OBSERVATIONS ON THE BREEDING BIOLOGY OF BLACK-BELLIED PLOVERS ON DEVON ISLAND, N.W.T., CANADA

DAVID J. T. HUSSELL AND GARY W. PAGE

Details of reproduction in many arctic shorebirds are poorly known, although excellent studies of some species have been published recently (e.g. Holmes 1966, Parmelee et al. 1968, Parmelee 1970, Jehl 1973). Particularly notable is the lack of data on growth of the young. Ricklefs' (1968, 1973) extensive compilations of growth rates in birds include only 5 species in the families Charadriidae and Scolopacidae. This dearth of information is undoubtedly related to the inaccessibility of many shorebird breeding ranges and to difficulties in studying breeding shorebirds under natural conditions.

In this paper we report on the breeding biology of the Black-bellied Plover (*Pluvialis squatarola*) at the northern limit of its known breeding range, on Devon Island. In North America this species breeds mainly in the high arctic region of Canada between 63°N and 76°N (Godfrey 1966), and on the north and west coasts of Alaska south to about 61°N (Gabrielson and Lincoln 1959). Some aspects of the breeding biology of the species have been described and earlier literature reviewed by Drury (1961), Parmelee et al. (1967), and Mayfield (1973). Our account is most complete for the later stages of breeding, including growth and development of the young, and tends to complement the work of other authors whose reports concentrate on the earlier events of the breeding cycle.

STUDY AREA AND METHODS

The study was conducted primarily between 7 June and 26 August 1968 on the Truelove Lowland (75°40'N, 84°35'W) about 24 km southwest of Cape Sparbo on the north coast of Devon Island. Additional data were collected there by Hussell and his assistants from 11 June to 14 August 1966, 9 June to 29 August 1967, and 8 June to 13 August 1969.

The Truelove Lowland is a coastal lowland situated between Jones Sound and the interior plateau of Devon Island (Fig. 1). It is traversed by a series of raised beaches, separated by numerous lakes, ponds, and poorly-drained meadows. Granitic and calcareous rock outcrops occur in several places. Plant life is sparse on the exposed beach ridges and outcrops, but is rich in the low-lying wet meadows. More detail on the topography and vegetation may be found in Bliss and Teeri (1971) and Barrett and Teeri (1973). At this latitude the sun remains above the horizon continuously from 27 April until 17 August. Summer temperatures rarely exceed 15°C and July temperatures average about 4°C. The breeding season of most birds on the Truelove Lowland is remarkably late, corresponding with a late melt (Hussell and Holroyd 1974).

In 1966 and 1967 most observations were made in the "census area" of about 308 ha shown in Fig. 1. General observations were recorded on Black-bellied Plovers and records

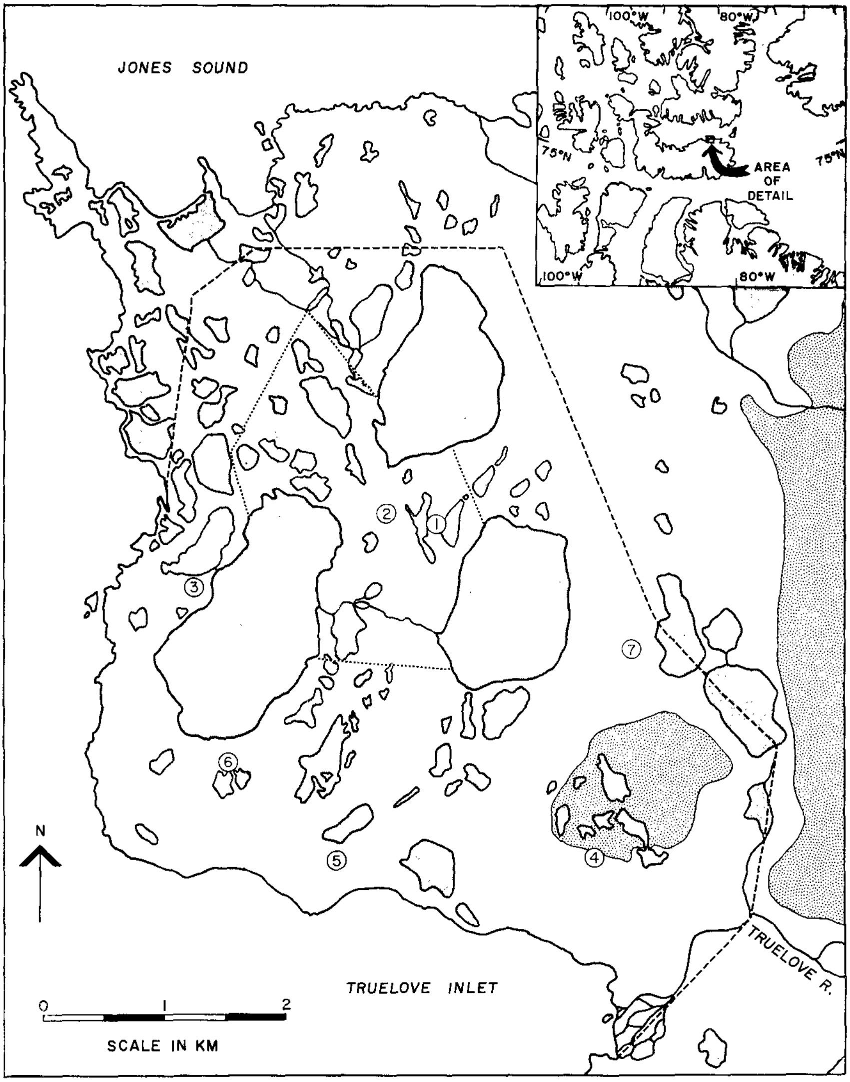

FIG. 1. Map of the Truelove Lowland, Devon Island. Numbered circles show locations of Black-bellied Plover nests found in 1968. Dotted and broken lines indicate limits of the "census area" and "study area," respectively (see text). Shaded areas are lakes or ponds. Land over 60 m elevation is stippled.

were kept of all nests. In 1968 a wider "study area" of 1940 ha was covered regularly (Fig. 1) and an effort was made to locate all plover nests in this area. From late July until our departure that year, Page spent most of his time working on plovers. In 1969 the census area and the eastern and central ⅔ of the study area were covered regularly, but although special attention was paid to the plovers, considerably less time was devoted to them than in the previous year.

