hatching. This figure compares well with similar nest-relief of the White-rumped Sandpiper. With much less data at their disposal, Drury (1961) and Parmelee *et al.* (1968) roughly estimated that females of that species are off the nest 20 to 30 per cent of the time.

The marked Sanderling left Nest 2 to feed, to pursue other Sanderlings, and to avoid birds and mammals, including predators. Most trips involved feeding.

The bird often flew north and fed along a small, melt-water creek that flowed southeastwardly some 200 yards from Nest 2. Other Sanderlings and some Knots also probed in the mud along this creek bed and slopes that rose gently from its banks. We were unable to determine precisely what food they found there.

Almost as often, the marked bird flew southeast, disappearing over the bank of the creek, doubtlessly following the creek bed down to a big marsh a quarter of a mile below the nesting ridge. Sometimes it flew straight down the precipitous south bank of the ridge and probed near the edge of a huge snow drift. Although at times it ran from the nest, when it went off to feed, it almost invariably flew directly from the eggs or chicks for about 30 to 50 feet and then suddenly gained some altitude before dropping down to the feeding spot.

On occasion it rose very rapidly, descended, rose again, and then plunged in an undulating performance; or it suddenly flew off twisting and turning. Once it did a quarter barrel-roll and the flight that began as a feeding excursion evidently developed into something else, possibly due to the presence of another Sanderling. Essentially, the feeding flight was direct.

Rarely, when the wind was not blowing hard, the marked Sanderling rose on rapidly beating wings straight up from the eggs before leveling off a foot or so above ground. MacDonald noted that the bird on leaving the nest in periods of low wind, "raises so legs are only about half straightened, then whirrs wings and rises almost vertically for about 12–18 inches." I once saw the bird rise a foot above the eggs, suddenly turn 180 degrees, and fly off in the opposite direction.

Returning to the nest was less spectacular. Nearly always the bird flew in on shallow wing-beats low above the ground, alighted one to 20, usually five to 15, feet from the nest, ran directly to the eggs or chicks, and sat without any preparatory behavior. At times the bird ran in from greater distances—as much as 125 feet. Never did we see this bird, or any Sanderling, flutter down on the eggs in the manner so characteristic of turnstones.

Most feeding trips lasted from three to 10 minutes and some barely a minute, hardly long enough for the bird to take a drink. Whether eating or drinking, it returned with a wet bill that sparkled on clear days.

The manner of feeding, seen so often at Nest 2, did not differ much from that observed at other Sanderling nests. The marked adult at Nest 7 fed briefly at a wet spot only 240 paces from the eggs. The one at Nest 8 flew a quarter-mile to feed for a few minutes at a marshy pond. The bird at Nest 11 flew a quarter-mile to a marshy pond and, during rapid-fire feeding there on 14 July, plucked insect larvae from water one to three inches deep.

The number of Sanderlings that visited the immediate vicinity of Nest 2 was astounding. We felt that quite a few of these birds were aware of Nest 2 because at times they ran up to or flew close to it. The incubating Sanderling reacted to these intrusions in various ways. Sometimes it crouched or flattened out on the nest, as it often did when a predator approached; sometimes it paid little or no attention to an odd Sanderling or even a flock; most of the time it flew at the intruders and chased them hard with some chases ending in genuine confrontations. We saw no less than 56 intrusions on the *sanctum sacerdotum* of Nest 2.

Most intrusions were by single individuals, some of which visited Nest 2 repeatedly. One very pale individual, believed to have been a male despite its appearance, chased Sanderlings about, including the bird at Nest 2, and performed flight displays in full song. Nest 2 had a special attraction for it. At 17:22 on 9 July, Taylor saw the pale bird alight 10 feet from the nest, walk up, and circle it with scapulars and other feathers erected. The marked Sanderling leaped off the eggs, forced it back, and then chased it on the wing. After such a flight, the marked bird, obviously agitated, returned to the nest with feathers erected.

The pale Sanderling was a nuisance—and at times disturbing. At 18:30 on 9 July, it approached Nest 2 when the owner was off feeding and from 40 feet began chattering. Then it ran straight to the nest and began jabbing the eggs with its bill. Fortunately, not one egg was damaged. We saw this pale bird a few more times before it disappeared like those before it and other Sanderlings replaced it.

Sixteen times we recorded the arrival of small flocks—from two to seven birds—which, although they did not go directly to the nest, sometimes approached it closely. At most any distance the presence of a flock was too much for the incubating Sanderling. For example, at 05:14 on 11 July, MacDonald observed three Sanderlings drop down to the ground 150 feet from Nest 2. The marked bird flew off the eggs straight for them and, with wings and tail spread, landed among them, scattering all three. Then it pursued them on the wing, actually catching one in midair and landing squarely on its back. Four minutes later it returned to its eggs. Definitely an incubating Sanderling is hostile to strange Sanderlings. On the other hand, a freshly killed Sanderling specimen of either sex, propped with wires near Nest 8, incited no response whatever from the incubating bird, probably a male.

Although we were not absolutely sure that one of the many Sanderlings that came to Nest 2 was not the mate of our marked bird, we were certain that

none of these birds actively took part in the incubation or brooding from 7 July onward. Conceivably the mates of incubating Sanderlings do visit the nest at times; clearly they play no real role. We can hardly accept Pedersen's belief (1942) that only the female Sanderling incubates, that the male Sanderling stays in the vicinity of the nest, meets her regularly when she goes for food, and, later, joins her and the brood in times of stress or emergency.

It soon became apparent to us that our marked bird was very much aware of strange birds and mammals that passed near or through its domain. In responding to all — predators or not — from buntings to caribou, it flattened out on the nest or ran quickly from the nest for a few to many feet and squatted low in a depression. Once the animal had passed through the area, the Sanderling quickly ran back to its eggs. Many times we first became aware of the presence of some bird or mammal by noting the behavior of the incubating Sanderling.

During long periods when it was incubating undisturbed, it held its head and neck upright and moved them back and forth often, turned about frequently, preened and arranged its feathers, moved the eggs, adjusted its brood patches and rearranged its feathers, picked at the saxifrage close by, and played with the lichens that lined the nest. It was quietest during the coolest hours and at such times usually appeared to sleep soundly, its head turned and bill tucked beneath the scapulars.

