

THE BREEDING BIOLOGY OF SHOREBIRDS ON BYLOT ISLAND, NORTHWEST TERRITORIES, CANADA

WILLIAM H. DRURY, JR.

INTRODUCTION

THIS paper compares the interactions of two species of plovers usually placed in separate genera (A.O.U. *Check-list*, 1957) with two species of sandpipers usually put into the same genus (A.O.U. *Check-list*, 1957).

The 1954 Bylot Island Expedition spent from 12 June to 29 July at the mouth of the Aktineq River, at approximately latitude 73° N, longitude 79° W, in southern Bylot Island. Bylot is between the Low and High Arctic just north of Baffin Island and south of the eastern end of Devon Island. A short description of the expedition has been published by the Drurys (1955), and a lively, popular account is given in Scherman (1956). A map showing the study area and locality names appears in Scherman and in Miller (1955). Faunal details and description of the study area have been published in Van Tyne and Drury (1959).

Observations were made by William Drury, Mary Drury, and Benjamin Ferris, who concentrated on the breeding birds; and by Josselyn Van Tyne, who gathered information in daily collecting trips outside the study area. A field map (Figure 1) shows localities in our study area. A vegetation map (Figure 2) shows location of nests.

The expedition was supported by a private grant and by the New York Zoological Society. Arrangements were made through the Arctic Institute of North America. I prepared this report while on sabbatical half-year at Harvard University in 1955 and made extensive revisions while with the Massachusetts Audubon Society. Josselyn Van Tyne's illness and death prevented the preparation of a combined report and delayed the publication of this material, but we were able to report several of these conclusions at the American Ornithologists' Union meeting in Boston (Van Tyne and Drury, 1955).

I. ECOLOGY AND DISPLAYS

AMERICAN GOLDEN PLOVER

Pluvialis dominica (Müller)

(Eskimo: Toódleehrátsuk)

We could easily differentiate the sexes because the face and underparts of the males in our area were almost solid black, whereas in the

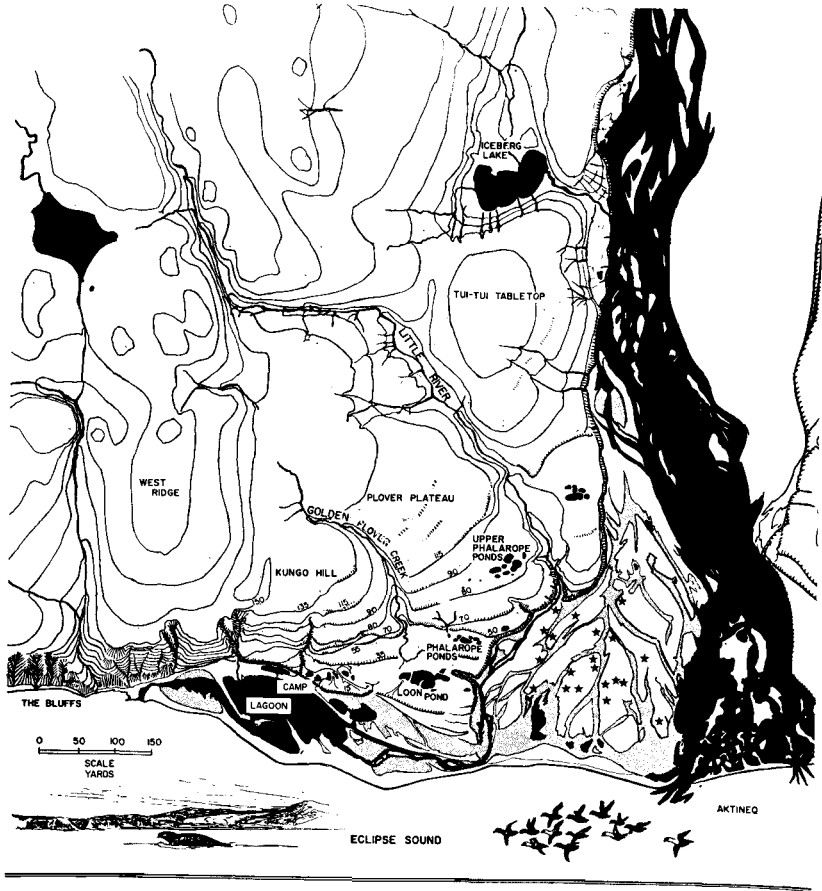


Figure 1. Field map of the study area.