Seventeen nests and 1 additional brood were located in the 4 years. On 31 July and 1 and 2 August 1968 we watched a nest from a blind during hatching, including 21 hours of continuous observation. At other times to observe plover behavior we concealed ourselves as best we could in the open habitat favored by the birds. Eggs found during the laying period were individually marked with ink, and laying and hatching times determined by repeated observations of the nests. During incubation we often avoided approaching nests closely as we thought that our visits might attract predators to the nests. Young plovers were banded when they were first found, usually within 24 h of hatching. Development was studied by measuring and weighing the young whenever they were found, and by collecting a series of known-age young. Eggs and young were weighed to the nearest 0.1 g with Pesola spring balances or an Ohaus triple-beam balance. Specimens are in the Museum of Zoology, University of Michigan, and nest records are in the Prairie Nest Records Scheme, Manitoba Museum of Man and Nature, Winnipeg.

In this paper "clutch size" refers to completed clutches determined by observations of the same number of eggs in a nest at 2 visits at least 48 h apart, or by a single observation of the number of eggs less than 25 days before the young hatched. "Incubation period" is the time from laying to hatching for the last egg in a clutch. "Fledging period" is the time from hatching to first flight for an individual bird. Times are in Mean Solar Time for the locality concerned.

RESULTS

Arrival and pre-nesting activities.—In the 4 years 1966–69, Black-bellied Plovers were first observed on the Truelove Lowland on 11, 12, 11, and 14 June, respectively. Most early arrivals were males, distinguished from females by their more boldly marked plumage (Van Tyne and Drury 1959). The majority of females arrived a few days after the males and by about 20 June each year pairs were scattered over the lowlands.

On Devon Island arrival dates are later than for most other parts of the breeding range (Table 1). At the southern limit of the range in western Alaska, Black-bellied Plovers arrive by the second week of May. They appear in the first week of June at many places in the Canadian arctic, and on Bylot Island (73°N), near the northern limit of the range, first arrivals are as late as on Devon Island.

Flight displays were observed infrequently each year, from as early as 12 June until late June. We have nothing to add to the descriptions of Drury (1961) and Parmelee et al. (1967) on the form of the display.

Copulation was observed by Hussell on 21 and 22 June 1969. In the first case the male, with head stretched out horizontally and wings drooped, ran quickly towards the female and straight onto her back, remained for about

TABLE 1

ARRIVAL DATES OF BLACK-BELLIED PLOVERS AT VARIOUS NORTH AMERICAN LOCALITIES

Locality	Latitude (°N)	No. of years	First arrival (range)	Sources
Devon Island	76	4	11–14 June	This study
Bylot Island	73	2	15–17 June	Tuck and Lemieux (1959) Drury (1961)
S. Banks Island	72	2	end of May–1 June	Manning et al. (1956)
Cambridge Bay, Victoria Island	69	3	28 May–4 June	Parmelee et al. (1967)
Jenny Lind Is.	69	1	4 June	Parmelee et al. (1967)
Southampton Is.	64	1	9 June	Sutton (1932)
Hooper Bay, Alaska	62	1	9 May	Brandt (1943)

20 sec while copulation occurred and then flew off to a distance of about 40 m. The male behaved similarly in the second case, except that during the run towards the female his head appeared more withdrawn. The tail was held slightly below the horizontal. This time the male remained on the female for about 30 sec, then flew about 10 m away. No special postures by the female were noted. The male's behavior was similar to the "rushing" which sometimes preceded copulation and often followed flight displays of Black-bellied Plovers on Victoria Island (Parmelee et al. 1967). The preliminary behavior of the adults prior to the copulations observed on Devon Island was not seen.

The pair observed copulating on 21 June was believed to be from Nest 3/69, which we found on 1 July. From hatching dates we estimate that the first egg was laid in it on 25 June. The pair seen copulating on 22 June was near the site of Nest 1/69, which contained 2 eggs when found on 26 June. The first egg in this nest was probably laid on 24 June.

Nest sites and breeding density.—Nests were depressions in the ground in relatively dry sites on or near raised beach ridges, and often on a prominent part of a ridge. Nest sites were usually on gravelly ground, sometimes with large boulders nearby, and typically sparsely vegetated with lichens, tufts of *Dryas integrifolia, Saxifraga oppositifolia, Salix arctica,* sedges (Cyperaceae) and grasses (Gramineae). Although many of these sites were among the first places free of snow in the spring, egg-laying did not usually start until the snow had disappeared from considerably wider areas (see Fig. 7).

We probably located all of the nests in the study area in 1968. Seven nests were found, but there were probably only 6 pairs of plovers, since the eggs

TABLE 2

BREEDING DENSITIES OF BLACK-BELLIED PLOVERS ON DEVON ISLAND

Year	Area[1]	No. of territories[2]	Density pairs/km^2
1968	S	6.5	0.34
1966	C	2.0	0.65
1967	C	3.0	0.97
1968	C	1.0	0.32
1969	C	1.5	0.49
mean	C	1.9	0.61

[1] "C" is the census area of 308 ha and "S" is the study area of 1940 ha (see Fig. 1 and text).

[2] No. of territories estimated from nests and broods found. Nests near the border of the area are counted as 0.5 territory. Numbers of nests involved for the census area are as follows: 3 in 1966; 4 in 1967; 1 in 1968; and 2 in 1969. For the study area in 1968, see text.

in Nest 1 disappeared before laying began in nearby Nest 2. One pair probably bred just outside the study area, as we found 2 large unbanded young from a previously undetected brood in the northwestern portion of the area on 23 August. Thus we count 6.5 pairs in the study area, giving a density of 0.34 pairs per km^2.

Estimated densities of breeding pairs in the census area each year are shown in Table 2. Densities were higher in 1966 and 1967 than in the following 2 years, a situation which was similar in Lapland Longspurs (*Calcarius lapponicus*) and Snow Buntings (*Plectrophenax nivalis*), and may have been related to the early melt in the first 2 years (Hussell and Holroyd 1974). We do not know whether breeding densities were higher for the entire lowland in 1966 and 1967, but the data in Table 2 support the idea that the density of 0.34 pairs per km^2 for the study area in 1968 may be lower than average for the Truelove Lowland. In 1969, only 3 nests were found in the study area. The wide distribution of these nests and absence of other territorial birds indicated that overall densities were at least as low as in 1968. In summary, the evidence suggests that densities of 0.3–1.0 pairs per km^2 are normal on the Truelove Lowland.

Breeding densities on Devon Island were similar to those on Victoria Island, but on Jenny Lind Island estimated densities were 1.2–2.3 pairs per km^2 (Parmelee et al. 1967). Drury (1961) found 4 nests in an area of less than 0.5 km^2 on Bylot Island.