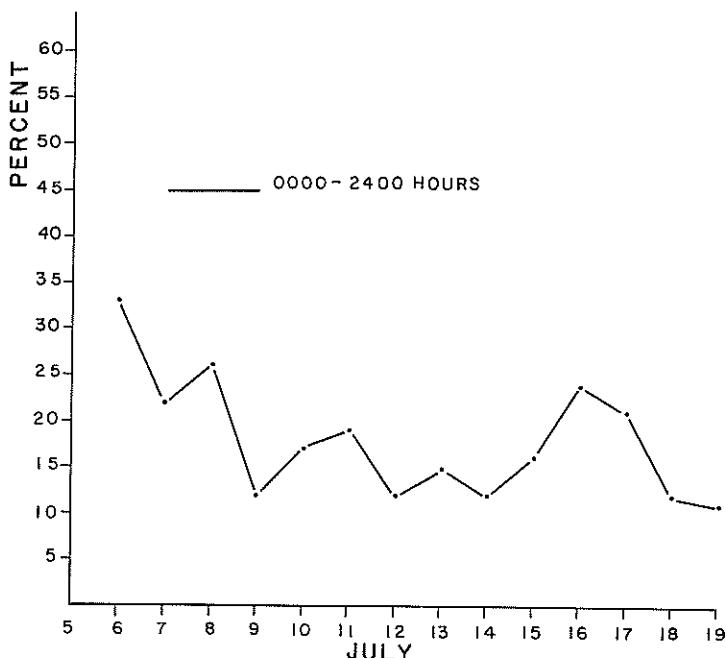


Figure 12. Graph showing the percentage of time that the incubating Sanderling was off Nest 2 during 00:00-24:00 hours for the period 6-19 July. This graph combines the data of Figures 10 and 11, and shows that the Sanderling spent 81 per cent of its time on the nest during two weeks in July.

Hatching

Although we did not determine precisely when each of the four eggs at Nest 2 became starred (developed cracks in shell), and later pipped (developed hole in shell), we recorded the times when we first observed the events. See Table 6.

From the data in Table 6 it is clear that almost five days (116.5 hours or more) may elapse from first indication of starring to hatching (Egg 2), or as little as two-and-one-half days (62.5 to 68.5 hours, Egg 4), even when allowing for an error of up to six hours; and that as many as 57.68 to 63.68 hours (Egg 1), or as few as 10.25 to 12.58 hours (Egg 3), may elapse from pipping to hatching.

At Nest 7, at least 84.25 hours elapsed between the first observed starring and the hatching of one egg; at Nest 8, at least 72.5 hours; at Nest 12, at least 110 hours. The interval from pipping to hatching was less than 24 hours for two eggs at Nest 13. Manniche's statement (1910) that the "bursting of the egg-shells will generally begin already some 3 days before the emergence of the young" is reasonable, but there appears to be much variation in the period between starring and hatching and between pipping and hatching.

Prior to hatching, the young Sanderling chips a circular path completely around the large end, or "cap," of the shell. At Nest 2, the parent flew off with the cap before the first chick had completely emerged from the remaining larger portion and it quickly flew off with the larger portion as soon as the chick was free of it. Exactly the same procedure took place with the second hatching—i.e., the parent flew off first with the cap while the chick was still in the larger portion of shell and later with the larger portion. The quick removal of the cap before the young emerged suggests that the parent may actually assist the chick in hatching, apparently the case with Stone Curlews (*Burhinus oedicnemus*) in the Old World (see Nethersole-Thompson, 1951:183).

TABLE 6
Timing of Events in Hatching of Eggs in Sanderling Nest 2

| Egg number | Starring first noted | Pipping first noted | Precise hatching time | Minimum time from starring to hatching | Minimum time from pipping to hatching |
|------------|----------------------|----------------------|-----------------------|--|---------------------------------------|
| 1 | 15 July (18:00) | 17 July (12:00)** | 19 July (21:41) | 99.68 hrs. | 57.68 hrs. |
| 2 | 14 July (18:00) | 18 July (18:17) | 19 July (09:30) | 116.5 hrs. | 15.21 hrs. |
| 3 | 16 July (18:30)** | 19 July (05:45)* | 19 July (16:00) | 69.5 hrs. | 10.25 hrs. |
| 4 | 16 July (18:30)** | 17 July (12:00)** | 19 July (09:00) | 62.5 hrs. | 45.0 hrs. |

*Error less than 2.5 hours since the third egg was not pipped at 08:25 on 19 July.

**Error less than 6 hours since the third and fourth eggs were not starred at 12:33 on 16 July, and the first and fourth eggs not pipped at 06:10 on 17 July.

The third hatching at Nest 2 took place during a downpour and the parent did not remove the half shells immediately. When the rain abated some minutes later, it ran off with the cap, dropped it about 20 feet from the nest, ran back, grasped the larger portion, flew off, and dropped it a hundred yards or so from the nest. It removed the two parts of the shell during the fourth hatching as it had the first two. With the one exception, the bird dropped all the shell parts from 100 to 200 yards from the nest and immediately returned each time.

When the parent was purposely flushed from Nest 7 during a routine check, we discovered that it had been brooding a chick which, judging by the wetness of its down, was perhaps 15 minutes old. An empty eggshell lay beside the chick in addition to a pipped egg and two slightly older young. As sometimes happens, the cap of the empty shell was firmly attached to the larger portion. When the parent bird returned to the nest, it at once flew off with the two pieces, still attached, for a distance of 125 paces, alighted, dropped the whole shell on a bare spot of ground without any attempt at hiding it in one of many cracks in the turf, and returned to the nest in a flash.

TABLE 7
Spread of Hatching Time in Sanderling Nest 2

| Young number | Partial band number | Time of hatching on 19 July | Final departure from nest on 20 July | Age when nest abandoned |
|--------------|---------------------|-----------------------------|--------------------------------------|-------------------------|
| 1 | 125121 | 09:00 | 10:47 | 25.78 hrs. |
| 2 | 125122 | 09:30 | 10:47 | 25.28 hrs. |
| 3 | 125123 | 16:00 | 10:47 | 18.78 hrs. |
| 4 | 125124 | 21:41 | 10:47 | 13.1 hrs. |

The parent at Nest 8 was so obsessed with brooding its newly hatched chicks in a high wind that it never removed the last empty shell with cap still attached. Nor did it fly off with this shell that we later weighted down with a small stone and placed beside the nest. Evidently, Sanderlings are reluctant to remove shells during inclement weather. Probably they do not remove addled eggs at any time. Such an egg remained in Nest 12 when the young left.

Manniche (1910) mentioned the immediate removal of eggshells by female Sanderlings following emergence of the young but gave no details. All tundra sandpipers, noted by us over the years, usually removed empty shells from the nest immediately or soon after the young emerged—or as soon as they were aware of the empty shells. Pioneer studies by Nethersole-Thompson and Nethersole-Thompson (1942) showed that variation in eggshell removal occurs both intraspecifically and interspecifically in shorebirds; but there can be no doubt that a good many shorebirds remove the eggshells before the young leave the nest.