female they were mottled with gray and white, and the white areas on the sides of the chest almost met. Golden Plovers were display-flying on Bylot Island when we arrived the evening of 12 June. We saw a flock of 90 to 100 flying rapidly southeast on 15 June, and 96 on 16 June flying north.

Habitat and density. The two nests of Golden Plovers in our study area (Figure 2), the 13 pairs at Ooyarashukjooeet, and the six pairs near Oonakuktooyuk were on the general tundra vegetation of mosses (Hypnaceae), sedges (Cyperaceae, Juncaceae), grasses (*Trisetum spicatum* [L.] Richt., *Poa rigens* Hartm., and *Arctagrostis latifolia* [R. Br.] Griseb.), Avens (*Dryas integrifolia* M. Vahl), and Arctic Willow (*Salix arctica* Pall.), where mat plants alternated with small

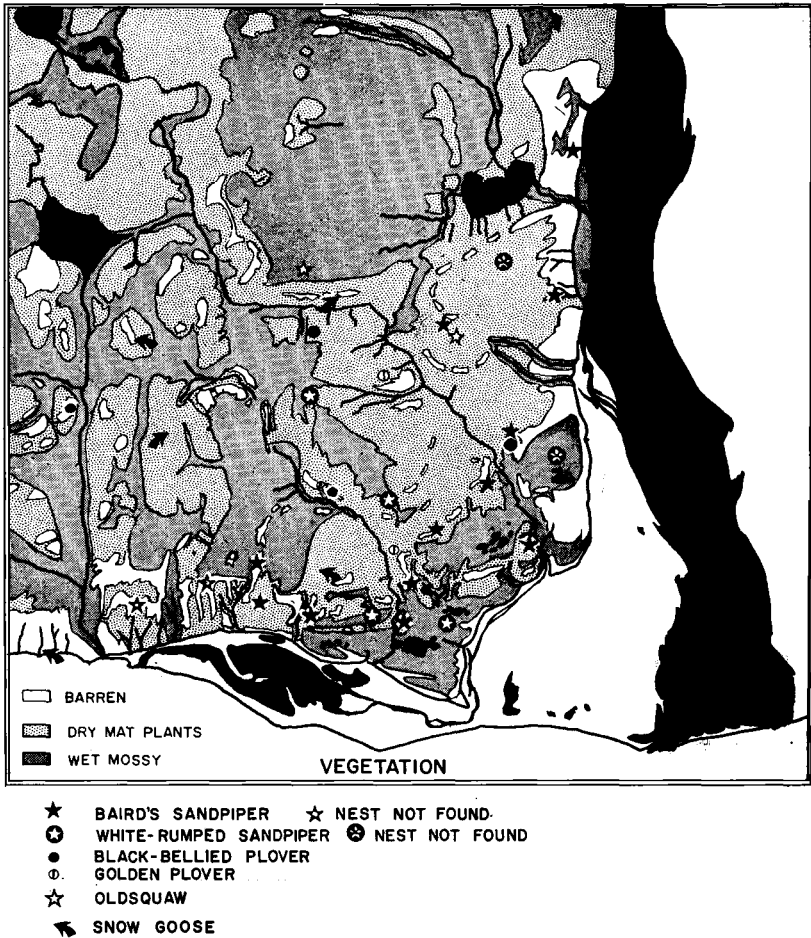


Figure 2. Vegetation and nests. The major types of vegetation in the study area are mapped. Symbols of the nest locations show the correlation of sites with vegetation.

patches of bare soil. In these places, Golden Plovers were on fine-grained soils disturbed by frost action into polygons and terracettes (Washburn, 1956). At Oonakuktooyuk, the slopes were so disturbed by slumping that the bare areas on the tops of the terracettes were larger than the mats of vegetation.