Laying, incubation and hatching.—Black-bellied Plovers laid 4 eggs at approximately 36 h intervals on Devon Island (Fig. 2). Thus about 4½ days elapsed between the laying of the first and last eggs in a clutch. Our observations are consistent with the hypothesis that the 4th egg was always

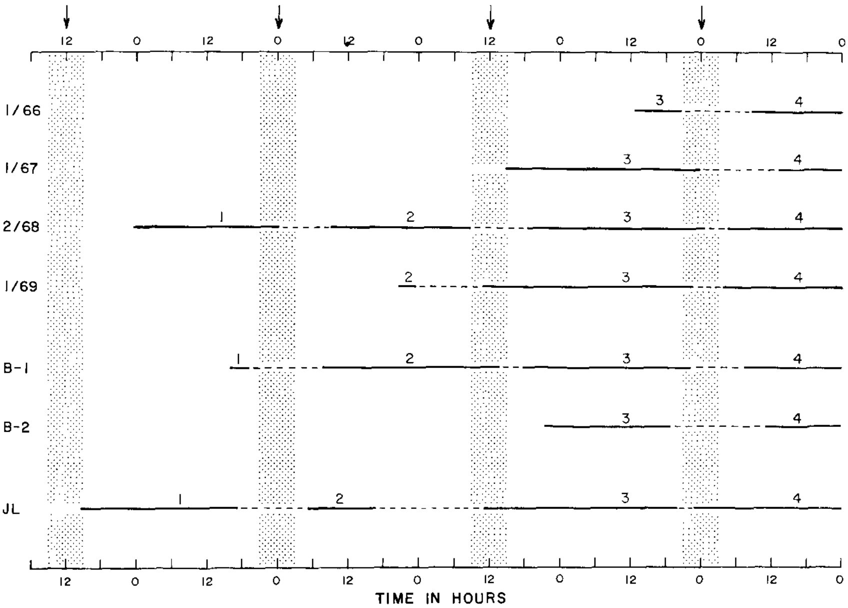

FIG. 2. Timing of egg-laying in 4 Black-bellied Plover nests on Devon Island, 2 on Bathurst Island (B-1 and B-2) (H. F. Mayfield, pers. comm.), and one on Jenny Lind Island (JL) (D. F. Parmelee, pers. comm.). Solid lines represent periods when indicated number of eggs were known to be present; dotted lines show periods during which egg-laying occurred. Arrows and stippled areas show hypothesized times of egg-laying. Nest histories are placed so that the night of clutch completion is below the right-hand arrow.

laid within about 3 h of midnight, and the 3rd, 2nd, and 1st eggs were laid within 3 h of noon, midnight, and noon, respectively. Records for 1 nest on Jenny Lind Island (Parmelee et al. 1967, and D. F. Parmelee pers. comm.), and 2 nests on Bathurst Island (H. F. Mayfield pers. comm.) also conform to this pattern.

We agree with other authors that completed clutches are almost invariably of 4 eggs. During our study 12 nests had completed clutches of 4 eggs, and 3 other nests containing 4 eggs were destroyed before we could determine if the clutch was complete.

During the laying period we found only the adult male in attendance at the nest, but after the clutch was complete both sexes shared incubation duties. On 5 occasions during the laying period the male was observed sitting on an incomplete clutch and on 7 occasions standing near the nest, but often no adult of either sex was found in the vicinity.

TABLE 3

AIR TEMPERATURES DURING EGG-LAYING

Nest(s) and year	Egg-laying dates	Daily temperatures °C[1] Minimum Mean and Range	Daily temperatures °C[1] Maximum Mean and Range
All 1966	20–28 June[2]	+0.7 (−2 to +1)	+6.0 (+5 to +8)
All 1967	19 June– 3 July	+1.7 (−1 to +4)	+5.0 (+2 to +8)
All 1968	26 June– 6 July	−0.7 (−4 to +1)	+2.1 (0 to +6)
All 1969	22 June– 30 June	−0.8 (−3 to +1)	+3.1 (+1 to +6)
No. 2 1966	23–28 June	+1.3 (+1 to +2)	+6.1 (+5 to +8)
No. 2 1968	1–6 July	−1.6 (−3 to 0)	+2.6 (0 to +6)

[1] For methods see Hussell and Holroyd (1974).

[2] Temperatures for 22–28 June 1966, only.

That the incomplete clutch is partially incubated by the male and is often left unattended, raises the question of whether the eggs are in danger of chilling during the egg-laying period. Air temperatures during the known egg-laying season each year, and for Nests 2/66 and 2/68 (each of which had hatching periods of over 30 h—see below) are shown in Table 3. Daily minimum temperatures averaged close to 0°C but never fell below −4°C during the laying period.

Males were observed incubating completed clutches on 12 occasions compared to 5 for females. In 8 of the 12 instances when the male was incubating, however, he went to the nest after we visited it and may not have been incubating when we first approached. Males were observed alone near the nest on 13 occasions during the incubation period compared to 4 for females. Höhn (1957) found only the more brightly-colored adult (presumably the male) on the nest during incubation and Drury (1961) found that the male did most of the incubating on Bylot Island. In contrast, Mayfield (1973) reported that the female at one nest on Bathurst Island incubated 60% of the time during 23 hours of observation near the middle of the incubation period. Bent (1929) and Sutton (1932) state that both sexes incubate after the clutch is complete; Parmelee et al. (1967) agree, but note that the female is more reluctant than the male to incubate when a person is near the nest, an observation with which we concur. Considering the difficulty of seeing the drab females at a distance and their reluctance to go to the nest when an intruder is nearby, we think that incubation may be shared more equally by the sexes than our observations indicate.

The incubation period was determined to be about 27 and 26.5 days at 2 nests on Devon Island. At Nest 2/68 the incubation period was between 26 days, 22 h, 41 min and 27 days, 2 h, 36 min; and at Nest 1/69 it was between 26 days, 6 h, 25 min and 26 days, 22 h. At 2 other nests the last young hatched about 26 days after the completed clutch was found. Mayfield (pers. comm.) determined 2 incubation periods of 26 days, 17 h (± 8 h) and 27 days, 8 h (± 4 h) on Bathurst Island, N.W.T., in 1973. These data, together with two 27-day periods reported by Holmes and Black (1973), add weight to Mayfield's (1973) conclusion that the incubation period is usually 26–27 days and reports of shorter periods are probably erroneous.

The 4 eggs in a clutch usually hatched over a period of 1 or 2 days, indicating that there may have been effective incubation before the clutch was complete, as suggested by Parmelee et al. (1967). In Nests 2/66 and 2/68 the hatching periods were at least 30 h and about 36 h, respectively. In Nest 2/68 the eggs hatched in the order in which they were laid. The first young hatched was about 1 h old when we first saw it, and its down was still wet. The second egg hatched 6 h and 35 min later, the third 12 h and 49 min after the second, and the fourth 15 h and 35 min after the third (based on times of shell removal). At 2 other nests the last eggs hatched at least 24 and 11 h after the others. Drury (1961) reports that the eggs of the Black-bellied Plover hatch over a 2-day period, and Parmelee et al. (1967) generally agree, stating that the hatching period is usually between 24 and 48 h and only occasionally less than 16 h. Mayfield (1973) reported a hatching period of about 12 h in 1 nest.