TABLE 8
Young Sandpipers Collected on Bathurst Island in 1968

| Specimen number* | Date collected | Days of age | Sex | Weight††† | Wing chord† | Exposed culmen†† | Tarsus† | Remarks |
|------------------|----------------|-------------|-----|-----------|-------------|------------------|---------|---|
| 55561 | 20 July | 2** | M | 9.4 | | 11.7 | 18.5 | Yoke sac present |
| 55562 | 28 July | 2** | F | 9.5 | | 11.4 | 21.0 | Yoke sac present; small stones and fragments of chitin in gizzard |
| | | | | | | | | |
| 55569 | 28 July | 4 or 5** | F | 13.3 | 23.0 | 13.3 | 20.5 | |
| 55570 | 28 July | 4 or 5** | F | 13.0 | 23.0 | 13.7 | 20.5 | |
| 55563 | 26 July | 7*** | M | 17.1 | 31.0 | 14.3 | 20.0 | |
| 55571 | 3 Aug. | 7** | ? | 17.4 | 30.0 | 14.7 | 20.0 | With adult female |
| 55572 | 3 Aug. | 10-11** | M | 27.4 | 57.0 | 14.7 | 21.5 | With adult female |
| 55573 | 4 Aug. | 15*** | M | 39.7 | 84.0 | 19.0 | 23.5 | |
| 55575 | 8 Aug. | 15** | M | 39.1 | 83.5 | 19.1 | 20.0 | With adult male |
| 55574 | 7 Aug. | 21-22** | F | 56.1 | 107.0 | 21.5 | 25.0 | Strong flying; with adult male |

* Specimens in Canadian National Museum of Natural Sciences.

** Probable age.

*** Known age.

† To nearest 0.5 millimeter.

†† To nearest 0.1 millimeter.

††† To nearest 0.1 gram.

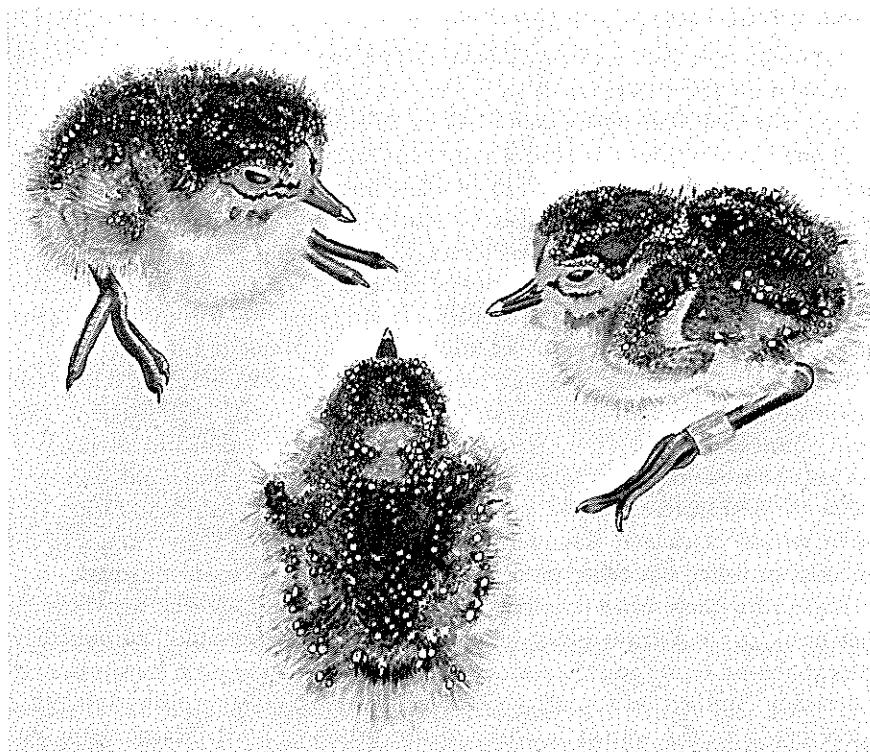


Figure 13. Fourteen-hour-old Sanderling. A chick in Nest 7 served as my model for this drawing. The chick hatched at about 04:00 hours on 24 July 1968 and was still in the nest at 18:00 when we made a detailed study of it. Juvenile plumage is not evident in a chick this age. Its eyes are black. The proximal two-thirds of its bill is dark gray or bluish gray, the distal third black except for the very tip and egg tooth. Legs and feet are black to bluish black with silvery highlights.

Since the chicks in one brood hatched at different times, they were obviously different ages when they left the nest together. The spread of hatching time was greatest in Nest 2 (12.6 hours); it was the least in Nest 11 (2.5 hours). See Table 7. At Nest 2, the only nest for which we have exact figures, the youngest chick was only 13.1 hours old when it faced the outside world. At Nest 8 we know that the youngest chick was not more than 13 hours old when it left — or was taken by a predator. The three chicks in Nest 12 probably hatched within an hour. All were wet when first seen. Since one egg in this nest was addled, we could not determine the hatching spread, nor did we know when the young left.

A Sanderling with wet down is a newly hatched chick. The down feathers dried and fluffed in a short time. Within 30 minutes the down of one was half dry; an hour later it was well fluffed though bits of membrane still adhered to the down. The fluffing of the down in other chicks took slightly longer. Figure 13 illustrates the fluffed-down pattern of a small chick.

Four newly hatched chicks at Nest 2 weighed 7.1, 7.5, 7.1, and 7.5 grams respectively. Attached to Chick 2 was an abnormally large egg sac that burst, spilling yolk onto the two pipped eggs. Later, the sac dried and the chick seemed none the worse.

*Probable age.
**Known age.
†To nearest 0.5 millimeter.
††To nearest 0.1 millimeter.
†††To nearest 0.1 gram.

Departure of Young from the Nest

Although we discontinued constant observations at Nest 2, following hatching of the last young on 19 July, I was in the blind and watched the final departure of the brood at precisely 10:47 on 20 July.

If one has any question as to whether the young Sanderling—or any other tundra sandpiper—ever returns to the nest once it departs, he can find the answer by spending some time near a nest. The young Sanderlings may run out of the nest and back to it many times, the more so as they gain in age and strength, and in time do so quite independently of the parent. However, the parent determines the final exodus and accomplishes this through persistent brooding at the nest followed by simulating feeding outside the nest.

Newly hatched chicks at Nest 2 were weak and almost helpless. Although capable of moving about in the nest, they remained mostly still, uttering low rasping *chucks*. Within an hour or so they were able to position themselves favorably beneath the adult. One chick, not more than 2.75 hours old, bounced outside the nest from beneath the parent and quickly crawled back. Either the first or second chick may have left the nest and ventured a few inches of its own volition when not more than three hours old, but it soon returned.

Except for these brief moments the young at Nest 2, as well as young at other nests, did not leave much before they were 12 hours old, though they were capable of doing so. They moved about freely in the nest, however, and on occasion climbed on top of the brooding parent, only to plunge and disappear again in the spread feathers of the brooding bird. Many times the brooding parent had difficulty in maintaining its balance when the brood moved about beneath it. Suddenly it rocked and wobbled, stood up with scapulars fully erect, turned about, hurriedly adjusted feathers, and plopped down on the squirming mass. When it flew off to feed, any chick less than 12 hours old stayed in the nest while older siblings ventured out and romped.