We found Golden Plovers on south-facing areas below 150 meters from which the snow disappeared early. All territories were within two miles of the coast. Seebohm and Harvie-Brown (1876) reported

this species nesting on exposed, rounded hilltops in the Petchora Valley; in western Alaska, Walkinshaw (1948) found one nest in a damp spot of tundra on a mound surrounded by sedges, another on "much higher, completely dry . . . land." Any comparison of nesting sites involving a large geographical area must allow for regional differences of vegetation. Full, accurate descriptions of vegetation are usually not available. Nearly all sites at Bylot Island were dry, in comparison with those studied by Walkinshaw in Alaska.

Territory. In display flight over Plover Plateau (Figures 1 and 3), a bird flew with hesitant flight like that of a Nighthawk (*Chordeiles minor*) or the fish flight of a Common Tern (*Sterna hirundo*), calling *ktoóólee ktoóólee*. It flew in either direction, or in "figure 8's," from Loon Pond to Iceberg Lake. A second flight pattern overlapped with this—over Tui-Tui Tabletop west to the West Ridge. We did not see two birds in the air at once, and we saw no conflicts. Walkinshaw (1948) reports a similar flight ending with a sudden drop almost to the ground, then a quick rise to pass far out over the tundra.

At times we heard only a *kleeeeee* given every 20 seconds, but when the bird came closer, we heard a fainter *tood* preceding the louder note. Displaying birds flew with their wings held largely above the horizontal. There was a slight hesitation at the highest point and a longer hesitation at the end of the downstroke (Figure 3). These flights were most frequent and longest on 12–15 June; and last recorded on 6 July. The usual times were 2100 to midnight and early in the morning.

Aggressive behavior. The parents at nest No. 2, on intrusion of a male Black-bellied Plover, took the posture described in Table 1 (Aggressive on Ground).

On 30 June at nest No. 1 the alarm cries of a pale bird brought up a dark bird, but when the dark bird (presumed male) came to within 30 meters, the "female" suddenly turned and drove him away. This may have been because he was not her mate or because she was confused and overexcited by me. As Williamson (1947) and Moynihan (1955) have suggested, the tendency to drive away the human intruder is re-directed to a substitute that will flee. When attacked, the male ran away a short distance, then both birds stopped. Again she ran at him, head down and back feathers ruffled, crying *túrdileeee* and *kleééar*; then flew at him with head stretched out in front, calling *eeeeeeooooo-eeeeeeooooo tswit-tswit*, *eeeeeeooooo-eeeeeeooooo eeeeeooooo-eeeeeeooooo*, or *kloo tswit-tswit kloo*. At each cry of *tswit-tswit*, the pursuer bobbed her head vigorously. Sometimes she pursued him in a short, rapid zigzag. He flew; she caught up and glided past while he flew on; she lit and he lit near her, and they repeated the "leap-frog" performance. When