At least 41 young hatched from 17 nests on Devon Island during our study. Five nests were destroyed during the incubation period, young hatched in 11 nests, and the fate of 1 nest was unknown. Four young were hatched in each of 9 nests not destroyed by predators, 3 eggs hatched in another and the 4th was infertile, and at least 2 hatched in the remaining nest. Based on the 15 nests for which full data are available, the plovers hatched an average of 2.6 young per nest.

Nesting success can be calculated more precisely on the basis of exposure (Mayfield 1961). The rate of loss of nests was 0.022 per nest-day after clutch completion, which represents a survival rate of 54.7% over the 27-day incubation period. Hatching success of individual eggs which survived the incubation period was 97.5% (39 out of 40), which gives an overall hatching success of 53.3% or 2.1 young hatched per completed clutch.

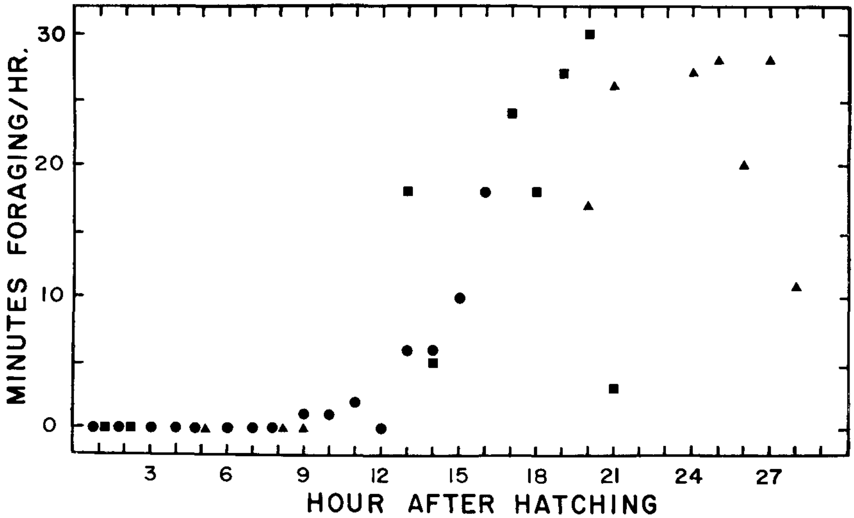

FIG. 3. Development of foraging behavior in young at Nest 2/68. Symbols show time spent away from brooding adult in relation to age: triangles, first hatched young; squares, second hatched young; circles, third hatched young.

Behavior during the hatching period.—At Nest 2/68 we saw eggshell removal by the adult female and the adult male after hatching of the 3rd and 4th eggs, respectively. In each case the bird picked up the shell and flew away with it. We did not determine the exact interval between hatching and shell removal in any case, but in only 3 other instances did we see shells in the nest with newly-hatched young, indicating that shells are removed quickly. Mayfield (1973) reported that shells were removed "within minutes after the young bird broke free."

The chicks remained in the nest for several hours after hatching while their down dried. Intensive observations at Nest 2/68 showed the progressive development of effective locomotory abilities and feeding behavior in the young (Fig. 3). The third chick hatched in this brood first left the nest 8 h and 25 min after hatching but returned under the brooding adult less than 1 min later. It appeared weak and stumbled frequently. During the next hour it made another short trip and pecked at something. In successive trips, this chick remained away from the brooding adult longer and strayed farther from the nest; by the time it was 13 h old it was definitely feeding.

On their trips from the nest, individual chicks foraged alone and were not assisted by adults in obtaining food. One young plover was observed pecking at a large midge (Chironomidae), but it hesitated and the midge escaped.

On another occasion a chick eyed a caterpillar near our blind. It turned away and moved off only to return seconds later and eye the caterpillar again. In this instance the bird did not attempt to eat it, but later one young plover, perhaps the same one, picked up a caterpillar and swallowed it after dropping it several times. On these feeding trips, the movements of the young were very like those of foraging adults—run, stop, peck. By the time the young were 24 h old they were venturing as far as 40 m away from the brooding adult.

During the observation period at Nest 2/68 the male spent 12 h and 13 min on the nest brooding the young compared to 7 h and 34 min spent by the female. The differing dispositions of the sexes to return to the nest after a disturbance may partially account for the greater amount of time we observed the male at the nest. The male returned to the nest 11 times after our activities had driven the brooding adult away, compared to only once for the female under similar circumstances.

The adults usually brooded quietly on the nest during the foraging trips of the young, but both sexes often used a quiet quivering trill when a chick was about to enter or leave the nest. At other times this note appeared to stimulate the chicks to come to the parent, particularly when a chick began peeping at some distance from the brooding adult. On the 3 occasions when this happened the adult responded with the trill note and the young plover returned to the parent brooding on the nest. When the adults had been disturbed by our activities and the young plovers were scattered nearby, one parent often brooded away from the nest while the other brooded on the nest. This occurred on 4 occasions when our activities caused all but the most recently hatched young to be away from the nest for an unusually long time.

When a person approached the nest either the brooding or the off-nest parent called in alarm when the intruder was as much as 250 m away. As the intruder came closer, one adult (usually the off-nest bird) flew to meet him and continued to call in alarm. Before he had approached to within 50 m of the nest, the brooding adult left and joined its mate, and the oldest chicks fled and crouched motionless nearby until the disturbance had passed. Close approach often elicited distraction behavior from the adults, as described by Drury (1961).

There was no noticeable difference in the reactions of adult male and female Black-bellied Plovers to predators near the nest at hatching, but their reactions were related to the species of predator and its behavior. In 2 instances when Glaucous Gulls (*Larus hyperboreus*) flew over the nest one of the parents called in alarm but made no attempt to chase the gulls. Long-tailed Jaegers (*Stercorarius longicaudus*) flew over on 4 occasions but did

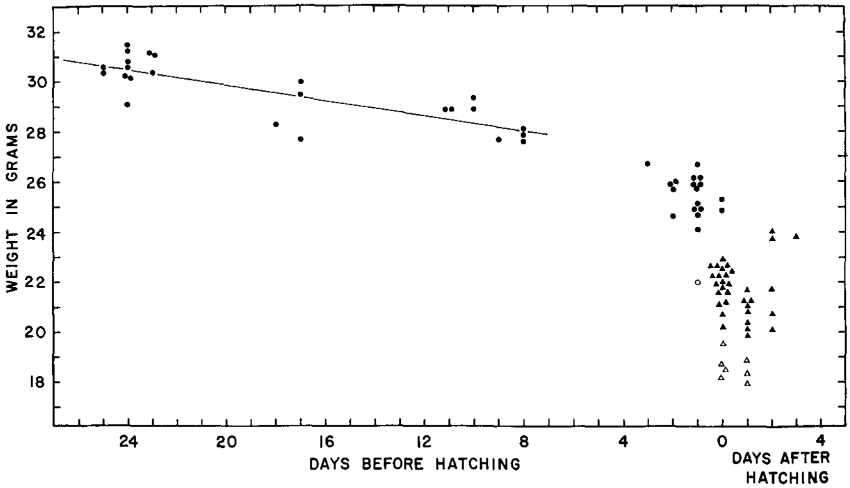

FIG. 4. Weights of eggs and newly-hatched young in relation to hatching date. Circles show weights of eggs; triangles, weights of young. Open symbols indicate weights of young and an egg in Nest 7/68. The line is a linear regression fitted to the data for eggs more than 7 days from hatching (see text).