When 19 and 18.5 hours old, respectively, the two oldest young ran nimbly for 15 feet before returning to the nest. One or both left the nest 13 times during the four-hour period, 04:15–08:05, that followed, indicating that they were ready to leave the nest most any time even in the cool hours. Each of the 13 trips averaged a minute and did not exceed two. They ran about probing with their bills but soon became chilled. Twice they left, and four times they returned, when the parent was away. The rest of the time they left and returned when the parent was on the nest. The third and fourth young did not leave the nest once at this time.

During this four-hour period, the parent flew off to feed nine times for a total of 56 minutes—24 per cent of the time. Each trip lasted five to eight minutes and averaged 5.6 minutes. The adult sometimes flew off even while its young were outside the nest. We noted the temporary abandonment of young by the parent at other Sanderling nests as well. For example, at Nest 8 on 16 July, while I lay on the ground only a few feet from the nest that held a chick and pipped eggs, the marked adult flew off to a distant marshy pond to feed four times in a 2.75-hour period. It stayed away for a total of 36 minutes (21 per cent of the observation period), each trip lasting five to 12 minutes and averaging nine minutes.

By 10:15 on 20 July, the morning of final departure from Nest 2, all four chicks were running hard. Now they all invariably ran from the nest when we purposely flushed the parent or when it flew off of its own accord to feed. They probed about, investigating everything they encountered. The oldest tested a purple saxifrage petal and swallowed plant bits. They became chilled after an expedition of two minutes and returned to the nest whether the adult was there or not. Twice the adult, on returning to an empty nest, waited for the chicks to run in, and this they most certainly did, one by one. Not once did the adult attempt to brood the chicks outside the nest.

At 10:47 the behavior of the brooding parent changed dramatically. Suddenly it called loudly from the nest. One chick ran off. Then the parent left and very deliberately walked about, jabbing the ground hard with its bill in simulating feeding. The effect was electrifying. The remaining three chicks bounded out of the nest and soon all four were scrambling behind the parent, probing as they went. At 10:49 two chicks, followed by the other two, ran to the adult. It brooded them where it stood, five feet from the nest, forever abandoned by the young.

Fledgling Period

Following the final departure of the brood from Nest 2, we watched them for nearly two hours, 10:47–12:37. The parent bird repeatedly abandoned the young briefly and left to feed just as it had done many times previously when attending eggs or chicks in the nest. During the nearly two-hour watch, it was away for a total of 27 minutes (24 per cent of the observed time), each trip lasting two to nine minutes and averaging 6.7 minutes per trip.

The adult did not fly off each time it left the brood. More often it jumped away from the young and continued its probing action, though apparently it did not eat anything. The chicks exploded in all directions, fanning out within five feet of the adult and probing. After a few minutes the parent squatted and the chicks ran to be brooded. When the parent was away and they became chilled, they ran to one another and pressed close together, at times in pairs; at other times all four huddled in one downy bundle.

As mentioned previously, the parent brooded the chicks of Nest 2 five feet from the nest following the final departure. It brooded them again only four minutes later 10 feet from the nest. Gradually the distance between nest and brood increased until by the end of the first hour they had moved 60 feet, and by the end of the second hour, 210 feet.

We then discontinued observations until 00:30 the following day, 21 July, when the young were 26.81 to 39.5 hours old. They were probing for food in a favorite feeding area of the adult, a small creek bed kept wet by melting snow only 150 yards northeast of the nest. However, they had probably moved about considerably more since they initially traveled due south of the nest. All, appearing to be much stronger, ranged freely 15 feet from the adult before running back to be brooded.

Young Sanderlings sometimes travel long distances the first day out of the nest. Manniche (1910) actually observed young that had moved 500 to 600 meters hardly an hour after leaving the nest. Our evidence suggests that, as a

rule, young Sanderlings and other young tundra sandpipers do not range far from the nest the first week of their lives. This was true of the brood from Nest 2. On 26 July, seven days after hatching, the marked parent tended three chicks in wet, hummocky tundra below a bank of snow only 553 paces from the nest. We collected one young (see Figure 14).

The good feeding areas close to Nest 2 may have kept the birds from moving far from the home ground. Unfortunately, we did not see them after 26 July, so we do not know whether they traveled to a new area or whether a predator found them.

That some Sanderling families move long distances from the nest was clearly evident when, at 22:10 hours on 3 August, Gray and Taylor caught and kept as a specimen one of the banded young from Nest 12 (see Figure 15). Almost 15 days old to the hour, not quite capable of sustained flight, and still with the marked parent, it had traveled fully two miles from a high, exceedingly barren slope to a lush, marshy valley. They saw no siblings.

An unbanded chick, collected on 8 August, was most likely the same age because it had nearly the same weight, measurements, and plumage development as the bird of known age (see Table 8). And like the latter, it could fly only a foot or two at a time just above the ground. The wing chords of both birds exceeded 80 mm (83.5–84.0) and no doubt were nearly long enough to support the birds in sustained flights for distances of 50 to 100 yards or more. White-rumped Sandpipers fly fairly strongly at 16 to 17 days of age when their

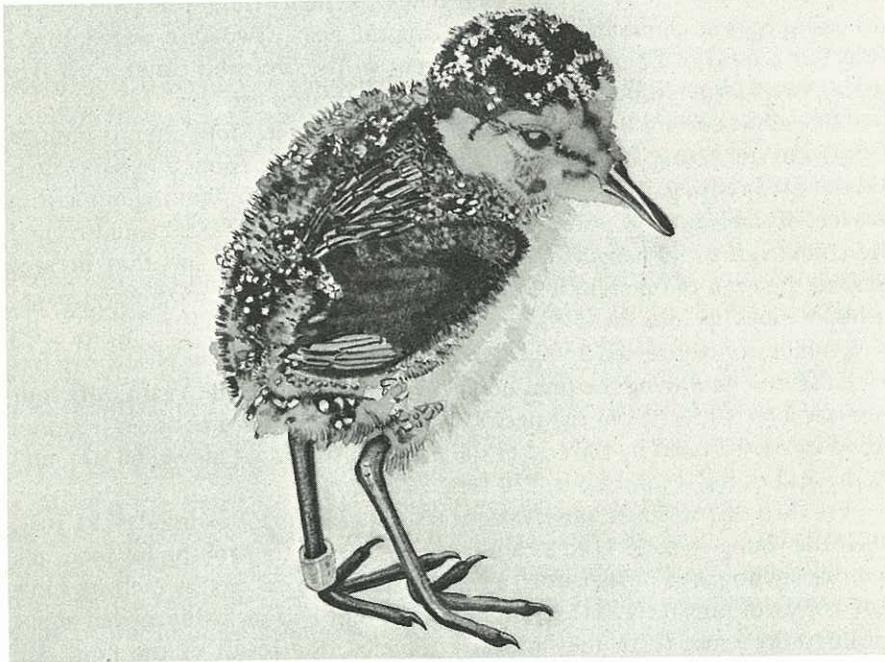


Figure 14. Seven-day-old Sanderling. I drew a chick that I had banded at Nest 2 on 19 July 1968 and found nearly seven days later with the parent and two siblings 553 paces from the abandoned nest. I returned to camp with the chick and preserved it at exactly seven days of age on 26 July. Although down is conspicuous on a chick this age, the juvenal plumage is developing rapidly above and below. The quills, about 13.0 mm, are starting to burst at the tips. Eyes, bill, legs, and feet are very dark, nearly black.