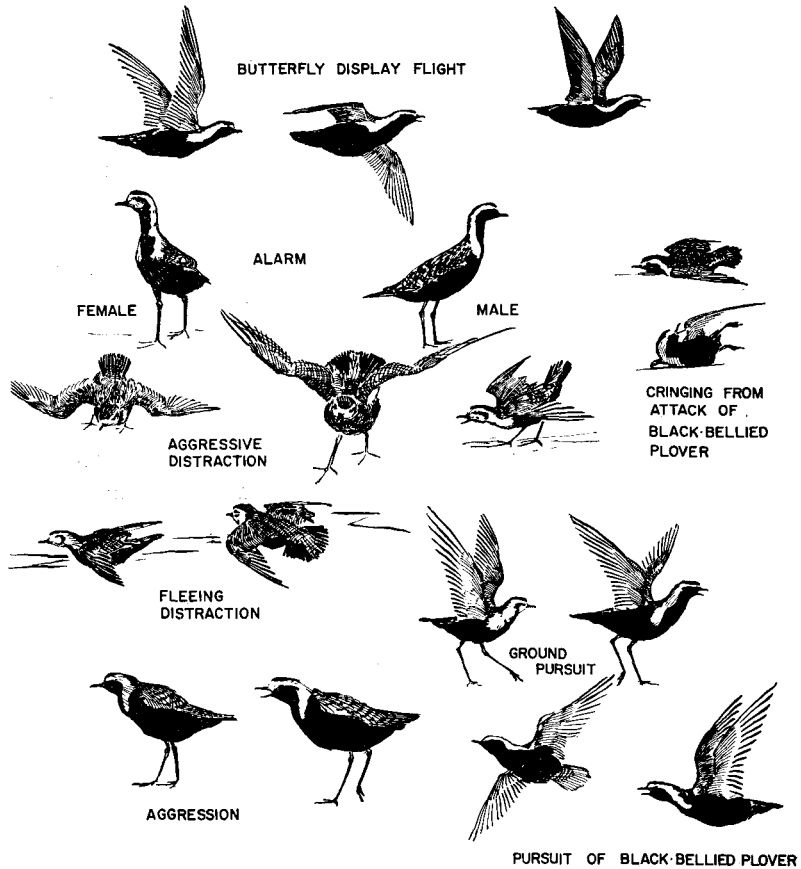


Figure 3. Golden Plover displays.

they landed, they held their wings over their backs and ran a few meters (Figure 3—ground pursuit). The colors of the axillars in the two closely related species of *Pluvialis* suggest that this posture, holding wings over the back, has "signal" function.

During a group flight over the uplands at Ooyarashukjooet on 12 July: (1) one bird flew in a meandering course over a circumscribed area, while another repeatedly flew from behind, set its wings at the limit of the upstroke, and coasted past, calling *toodleéka-toodleéka*, bobbing its head violently; (2) two birds on one occasion and three on

another, pursued each other with rapid zigzagging, hairpin turns, steep dives, and towering climbs, swerving and spreading their tails. They spread their tails simultaneously many times during the flight, even when flying straight. They called *tsee-witwit-tsee* or *tswit tswit*. We heard these calls only when a Golden Plover was driving away another Golden Plover, a Black-bellied Plover, a Parasitic Jaeger (*Stercorarius parasiticus*), or a Long-tailed Jaeger (*Stercorarius longicaudus*).

These displays resemble those described for the European Golden Plover (*P. apricaria*) by D. Nethersole-Thompson (Witherby, *et al.*, 1940).

Appeasement display. On 22 June I watched a presumed female at the mouth of Golden Plover Creek. A second bird flew down from the plateau and lit about 20 meters away, then with head lowered and shoulders hunched, ran a short way toward the female with his wings raised, folded his wings and ran forward again. When he was about one meter away he cried *witwit* very rapidly, then stood with his head and neck stretched upward (Figure 3, male). The other bird remained motionless, with head raised (Figure 3, female), then took a few slow steps and pecked the ground, and took a few more steps. The new bird followed for a few moments, then they moved apart, feeding.

*Nest and eggs.*¹ The three Golden Plover nests that we found (mapped in Figure 2—dry mat plant areas) were in slight hollows surrounded with scattered mat plants.

From date of hatching of our earliest nest, the clutch (4) was completed between 18 and 20 June. The first egg was probably laid on 13 June. In some Golden Plover eggs there is a greenish tint to the background color in contrast to the pastel gray of the Black-bellied Plover, but our examinations in the field and in egg collections showed no reliable way of distinguishing the eggs of the two species.