not elicit any reaction from the plovers, other than causing the brooding female to flatten on the nest on one occasion. When a Long-tailed Jaeger landed near the brooding male, however, the female appeared quickly and chased the jaeger off. In contrast to the mild response to airborn Long-tailed Jaegers, on the only occasion when Parasitic Jaegers (*Stercorarius parasiticus*) flew over the nest, the male called several times in alarm, left the nest, and chased the jaegers until they left the vicinity.

After the last-hatched young had been brooded for several hours the plovers deserted the nest. At Nest 2/68 this occurred sometime between 8 and 15 h after the 4th egg hatched.

The behavior of Black-bellied Plovers at the time of hatching is poorly documented in the literature. Parmelee et al. (1967) found that both sexes were equally solicitous of the newly-hatched young at nests on Victoria Island and that after the young deserted the nest there was no evidence that they ever returned. Their findings are supplemented by Drury's (1961) observation that the young spent 1 night in the scrape after all had hatched in the 1 nest he examined. Mayfield (1973) mentions that while other young were hatching, the earlier hatchlings ventured only as far as 20 cm out of the nest and alternated sleep with vigorous activity within and outside the nest. His observations of the behavior of the young appear to correspond

TABLE 4

GROWTH OF YOUNG BLACK-BELLIED PLOVERS FROM HATCHING TO FLEDGING

UMMZ No.	Nest No./Yr.	Age			Sex	Weight g	Tarsus mm	Culmen mm	Wing chord mm	Outer primary mm	Outer rectrix mm
		Minimum days–hr	Maximum days–hr	Est. days							
212791	2/66	0–02	0–23	0.5	–	–	33.4	12.6	–	–	–
215889	4/67	0–01	1–02	0.5	M	19.8	32.3	12.5	–	–	–
215906	4/68	3–00	4–02	3.1	F	23.6	34.1	13.1	–	–	–
215907	7/68	6–04	7–02	6.5	F	35.1	36.2	15.4	–	1	–
215908	6/68	6–02	7–03	6.7	F	48.0	37.1	16.9	–	6	–
215909	7/68	12–02	–	12.5	F	84.9	42.0	20.0	66	27	8
215944	1/69	17–23	–	18.4	M	154.0	45.0	25.3	116	64	28
215911	2/68	20–09	20–09	20.4	M	158.2	46.4	24.1	123	71	34
215910	7/68	20–22	–	21.4	M	152.8	43.3	23.5	117	61	27
215912	2/68	23–08	23–08	23.3	M	186.9	45.7	25.1	137	81	37
	–	–	–	5.0[1]	M	32.2	37.0	15.5	–	–	–
Full-grown birds (means)					M	185.0[2]	45.5[3]	27.8	183	126	70
					F	168.4[4]	43.8[5]	26.8	177	125	67

[1] Data for specimen from Jenny Lind Island (Parmelee et al. 1967:221).

[2] Mean weight of 1 young male in the Royal Ontario Museum (R.O.M.) from N.W.T. in September and 2 fledged males from N.W.T. in August from Parmelee et al. (1967).

[3] Mean measurements of 7 young males in R.O.M. from N.W.T. and Ontario in September.

[4] Mean weight of 1 young female in R.O.M. from N.W.T. in September and 3 fledged females from N.W.T. in August from Parmelee et al. (1967).

[5] Mean measurements of 7 young females in R.O.M. from N.W.T. and Ontario in September.

with ours for chicks less than 12 h old; that he did not see greater activity by the young is probably related to the shorter hatching period (about 12 h) and time spent at the nest (less than 15½ h) for the brood he observed.

Development and fledging of the young.—During the chick's embryonic development, the weight of the egg decreased by nearly 20% (Fig. 4). Twelve eggs weighed within 5 days of clutch completion averaged 30.6 g (S.D. = 0.6 g) in contrast to 12 pipped eggs which averaged only 25.2 g (S.D. = 1.3 g) on the day prior to hatching. The mean weight of fresh eggs is estimated at 31.0 g (S.D. = 0.26 g) and the average rate of weight loss is about 0.15 g/day during the first 20 days of incubation.

Twenty-three newly-hatched young (less than 1 day old) weighed considerably less than the pipped eggs, averaging 21.4 g (S.D. = 1.4 g). After hatching the young decrease in weight for several hours. The first chick hatched in Nest 2/68 weighed 20.7 g when about 3 h old, was down to 20.1 g at 18 h and had increased again to 20.7 g at 39 h. Likewise, the 3rd chick in Nest 1/69 weighed 21.9 g about an hour after hatching, was 0.7 g lighter 11 h later, but had regained 0.5 g after an additional 10 h. This trend of weight loss followed by recovery during the first 48 h after hatching can also be detected in Fig. 4.

The yolk sac was large in newly-hatched young and it had not entirely disappeared in 1 chick which was between 3 and 4 days of age. The contents of the yolk sac provide nourishment for the chick for the first day or 2 after it hatches and is learning to forage.

Eggs and newly-hatched young in Nest 7/68 were substantially lighter in weight than those in any other nest we observed (Fig. 4). On the day of hatching the 4 young averaged 18.8 g, about 12% below the mean for all newly-hatched young. This difference apparently persisted throughout the development of the young from this brood (see below).