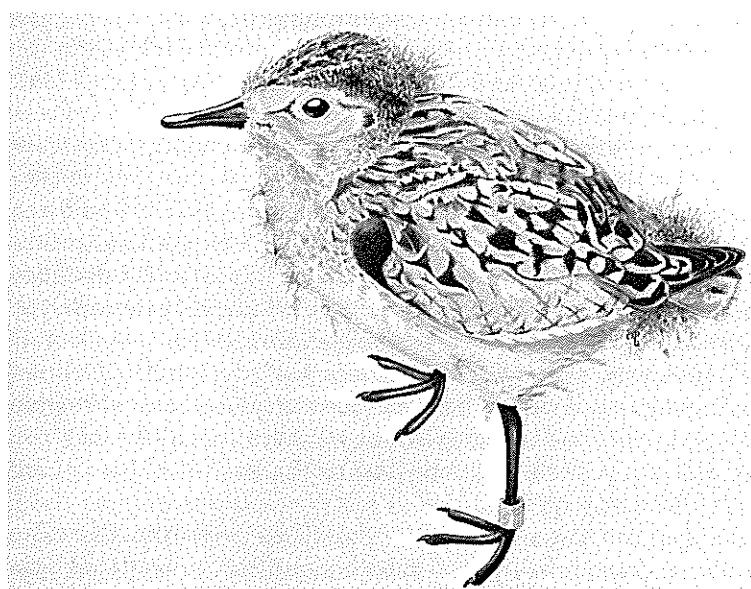


Figure 15. Fifteen-day-old Sanderling. I drew this illustration of a banded young caught on 3 August 1968 two miles from abandoned Nest 12. The drawing is also based on an unbanded young believed to have been 15 days old on 8 August. A Sanderling this age is not quite capable of sustained flight. Its juvenal plumage is conspicuous above and below. Down is still plentiful on parts of head, neck, mid-pectoral region, base of tail, and legs. Color of eyes, bill, legs, and feet is similar to that of seven-day-old.

chords exceed 80 mm (Parmelee *et al.*, 1968). However, Sanderling juveniles weigh considerably more than White-rumped Sandpipers of the same age and for this reason may require slightly longer wings before they become airborne. This aspect of fledgling needs study.

If we use the criterion of sustained flight for a distance of at least 50 yards, the fledging period for the Sanderling probably averages close to 17 days. Certainly the "12 to 14"-day period, the so-called fledging period, given by Manniche (1910) and quoted by many authors thereafter, is too short.

Allowing 17 days from time of hatching to time of first sustained flight, we estimated that some young flew as early as 2 August on the Bathurst breeding ground in 1968. Most young probably flew by 2–9 August though a few, such as those from Nest 10 where laying was late, may not have flown much before 20 August.

On 7 August we shot one of two strongly flying juveniles and an adult male flying with and defending them at the time. This specimen was well developed (see Table 8) with wing chords 107 mm long. If we make a rough comparison between it and White-rumped Sandpipers of known age, the Sanderling was 22–23 days old.

Departure from Breeding Grounds

Other investigators in different places have noted the early flocking of Sanderlings on the breeding grounds. The flocks, made up of both bright and pale individuals, probably start forming in late June and become noticeable

ot range far
d from Nest
ended three
ces from the

birds from
e them after
or whether a

he nest was
caught and
Figure 15).
ght, and still
igh, exceed-

the same age
age develop-
; it could fly
ards of both
ng enough to
rds or more.
e when their

2 on 19 July 1968
m the abandoned
of age on 26 July.
veloping rapidly
yes, bill, legs, and

in early July and conspicuous by mid-July. According to Manniche (1910), the flocks are composed solely of males which have abandoned the females at the nest. Others have suggested that the flocks are composed not only of males but also of females which have lost eggs to predators. I believe that the flocks contain both sexes, non-breeding individuals and breeding individuals that have lost eggs.

The flocks seen on the Bathurst Island breeding ground usually numbered from four to six birds, and no flock exceeded 10 although larger flocks probably occur. We do not know when these birds left the area. It appeared that they flocked for some time before departing. In 1968 the flocks became scarce by late July and we saw no flocks anywhere from Bracebridge Inlet to Goodsir Inlet during 7–10 August when we noted only a few adults, all but one of which attended young well inland. We saw one lone adult a quarter mile from the beach of Goodsir Inlet on 10 August. In the southern part of the archipelago, I observed as many as 50 adults at one time on the beaches of Jenny Lind Island during 3–10 August 1966.

Autumnal departure dates for adult Sanderlings from the Canadian breeding grounds are scarcer than arrival dates because little attempt has been made to separate old birds from birds-of-the-year in the fall flocks. We have, however, no reason to doubt Snyder's conviction (1957) that the majority of adults leave by mid-August and a few linger with young birds well into September. Some of these unpredictable adults conceivably migrate south with young (see Sutton, 1932:149). In Greenland, where departures are well documented, the fall migration of adults takes place in late July and the first half of August (Salomonsen, 1950–1951).

Although we made a special effort to locate Sanderlings-of-the-year on the marine beaches of Bathurst Island in 1968, not a single young shorebird of any species did we find on the sandy beaches at the head of Bracebridge Inlet on 7 August, and only one – a lone Sanderling – on the beach at the head of Goodsir Inlet on 10 August. The paucity of young shorebirds clearly indicated a poor breeding season. Nevertheless, the Sanderling was one of very few bird species that produced even a few young that year.

Predation and Survival

We have no evidence of predation on adult Sanderlings. Presumably some losses occur although these quick, swift-flying birds are able to cope with most predators. They also are tough and well adapted to the Bathurst environment. We saw no signs of suffering among the early arrivals such as that described elsewhere. Pedersen (1942), for example, stated that Sanderlings suffered greatly from cold and scarcity of food immediately after arriving on the Greenland breeding ground. He reported birds sitting on the snow in small groups, obviously cold, although he found only a few dead.