Activities during incubation. At nest No. 1 the female (judged by plumage) was nearly always at the nest, and we rarely saw the male during nest-checking rounds. We have moving pictures of the dark-plumaged bird performing distraction displays, however, and know that both members of the pair stay close to the nest during incubation. Allen (1934) reported that both parents incubated at Churchill, Manitoba. Walkinshaw (1948) reported that in "Pacific" Golden Plover (*Pluvialis dominica fulva*), both parents incubated. My experience

¹ Detailed descriptions of nests of the plovers and the sandpipers are available at the Hatheway School in South Lincoln, Massachusetts. These descriptions include elevation, location and description of site, details of the surrounding vegetation, and materials used in the scrape. They also include the daily observations, date of finding, and times of hatching.

TABLE 1
SUMMARY COMPARISON OF THE PLOVERS

<i>Black-bellied Plover</i>	<i>Golden Plover</i> Nesting Site	<i>Ringed Plover</i>
Wind-blown, Gray Lichen-strewn areas early free of snow, exposed; on ridge or terrace with a wide view.	More protected, moss- and mat plant-grown areas commanding good view but not exposed; on slope below ridge.	Gravel pavements nearly free of vegetation, on raised beaches, sea beaches, or abandoned river bars.
On bare soil surrounded by Gray Lichen; nearly smooth surface; coarse soil.	Scrape Surrounded by mat plants; irregular surface with terracettes, fine-grained soil.	Not seen.
Head on shoulders; back feathers ruffled; wrists not seen to be lowered. (Wrists are lowered in aggressive display on migration.)	Displays <i>Aggressive on ground</i>	Horizontal stand, head down and forward, back feathers ruffled, tail raised and barely fanned; <i>tché-rick</i> crescendo call becoming a rattle; fast runs (glides) at opponent.
Sleeking of feathers inconspicuous; head held up without raising breast.	<i>Flee-appeasement</i>	Breast and head high; body feathers sleeked.
Pursuit and running parallel in aggressive posture. <i>Kléécar</i> . No head bobbing seen.	<i>Ground display</i>	Not seen.

TABLE 1
(Continued)

Flight display

Single male butterfly flight at 30 meters over territory. *Koótiloo*, followed by swerving zigzag, alone or as pursuit.

Not seen.

Single male butterfly flight at 75 meters over territory, calling *koódléc*.

Butterfly flight at 3-10 meters, calling *tché-rick* crescendo.

Paired flight display

a) A rapid flight with towering and swerving.

Not seen.

b) One sets wings as a pigeon does and glides past companion, crying *toodléeka* with head-bobbing.

Alarm call

a) *Kleeec, koódléc*.
b) *Kécku-kudlécah*.

a) *Kléécar, túrdeléc, killik-killik*.
b) *Túdleca-túdleca*.

Churi (short and rich), or *kléécur*.

Distraction display

Low intensity

1. At first, head-up alarm; displacement feeding.
2. Runs 10-25 meters with head lowered, stretched far forward; wings drooped; tail barely fanned and tilted to intruder; back feathers much ruffled—cries *léec*; frequently settles with fast squirming, as if on eggs, but head along ground as if to hide; occasionally rushes in with feathers ruffled, looking white all over; displacement feeding.

1. At first (about 75-50 meters) head-up alarm; displacement feeding.
2. Runs with head up, back ruffled, tail barely fanned and tilted—cries *kléécar eec, túrdéec, túdle-túdleca, kicéit* or *killik-killik*; when stops, stands up, may crouch, though seldom; displacement feeding.
3. Runs diagonally to the side, crouched, both wings and tail partly spread, near wing more so; when beside intruder, stops, stands, calls; displacement feeding.