Weight increased rapidly throughout the fledging period (Table 4, Fig. 5) and the value of *K* for a fitted logistic curve (Ricklefs 1967) is 0.194 with an asymptote of 205 g. The primaries and rectrices grew rapidly after about the 6th and 10th days, respectively, but the bill and tarsus, which were already well developed at hatching, grew more slowly. There was no trace of the juvenal plumage on the freshly-hatched downy young (Fig. 6). By the

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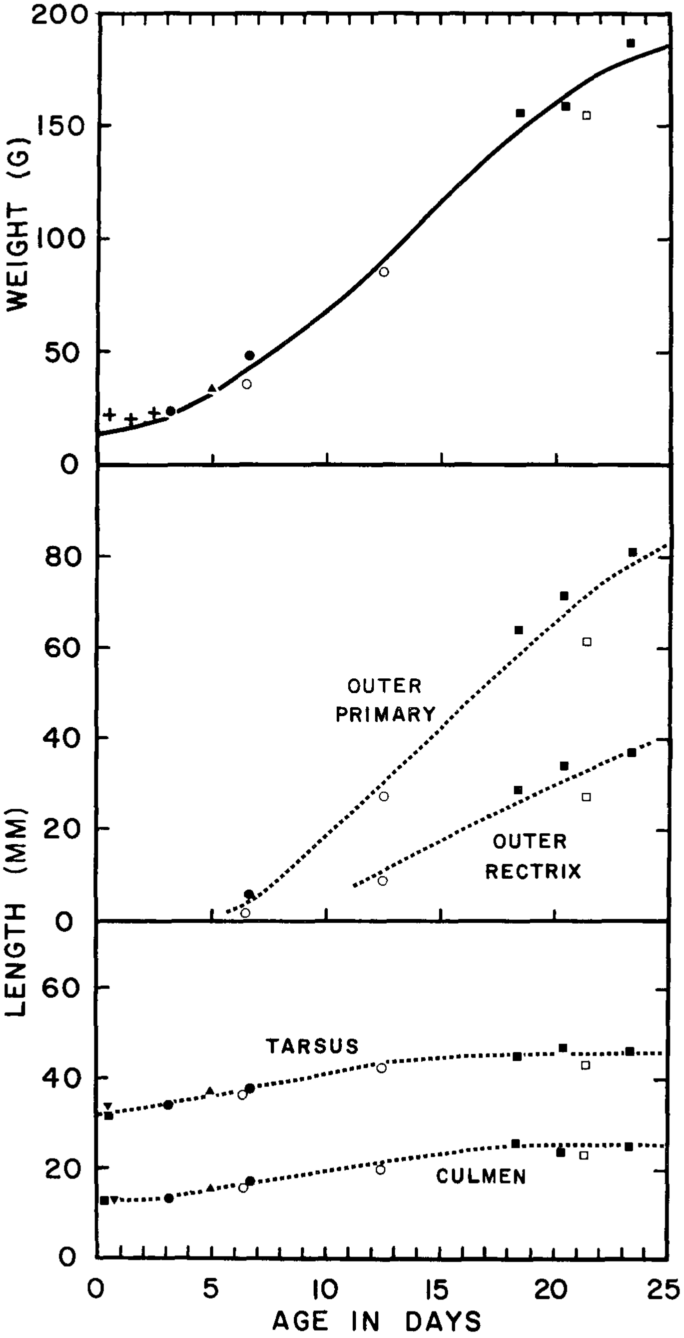
FIG. 5. Growth of young Black-bellied Plovers: squares—males; circles—females (open symbols are for young from Nest 7/68), triangle—data for one male on Jenny Lind Island (from Parmelee et al. 1967:221). Crosses indicate mean weights of 23, 11, and 5 young which were known or estimated to be 0–24, 24–48, and 48–72 hours old, respectively. The curve for growth in weight is a logistic fitted to the mean and individual weights of young more than one day old. All other curves were fitted by eye.



WEIGHT (G)
200
150
100
50
0
LENGTH (MM)
80
60
40
20
0
OUTER PRIMARY
OUTER RECTRIX
60
40
20
0
TARSUS
CULMEN
0
5
10
15
20
25
AGE IN DAYS

3rd day after hatching, however, the sheaths of the dorsal and ventral body feathers were visible beneath the skin and the primary feather sheaths were beginning to protrude through the skin. In a 6–7-day-old young (UMMZ No. 215,908), feather sheaths were protruding from the breast, abdomen, upper back and wings, and the 10th primary was 6 mm long. Juvenal feathering was noticeable over the entire body of a bird 12–13 days old (UMMZ No. 215,909), but the overall appearance was still that of a large downy young. The juvenal plumage is prominent in young 18–23 days old, with progressively less down adhering mainly to the nape, rump and underparts. There was considerable individual variation in growth rate and it was particularly noticeable that young from Nest 7/68 were retarded both in weight increase and feather development compared to birds from other broods.

The fledging period was determined as 23 days for 1 young plover in 1968. Although this bird's flight feathers were still growing, it made uninterrupted flights of about 150 m when it was 23.3 days old (UMMZ No. 215,912). Other chicks about 18.4, 20.4, and 21.4 days of age made no attempt to fly and were captured by hand.

Both parents were observed brooding young for up to 2 days after the chicks left the nest. The adults probably brooded older young but we did not see it. During the fledging period the adults acted as sentinels, using alarm calls to warn their foraging offspring of approaching danger. In response to the alarm calls, the young usually crouched motionless and consequently were difficult to find. They evidently fed in moist, grassy areas judging from the locations where specimens were collected, and the broods usually remained within about 1.5 km of the nest site. One young from Nest 7/68, however, was found about 3 km away when it was 21 days old.

The female parent deserted the brood before the male. In 1968 a female was last seen with a brood when the chicks were about 12 days old. In contrast, a male was still with young which were 23 days old. That year the last adult female was seen on 17 August, but males were still present on 25 August when we left. Parmelee et al. (1967) found that adult males sometimes attended fully fledged juveniles on Victoria Island; but adults of both sexes abandoned the nesting grounds soon after the young fledged, before the latter departed. We left Devon Island too early to determine when adult males deserted their broods and the Truelove Lowland, or when the young left the area.

Timing and length of breeding season.—Assuming that laying, incubation, and fledging periods are 4.5, 27, and 23 days, respectively, we can estimate the dates of the main events in the breeding cycle for the majority of the Black-bellied Plover nests on Devon Island (Fig. 7). The entire cycle, from laying of the first egg to fledging of the last young occupies about 55 days