For young Sanderlings in Greenland, which must have a remarkable survival rate some years, we have quite a different picture. According to Manniche (1910), the brood of the Sanderling seems to suffer very little from hostile persecution, a fact which may be due to the "accomplished vigilance and prudent behaviour of the old female and the young as well as the extremely

he (1910), the females at the ¹/₂ of males but he flocks con-
tinue that have
sually numbered
flocks proba-
bly that they
ame scarce by
et to Goodsir
ll but one of
ter mile from
f the archipel-
of Jenny Lind

the Canadian
empt has been
ocks. We have,
he majority of
irds well into
migrate south
tures are well
ly and the first
-of-the-year on
ig shorebird of
cebridge Inlet
at the head of
early indicated
f very few bird

esumably some
cope with most
t environment.
that described
rlings suffered
g on the Green-
n small groups,

a remarkable
ording to Man-
tle from hostile
vigilance and
s the extremely

suitably coloured clothing of these." Despite an abundance of predators, he did not find a single defective among "some 50 broods of downy young." Taken literally, every brood had four young!

Young Sanderlings on Bathurst Island did not fare so well. Of nine nests, not counting two collected, three were destroyed before hatching and one during hatching. Of a dozen broods seen out of the nest, nine were incomplete.

The Parasitic Jaeger and Long-tailed Jaeger (*Stercorarius parasiticus* and *S. longicaudus*) were the principal avian predators of Sanderling eggs and chicks in 1968. Both patrolled the breeding areas systematically. On 3 August, Taylor saw a Parasitic Jaeger catch a Sanderling chick. A few Glaucous Gulls (*Larus hyperboreus*) and Snowy Owls (*Nyctea scandiaca*) also hunted throughout the Goodsir-Bracebridge area. We do not know what effect these birds and the much rarer Gyrfalcon (*Falco rusticolus*) had on the Sanderling population.

The following mammals occurred in the Sanderling nesting areas and, though we have no direct evidence, may have been potential predators. The arctic fox (*Alopex lagopus*) was fairly abundant and probably the principal mammalian predator on birds in 1968. Wolves (*Canis lupus*), which occasionally investigated our observation blind, came dangerously close to Nest 2. Though not predatory in the usual sense, caribou (*Rangifer rangifer*), muskoxen (*Ovibos moschatus*), and particularly arctic hares (*Lepus arcticus*) frequented the Sanderling ridges and could have stepped on a few nests accidentally. Nest 2 had its closest call when a baby hare ran over the eggs and dented one with its toenails.

On the approach of a bird or mammal, the incubating Sanderling either crouches or runs from its eggs and squats some distance away — a behavior seen a number of times from the blind at Nest 2. Since a man's relatively slow approach gives ample warning, very likely the Sanderling leaves its eggs long before the man is close to the nest. At least it leaves the first time or until it becomes accustomed to such approaches. The fact that the Sanderling usually runs from the eggs at the approach of danger explains why Sanderling nests are difficult to find and has led some investigators to believe that the Sanderling does not engage in the "rodent-run" and "injury-feigning." The truth is that the incubating Sanderling, at the approach of a man, may occasionally leave the nest at the last moment and creep away like a lemming; or it may beat its wing furiously on the ground, partially or fully spreading its down-turned tail, and scuttle and drag itself over turf and bare ground, crying pitifully as it goes — reminding one of a Knot that has just left its eggs.

We found Nest 9 by first seeing the incubating bird feigning injury a long way from the nest and then watching it run back to the eggs. Although we visited Nest 9 rather frequently and often watched the site from afar, the marked adult always ran from the eggs before we were close enough to see it leave. However, this bird quickly returned to the nest. Other Sanderlings, once their nest was discovered, behaved differently. They, like the adult of Nest 2, often could be approached closely and photographed from only inches away. Nevertheless, we knew they were under stress by their involuntary trembling. Even the highly conditioned adult of Nest 2 trembled some when we were too close.

A distress call, often repeated, was sometimes given near the nest by adult females.

The facts that the Sanderling is inclined to run from the nest in the presence of danger, and that it leaves both eggs and young during routine feeding excursions, point up the importance of cryptic coloration in eggs and young of the species. One seemingly serious flaw in the Sanderling's behavior, first noted at Nest 2, is that Sanderling chicks move about conspicuously in and out of the nest while the parent is away feeding, which is about 19 per cent or more of the time. When running about unattended, they are conspicuous to the human eye and, we have reason to believe, particularly vulnerable to predators.

When the adult is on hand and danger approaches, it gives a sharp *wheat* or rapid *wit-wit-wit*, either of which stops the chicks at least momentarily. We first heard these quieting notes at Nest 2. There the adult began calling *wheat* or *wit* before the young hatched. Seemingly, the peeping of the chicks within the shells stimulated the parent. Unfortunately, we did not record these calls.

The adult attending the brood is highly solicitous of the chicks and defends them by attempting to lead potential enemies away. The quieting notes are a dead giveaway that chicks are in the vicinity. Locating Sanderling chicks is easy because the parent is prone to return quickly to them, even more quickly than to the eggs.

In addition to predators, the temperature in the Arctic subjects the Sanderling chicks to considerable stress. They are highly sensitive to cold and die quickly if not brooded regularly at short intervals. Although we did not determine the lethal limits of exposure, we do know that, after two minutes in temperatures approaching freezing, a small chick is under great stress and, after 15 minutes, it is so numb and stiff that it barely can move its legs. Two chicks, carried in a telescope case by Manniche (1910), were "both lying dying in convulsions" after 15 minutes of exposure. No one has yet determined the age when a young Sanderling is able to withstand cold.

The brooding Sanderling, which may occasionally abandon its eggs for unbelievably long periods, will remain with the chicks under adverse conditions — a behavior also noted by Manniche (1910). This certainly was the case following hatching of the first two chicks at Nest 2 on 19 July. Rain fell unusually hard that day and drenched the parent bird attempting to shield both eggs and young. So wet was the bird that it at times stood up and shook its body feathers violently, sending sprays of water out in all directions. Then it settled down and very deliberately stripped the remaining water from each primary with its bill. Once during a severe downpour it did not leave the nest even to carry off the shells of a newly hatched chick.

Banding Returns

To date we have had three recoveries of Sanderlings, banded on the Bathurst breeding ground. An adult male, banded at Nest 5 on 2 July 1968, was collected at Nest 14 on 28 June 1969. The two nests of different years were only 110 paces apart. Collecting the bird verified the sex, which we thought was a male from the start of observations at Nest 5.