1. Flies to intruder and stands very tall at about 50 meters with breast fluffed out; displacement feeding; occasionally flies at intruder (20 meters), then stands sleeked.
2. Lowers head and spreads and tilts tail to intruder; slightly spreads near wing, drags or beats it, facing away from intruder.

TABLE 1 (Continued)

<i>Black-bellied Plover</i>	<i>Golden Plover</i>	<i>Ringed Plover</i>
<i>High intensity</i>		
3. Prostrate, breast on ground in a hollow; bill thrust forward, chin along ground; tail cocked and fanned; wings almost fully spread, beating spasmodically (a second between beats), primaries brushing ground noisily; feet stamping though obscured; usually faces to one side of intruder, head turned to one side; occasional hoarse <i>klee</i> .	4. Deep bow or breast on ground, hunched, feet stamping but legs not in crouch; tail often fanned and usually barely cocked up; head pulled in; wings partly opened and spread (resembles a threatening owl), slowly beating noisily on the ground; occasionally crouching; usually faces intruder. Stands or crouches, but not seen prostrate.	3. Wiggles away over the ground, tilted on one side, beating one wing up in the air. 4. Freezes crouched, back to, in a hollow; head down, tail partly fanned and lowered, back feathers ruffled; held until 10 meters. When ignored, scolds, displacement feeds, runs closer—to start again.
4. Runs off, low rolling from side to side, with wings folded and slightly lowered, tail spread; head down, thrust forward, but watching intruder; back ruffled; stops in hollow and beats wings slowly; prostrate again with wings widespread. No use of wings as runs.	5. (a) Runs off crouching, with wings open and down at sides, beating and shuffling as if forelegs; looks over shoulder; breast along ground; tail canted down and partly fanned (rarely furled and cocked up); watches intruder. (b) Runs rapidly, fluttering.	5. Runs crouching, tail slightly raised and furled; wings folded, gliding over ground; then crouches again.
Male has more complete spring plumage than the female.	Male has more complete spring plumage than the female.	Male has more contrasting colors in black vs. brown plumage than the female.
Male incubates most of the time. Female rarely seen to incubate. Started at earliest nest 26 June. Incubation period at two nests 27 days.	Female incubates most of the time. Male rarely seen to incubate. Started at earliest nest 17–20 June.	Both sexes.
22–29 July. Young brooded in scrape two nights.	15–23 July. Young brooded in scrape one night.	Fast-running, downy young—20 July.
	Hatching	

with the European Golden Plover in Finland indicates that both sexes incubate.

Hatching and care of the young. The eggs in nest No. 1 hatched 15 and 16 July. One egg in nest No. 2 pipped 20 July, three hatched 22 July; all by 24 July. We found two young and their parents on 17 July in the marsh at the northwest corner of Plover Plateau when the young of nest No. 1 were at Loon Pond. The young stayed in the nest until all eggs hatched; then all four left, but returned to the scrape the first night, presumably to be brooded. On the following day they moved to marshy places. Both parents accompanied the young for at least two weeks. For a discussion of the plumage of juvenals, see Van Tyne and Drury (1959).

Reactions to predators. D. Nethersole-Thompson (Witherby, 1940) said that injury feigning is not common in the European Golden Plover, but we found it commonplace and conspicuous at Bylot Island as soon as clutches were complete, as did Williamson (1948). My experience with European Golden Plover in Finnish Lapland in 1958 was that they cried noisily, but did little distraction display.

For distraction display at various levels of concern see Table 1. Between distraction displays the bird ran, pecked stiffly and called *khllleeeeeooo* in alarm. As it circled it often ran in closer, when it was behind us with the sun behind it. There was a complete gradation of intensity from the early alarm call at leaving the nest to the violent wing flopping.