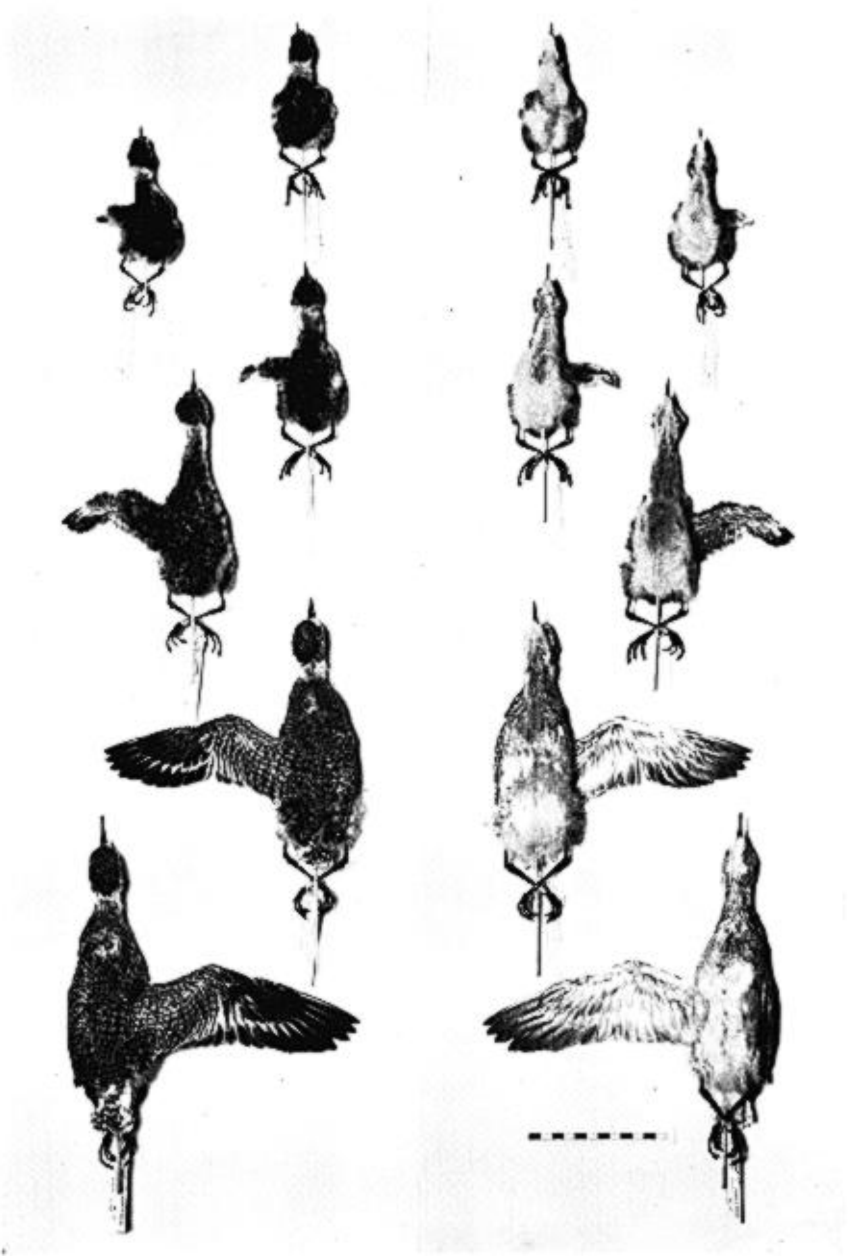


FIG. 6. Specimens of young Black-bellied Plovers collected on Devon Island. Known or estimated ages (from top to bottom) are 0.5, 3.1, 6.7, 12.5, 18.4, and 23.3 days (UMMZ Nos. 212791; 215906; 215908; 215909; 215944; and 215912). Each division on the scale at lower right is 1 cm.

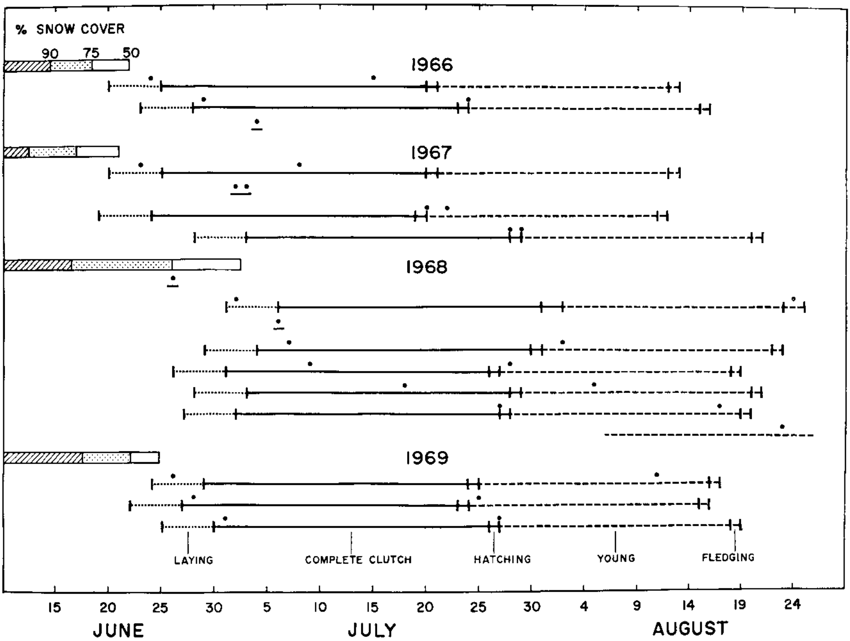


FIG. 7. Breeding phenology for 18 Black-bellied Plover nestings on Devon Island. Projected dates of laying, hatching, and fledging are shown for all nests for which sufficient information is available, including those known to have been lost to predators. See text for methods of calculation. Dates of first and last observations of a clutch or brood are indicated by a dot above the record for that nesting. Percent snow cover is based on estimates for the land surface within the "census area."

for a single nesting and about 68 days for the population as a whole. Median dates (and ranges) for starting laying, last egg hatching, and last young fledging were 25 June (19 June–1 July), 27 July (20 July–2 August), and 19 August (12–25 August), respectively. Although the sample is small, it appears that breeding was generally delayed in the cold, late season of 1968, and was more closely synchronized in any one year than indicated by the overall range of 13–14 days for all years.

At Cambridge Bay and at Jenny Lind Island, N.W.T., breeding apparently starts 7 to 10 days earlier than on Devon Island (Parmelee et al. 1967). Eggs from a "late nesting" on Jenny Lind Island hatched 26–28 July, which approximates the median date for Devon Island nests. Bylot Island hatching dates at 3 nests were 26–29 July and at another 22–24 July (Drury 1961), indicating that breeding is as late as on Devon Island. At these high arctic localities many young are not fledged until after the 3rd week of August and they may face severe problems in completing their growth and mobilizing energy for migration prior to the onset of adverse weather conditions.

DISCUSSION

Among the shorebirds, sandpipers exhibit a wide range of breeding systems (Pitelka et al. 1974) but plovers, and apparently other Charadriidae, are relatively uniform: they are usually monogamous and parental duties are shared almost equally by the sexes. This appears to be true for the Eurasian Golden Plover (*Pluvialis apricaria*) and the American Golden Plover (*P. dominica*), as well as for the Black-bellied Plover (*P. squatarola*), and perhaps for the majority of species in the genus *Charadrius* (Palmer 1967). The Dotterel (*Eudromias morinellus*) is polyandrous, however, and males take the major share of incubation and parental care (Pulliainen 1970, Nethersole-Thompson 1972); while Mountain Plovers (*Charadrius montanus*) often lay 2 clutches in quick succession, the first incubated by the male and the second by the female (Graul 1974).