An adult male, banded at Nest 7 on 16 July 1968, was trapped and then released at Nest 13 on 6 July 1969. The two nests of different years were fully two miles apart on ridges separated by a broad valley. We verified the sex of this bird in 1969 when we observed its unbanded mate

nest by adult

nest in the
aring routine
n eggs and
g's behavior,
spicuously in
ut 19 per cent
e conspicuous
vulnerable to

a sharp *wheat*
mentarily. We
calling *wheat*
chicks within
ord these calls.
e chicks and
The quieting
ng Sanderling
em, even more

c subjects the
ive to cold and
gh we did not
two minutes in
eat stress and,
e its legs. Two
oth lying dying
etermined the

on its eggs for
adverse condi-
ily was the case
July. Rain fell
pting to shield
l up and shook
rections. Then
water from each
t leave the nest

Bathurst breeding
Nest 14 on 28 June
he bird verified the

released at Nest 13
ridges separated by
its unbanded mate

laying eggs and we saw him on 31 July 1969 with his young at Nest 13.

A bird-of-the-year, banded when newly hatched at Nest 11 on 20 July 1968, was shot in the Gulf of St. Lawrence at Dune du Sud, Magdalen Islands, Quebec, on 20 October 1968. This recovery is important because it indicates that Bathurst Island Sanderlings, unlike the Knots of this area, migrate south to the New World rather than to Old World wintering grounds. J. Claude Baudreau made the recovery.

Specimens of Young Sanderlings

The probable age, weights, and measurements of 10 young, collected on Bathurst Island in 1968, are given in Table 8. A description of body-plumage development and colors of soft parts is outlined below:

Probable Two to Five-day-old Young

Down conspicuous everywhere; feather sheaths of juvenal plumage appearing on interscapular, humeral, dorsal, sternal, and axillar regions of two larger chicks.

Soft parts: eyes black; proximal two-thirds of bill dark gray or bluish gray, distal third black except for small whitish tip; legs and feet black to bluish black with silvery highlights.

Seven-day-old Young

Down conspicuous. Juvenal plumage inconspicuous but developing rapidly: sheaths well developed and bursting at tips on interscapular, humeral, and dorsal regions; sheaths well developed on lower cervical, sternal, and axillar regions. Quills, about 13.0 mm, starting to burst at tips. Wing chord length and juvenal plumage development similar to those of a White-rumped Sandpiper, six and one-half days old, except that the sheaths on the dorsum of the White-rump were not bursting noticeably.

Soft parts: eyes black; bill dark gray to nearly black, being darkest at tip except for trace of whitish; legs and feet very dark greenish gray to black.

Probable 10 to 11-day-old Young

Down about as conspicuous as juvenal plumage, especially noticeable on head, neck, mid-ventral, upper wing, rump, and thigh regions. Feathers conspicuous only on coronal and auricular regions of head, but well developed and fluffed on interscapular, humeral, and dorsal tracts above and on lower cervical, sternal, axillar, and abdominal regions below. Crural regions mostly downy with incoming juvenal feathers apparent. Remiges, including wing-bars, obvious. Compared well to White-rumped Sandpiper of known age.

Fifteen-day-old Young

Down less conspicuous than juvenal plumage but still plentiful on head (except on coronal and auricular regions), neck, mid-pectoral region, base of tail (pelvic and abdominal regions), and legs (crural region). Juvenal plumage conspicuous above and below; the grayish buff of lower throat, pectoral region, and along sides of body distinct from white belly. Wing chord length and juvenal plumage development similar to that of a White-rumped Sandpiper, 15 and one-half days old, except that more down showed on the Sanderling's head.

Soft parts: similar to those of seven-day-old, at most a shade or so lighter.

Probable 20 to 21-day-old Young

Down still conspicuous at base of bill, throat, above and behind eyes, neck, above and below base of tail, and on thighs; traces on pectoral region; otherwise juvenal plumage highly developed and conspicuous. Compared well to White-rumped Sandpiper of known age.

Conclusion

The Arctic summer is brief for man as well as birds and the pressure to see and record every action tremendous. In working over the notes and summarizing the material amassed by the members of the 1968 and 1969 expeditions, I realize that we added a lot of information on the mating and nesting behavior of Sanderlings. The chance to follow one nest from the laying of the eggs to the successful departure of the brood was an opportunity not even anticipated. I am also aware that there are many gaps — phases of the life history that we neglected or could not observe. However, the details that we

now have on pairing, mating, and nesting should make future work on this species easier and the prospects of additional studies more appealing, especially since the Sanderling appears to have one of the most complex breeding behaviors of any scolopacid studied to date.

Summary

This paper describes a study of the Sanderling (*Crocethia alba*) conducted on Bathurst Island near the 76th parallel in the Canadian Arctic during the summers of 1968 and 1969. It emphasizes courtship and mating activities, pair-bond relationship, and the role of the sexes in the care of the eggs and young. Working inland, between Goodsir and Bracebridge Inlets, where dry and wet habitats are extensive and suitable, we made observations on 14 nests, one of which we kept under constant surveillance for 14 days. We also banded and color-marked nine birds with eggs or broods and banded 23 young of known age and 15 of uncertain age.

The Sanderling pairs were thinly scattered, not more than six or eight pairs to one square mile in 1968 and much less in 1969, even on the choicest nest ground.

Both sexes arrived together in small flocks between 3–9 June 1968 and 8–15 June 1969. Some appeared paired on arrival; others loafed and fed in pairs soon after; few appeared to be unmated. We observed single males advertising for mates and defending territories, flight chases, flight displays, and ground displays.

Sanderlings use precopulatory scrapes apart from nesting scrapes for mating purposes. A description is included.

Nests were slight hollows containing dry leaves and lichens. With one exception, the clutches had four eggs. Eggs were laid at intervals of 26 to 29 hours. The incubation period for two nests varied: 24.2 days in one, 31.6 days in the other. The pair-bond dissolves before incubation begins and only one adult, either male or female, incubates the eggs and attends the young.

The details of the activities and behavior of a nesting Sanderling are based primarily on a round-the-clock observation of over 14 days and include times on and off the nest, reactions to the observers, mammals, and other birds, hatching and behavior of the brood, and the final departure from the nest.

The period from hatching to first sustained flight was close to 17 days and an adult defended one strong flying young for five or more days longer. Most Sanderlings probably flew strongly for the first time during 2–9 August.

Flocks, composed of adults of both sexes, occurred in early July, were conspicuous in mid-July, and diminished in late July.

Adult Sanderlings resisted predation, weather, and lack of food; eggs and young were victims principally of jaegers and probably foxes.

Recoveries in 1969 of Sanderlings, banded in 1968, showed that at least some males return to the same breeding grounds and nest close to or far from the former nest. The recovery of a banded bird of the year in the Gulf of St. Lawrence indicated that Bathurst Island Sanderlings migrate south in the New World.

The weights, measurements, and a brief description of plumage development and colors of soft parts are given for 10 young collected in 1968.