At both nests the dark-plumaged birds (presumably males) consistently were more shy, performed less-intense distraction displays, and remained at a greater distance. After watching a pair near Oonakuk-tooyuk for 10 to 15 minutes on 20 July, I shot the dark-plumaged bird, and it was a male. When the bird rushed at us and threw its breast into a hollow with wings spread, it closely resembled postures illustrated by Hosking for Avocet (*Recurvirostra avosetta*) in Simmons (1955) and for Killdeer (*Charadrius vociferus*) by Deane (1944).

BLACK-BELLIED PLOVER

Pluvialis squatarola (Linnaeus). (Eskimo: Toódlée-hrátsuk)

The Eskimos called this species by the same name as the Golden Plover, although they recognized two different species. Reasons for including *squatarola* in *Pluvialis* are given below (Behavior and Systematics), and in Van Tyne and Drury (1959).

Males were in full, dark-breasted plumages; females were much less fully spring plumaged and varied in the amount and position of black

patches and speckling. The female at nest No. 3 showed no black below. We first saw this species on 17 June at camp, and never saw flocks. We heard the typical fall cry, *keéleeeóó*, first on 22 July from a bird flying south over the Aktineq.

Habitat and density. Sutton (1932) and Brandt (1943) speak of the exposed nature of the Black-bellied Plover's habitat, remarking that they nested on high, exposed ridges. Four nests and two territories near camp (Figure 2), two pairs east of the Aktineq, 10 July, three pairs at Ooyarashukjooeet, 14 July, and two territories near Oonakuk-tooyuk, 20 July, were all associated with the driest, most exposed ridges, river banks, or raised beaches, within a mile of the sea.

These areas were among the first to be free of snow, and were characteristically on sand or gravel scattered with cobbles and black lichens, clumps of Grass Rush (*Luzula confusa* Lindeb.) and Gray Lichen (*Stereocaulon paschale* [L.] Ach.). There was a sparse growth of mat plants (Arctic Willow, and Bell Heather, *Cassiope tetragona* [L.] D. Don), and clumps of Alpine Sweetgrass (*Hierochloe alpina* [Sw.] R. & S.), Poppy (*Papaver radicum* Rottb.), and Purple Saxifrage (*Saxifraga oppositifolia* L.). Seebohm and Harvie-Brown (1876) report the nesting of Black-bellied Plover on peat ridges in wet marshes, and Walkinshaw (1948) reports a nest on a mound on a flat above a lake. (In western Alaska the term "flat" usually refers to a compound peat bog of great extent.)

Territory. We saw display flight and ground displays 19 and 20 June near Loon Pond. The flying bird stayed at about 30 meters above the ground, flapping slowly and hesitantly as does a butterfly (Simmons, 1953), or a Short-eared Owl (*Asio flammeus*)—(Figure 4). The displaying bird flapped more slowly and had a shorter hesitation at the top of the upstroke than a Golden Plover. It called *kehweh*, or *kúdíloó*, like its own fall cry, but with the quality of the call of a European Curlew (*Numenius arquata*). The first and last syllables were accented, and were longer and lower than the middle syllable. At the end of the slow flight, the bird suddenly flew very fast, swerving and towering, and occasionally dashing at the ground. We have often seen diving flight, on spring migration, and it has been reported by Seebohm and Harvie-Brown (1876), Haviland (1915), and Sutton (1932). At 2330 on 3 July a Black-bellied Plover was still slowly display flying over Tui-Tui Tabletop and the Little River, calling *koódleeeóó* about once a minute.