Pitelka et al. (1974) have explored the ecological determinants of social systems and sexual dimorphism in sandpipers, and Norton (1972) has studied relationships between the mating system and incubation behavior, but relatively little attention has been given to the interaction between energetic factors, such as egg size and growth of the young, and the social system in birds with precocial young. Parmelee and Payne (1973) point out that laying of multiple clutches in both Temminck's Stint (*Calidris temminckii*) and Sanderling (*C. alba*) is associated with unusually small eggs relative to body size, and the same is true of the Dotterel and Mountain Plover (Graul 1974). Unfortunately growth rates of most shorebirds are so poorly known that it is difficult to assess the significance of the developmental patterns of the few species which have been studied.

The *Pluvialis* plovers have exceptionally large eggs (16–20% of body weight) for their size (Lack 1968:206, 210). Within a period of 4½ days the female Black-bellied Plover lays a clutch of eggs which weighs approximately 70% of her body weight. To produce these eggs she probably must spend a large proportion of her time feeding, so it is not surprising that only the male incubates during the egg-laying period.

Hatching is usually thought to be highly synchronous in shorebirds, but this was not true of Black-bellied Plovers; asynchrony extended to as much as 36 h in some nests. That the hatching period is not longer is no doubt due to incubation being incomplete (by the male alone) during the laying period. It is often assumed that there is strong selection for synchronous hatching in birds with precocial young, because it would tend to facilitate parental care (Lack 1968). In the Black-bellied Plover there was no evidence that late hatching eggs were abandoned, as Jehl (1973) reported for the Stilt Sandpiper (*Micropalama himantopus*). Although precise documentation is sparse, asynchrony in hatching of as much as 24 to 36 h may not be unusual in the Charadriidae, but there appears to be a greater degree of synchrony in the Scolopacidae (e.g. Davis 1943, Williamson 1948, Sutton and Parmelee 1955, Wilcox 1959, Parmelee et al. 1967, Parmelee et al. 1968, Parmelee 1970, Jehl 1973).

The hypothesis that asynchrony is a side-effect of selection to protect the egg from chilling during the egg-laying period is attractive, but is unsupported by evidence. First, minimum air temperatures during egg-laying are not extreme (Table 3). Second, other species can successfully hatch eggs which have been unattended for several days in similar high arctic conditions (Parmelee 1970). And third, there is evidence that some passerines can prevent chilling of eggs without raising the nest temperature enough for effective incubation (Haftorn 1966). Thus if there is strong selection for synchrony, there are ample reasons for supposing it could be achieved without danger to the eggs.

The incubation period of about 27 days is remarkably long for a bird breeding in the short arctic summer, but is similar to that in the Eurasian and American Golden plovers (Witherby 1940, Parmelee et al. 1967). Plovers generally have longer incubation periods than scolopacids: 23–26 days in the smaller *Charadrius* (but 27–28 days in the Piping Plover, *C. melodus*) (Palmer 1967) compared to 18–22 days for most small sandpipers (Godfrey 1966, Palmer 1967, Parmelee et al. 1967) and no more than 24 days for some of the larger species such as the Hudsonian Godwit (*Limosa haemastica*) and Whimbrel (*Numenius phaeopus*) (Jehl and Hussell 1966). The Charadriidae and Scolopacidae as a whole do not differ greatly in relative egg weight (egg weight as % of body weight), although there is much variation within each group (Lack 1968). Whether the long incubation period of plovers and the large eggs of *Pluvialis* are associated with characteristic embryonic developmental patterns remains to be determined.

Growth rates of shorebirds are poorly known and data for only 1 other plover, the Ringed Plover (*Charadrius hiaticula*), are given by Ricklefs (1973). This species has a growth rate (K) of about 0.13 (converted from Rickleff's data), slower than the 0.19 of the Black-bellied Plover. The significance of this difference is difficult to assess until information is available for more species, but it indicates that the range of variation in growth rates in the plovers may be as great as in the sandpipers. In view of the usual inverse relationship between growth rate and size it might be expected that the small plovers in the genus *Charadrius* would have a faster growth rate than *Pluvialis*, but the present evidence indicates otherwise. The few data given by Wilcox (1959) show a remarkably slow growth rate in the Piping Plover (*C. melodus*) and the feather development of a 17-day-old Semipalmated Plover (*C. semipalmatus*) photographed by Sutton and Parmelee (1955) appears little further advanced than that of a 12-day-old Black-bellied Plover specimen.

Fledging ages of shorebirds are also inadequately documented. In the sandpipers there is evidence of a fledging period of less than 14 days in the Semipalmated Sandpiper (*Calidris pusillus*) (Parmelee et al. 1967), 16–17 days in the White-rumped Sandpiper (*C. fuscicollis*) (Parmelee et al. 1968) and about 17 days in the Sanderling (*C. alba*) (Parmelee 1970). Among the plovers, fledging ages of 24 days and 21–23 days have been reported for the Ringed Plover (Palmer 1967, Ricklefs 1973), between 22 and 31 days in the Semipalmated Plover (Sutton and Parmelee 1955), 21–24 days in the Little Ringed Plover (*Charadrius dubius*) (Witherby et al. 1940), 30–35 days in the Piping Plover (Wilcox 1959), 33 days in the Eurasian Golden Plover, 33–34 days in the Mountain Plover (Graul 1975), and 39 days in the Lapwing (*Vanellus vanellus*) (Witherby et al. 1940). Thus the 23-day period for the Black-bellied Plover appears to be unusually short among the larger plovers.

SUMMARY

Black-bellied Plovers arrived on the north coast of Devon Island in the second week of June and occupied the coastal lowland at a density of 0.3–1.0 pairs per km^2. Most clutches were initiated in the last 10 days of June.

Four eggs were laid at about 36 h intervals. Fresh eggs averaged 31.0 g and lost 0.15 g per day during incubation. The incubation period is about 27 days. The interval between hatching of the first and last eggs in a clutch was sometimes as much as 36 h. Chicks remained inactive in the nest for 10–12 h after hatching. Older young foraged alone up to 40 m from the nest and brooding adult until the last-hatched young became active and the nest was deserted. The weight of newly hatched young declined for the first few hours then increased rapidly. Growth and development from hatching to fledging were described from a series of known-age specimens. The fledging period was about 23 days. Male and female adults both incubated and cared for the young, but the females deserted the broods earlier than the males, before the young had fledged.

The breeding cycle from first egg to last fledging took about 55 days for a single pair and about 68 days for the Devon Island population. Most young are fledged no sooner than the 3rd week of August.

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LONG POINT BIRD OBSERVATORY, P.O. BOX 160, PORT ROWAN, ONTARIO N0E 1M0; AND POINT REYES BIRD OBSERVATORY, BOX 321, BOLINAS, CA 94924. ACCEPTED 9 SEPT. 1975.