Acknowledgments

The Canadian National Museum of Natural Sciences and the Canadian Polar Continental Shelf Project, Department of Energy, Mines and Resources, financed the expeditions to Bathurst Island in 1968 and 1969. A faculty research grant-in-aid (NSF GU-2225 Institutional Grant No. 40) at Kansas State Teachers College provided my transportation to and from Bathurst Island in 1969. I initiated my study of the Sanderling in arctic Canada in 1966 through a research grant-in-aid (GB-4904) from the National Science Foundation.

David R. Gray, Cy G. Hampson, F. Pierre Lamothe, S. D. MacDonald, George Miksch Sutton, and Philip S. Taylor directly assisted my study on the Bathurst breeding ground. E. L. Bousfield, W. Earl Godfrey, F. P. Hunt, Jean M. Parmelee, and Ernest Frederick Roots have helped immeasurably. A. E. Porsild identified the plants, and the Canadian Wildlife Service provided permits for securing specimens and banding birds.

I am especially grateful to S. D. MacDonald who was largely responsible for establishing the Bathurst Camp and leading the expeditions. I also wish to express my sincere gratitude to George Miksch Sutton for the use of his painting of the adult Sanderling, and to Don Petz, who prepared the maps.

LITERATURE CITED

- BANNERMAN, D. A.
1960 Birds of the British Isles. Volume 9. Oliver and Boyd, Edinburgh.
- BENT, A. C.
1927 Life histories of North American shore birds. Part 1. U.S. Natl. Mus. Bull. 142.
- BIRD, C. G., and E. G. BIRD
1941 The birds of north-east Greenland. *Ibis* (Ser. 14), 5:118-161.
- DALGETY, C. T., CAPT. J. H. MCNEILE, and M. J. INGRAM
1931 Birds observed in Spitsbergen in 1930. *Ibis* (Ser. 13), 1:243-254.
- DRENT, R. H.
1967 Functional aspects of incubation in the Herring Gull. *Behaviour Suppl.* 17.
- DRURY, W. H., JR.
1961 Breeding biology of shorebirds. *Auk*, 78:176-219.
- FEILDEN, H. W.
1877 List of birds observed in Smith Sound and in the polar basin during the Arctic Expedition of 1875-76. *Ibis* (Ser. 4), 1:401-412.
- GODFREY, W. E.
1966 The birds of Canada. Natl. Mus. Canada Bull. 203.
- HENNESSEY, F.
1910 Report of Mr. Frank Hennessey, on the birds, animals, crustacea and fauna collected on the expedition of the 'Arctic' in 1908-1909. In: Bernier (1910):502-513.
- HARINGTON, C. R.
1961 Unpublished notes on file in Canadian National Museum of Natural Sciences.
- LOEPPENTHIN, B.
1932 Die Vögel Nordostgrönlands zwischen 73°00' und 75°30' N. Br., samt Beobachtungsergebnissen von der Dänischen Godthaab-Expedition 1930. *Medd. om Groenland*, 91:1-128.
- LOW, A. P.
1906 Appendix II. List of birds and eggs identified or collected. In: Report on the Dominion Government expedition to Hudson Bay and the Arctic islands on board the D.G.S. Neptune, 1903-1904. Ottawa.
- MACDONALD, S. D.
1954 Report on biological investigations at Mould Bay, Prince Patrick Island, N.W.T. Ann. Rept., 1952-53, Natl. Mus. Canada Bull. 132.
1959 Biological investigations at Isachsen, Ellef Ringnes Island, N.W.T. Contrib. to Zool., 1959, Natl. Mus. Canada Bull. 172.
- MACFARLANE, R.
1908 List of birds and eggs observed and collected in the North-West Territories of Canada, between 1880 and 1894. In: Through the Mackenzie Basin, by Charles Mair, William Briggs, Toronto.
- MACPHERSON, A.H., and T. H. MANNING
1959 The birds and mammals of Adelaide Peninsula, N.W.T. Natl. Mus. Canada Bull. 161.

- MADSEN, C.
1925 Ornithologiske Jagttagelser fra Øestgrønland. Dansk Ornith. Foren. Tidsskr., 19:33-41.
- MANNICHE, A. L. V.
1910 The terrestrial mammals and birds of north-east Greenland. Biological Observations. Medd. om Grønland, 45:1-200.
- MANNING, T. H., E. O. HÖHN, and A. H. MACPHERSON
1956 The birds of Banks Island. Natl. Mus. Canada Bull. 143.
- MANNING, T. H., and A. H. MACPHERSON
1961 A biological investigation of Prince of Wales Island, N.W.T. Trans. Royal Canadian Inst., 33 (pt. 2):116-239.
- MYERS, B. W.
1966 Nesting habits of the Mourning Dove in the Flint Hills area of Kansas with important trapping techniques. Unpublished Research Project, Kansas State Teachers College, Emporia.
- NETHERSOLE-THOMPSON, C., and D. NETHERSOLE-THOMPSON
1942 Egg-shell disposal by birds. Brit. Birds, 35:162-69, 190-200, 214-23, 241-50.
- NETHERSOLE-THOMPSON, D.
1951 The Greenshank. Collins, London.
- 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. Canada 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. Canada Bull. 222.
- PALMER, R. S.
1967 Species accounts. In: The shorebirds of North America, G. D. Stout, ed. Viking Press, New York.
- PEDERSEN, A.
1930 Fortgesetzte Beiträge zur Kenntnis der Säugetier- und Vogelfauna der Ostküste Grönlands. Ergebnisse einer zweijährigen zoologischen Untersuchungsreise in Ostgrönland. Medd. om Grønland, 77:341-508.
1942 Säugetiere und Vögel von "Dansk Nordøstgrønlands Expedition 1938-39. Medd. om Grønland, 128:1-119.
- SALOMONSEN, F.
1950-1951 The birds of Greenland. Ejnar Munksgaard, Copenhagen.
- SNYDER, L. L.
1957 Arctic birds of Canada. University of Toronto Press, Toronto.
- STOUT, G. D., Editor
1967 The shorebirds of North America. Viking Press, New York.
- SUTTON, G. M.
1932 The birds of Southampton Island. Mem. Carnegie Mus., 12 (Pt. 2, Sec. 2):1-275.
- TUCK, L. M., and L. LEMIEUX
1959 The avifauna of Bylot Island. Dansk Ornith. Foren. Tidsskr., 53:137-154.
- URBAN, E. K.
1957 Birds observed at Resolute Bay, Cornwallis Island, Northwest Territories. Passenger Pigeon, 19:73-75.
- WITHERBY, H. F., F. C. R. JOURDAIN, N. F. TICEHURST, and B. W. TUCKER
1940 The handbook of British birds. Volume 4. H. F. and G. Witherby, London.

DEPARTMENT OF ECOLOGY AND BEHAVIORAL BIOLOGY
JAMES FORD BELL MUSEUM OF NATURAL HISTORY
UNIVERSITY OF MINNESOTA, MINNEAPOLIS