Aggressive behavior. The Rosins (Drury and Drury, 1955) described Black-bellied Plovers on 19 June endlessly running past each other—one with head lowered, the other with head raised. This may

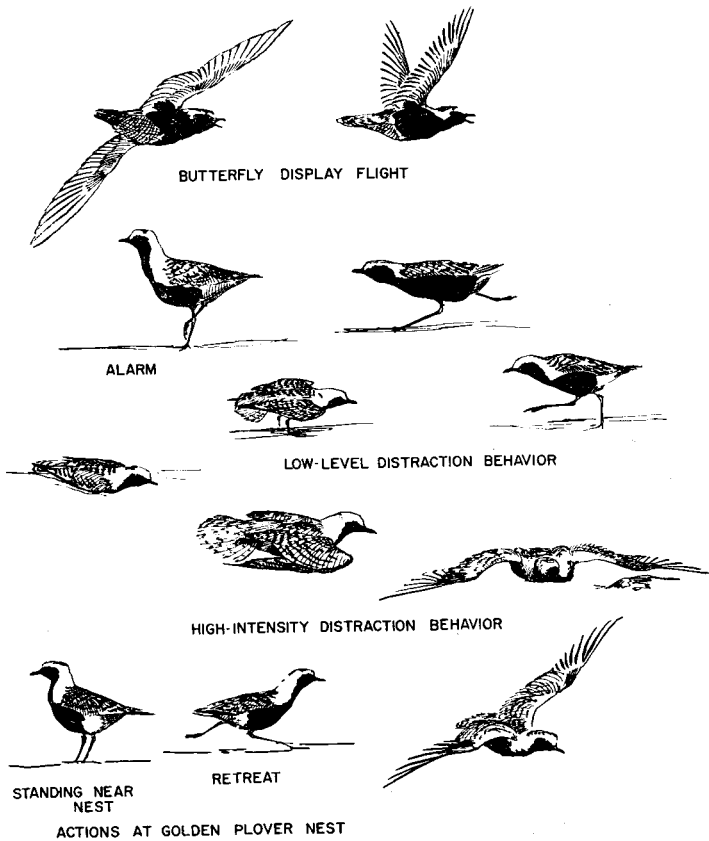


Figure 4. Black-bellied Plover displays.

be similar to behavior of Golden Plovers described by Williamson (1948). Birds at the nest "directed" similar running at an intruder, which suggests aggression (Simmons, 1955). The male at nest No. 4 briefly redirected hostility toward his mate. He ran at her with head down, calling *kleéear*. She ran to one side with head held very high (see Competition between Black-bellied Plover and Golden Plover under Ecological Interactions).

I have seen aggressive postures among birds in breeding plumage on fall migration in August in Massachusetts. At its most intense expression, when "standing off" an opponent, one bird bows deeply with head stiffly held down in line with the body, back ruffled, tail fanned and raised, breast feathers fluffed. The birds may crouch in this posi-

tion and then, standing stiffly, peck at the ground and flick pebbles or bits of weed over the shoulder. They may edge around each other, crouching and bowing, wrists partly lowered and tail canted and mostly spread; then they stop and flick pebbles again. When aggressive, migrant birds move toward an opponent, they stalk stiffly, suggesting differences from the actions the Rosins described. Much more detail is needed.

Nest and eggs. The four nests that we found (Figure 2) were all in bare areas among widely scattered patches and clumps of plants. We found a nest with three eggs on 30 June. In this and two other nests, eggs hatched 26–29 July. In another nest, eggs hatched 22–24 July, which suggests that the first egg was laid about 20 June. Clutch size was four in all nests.

Activities during incubation. At the nests studied, the male did almost all the incubating, but we saw the female near nests Nos. 1, 3, and 4 repeatedly. At nest No. 3 the female stayed in a sedgy marsh about 100 yards away and occasionally approached the nest when intruders came. On one visit after a long disturbance the male returned to incubate, but an hour later the female was on the nest. The female as well as the male incubated at nest No. 1. In 15 visits to each nest we found both birds absent two or three times for each. Shyness may have made the parent (female?) leave so early that the nest checker missed it. Pickwell (1942) called such action "casual abandonment" and suggested that it is of survival value in concealing the nest of Prairie Horned Larks (*Otocoris alpestris praticola*).

Hatching and care of young. The last egg in nest No. 1 was laid on 1 July or early in the morning on 2 July; it hatched the night of 27 July or early on 28 July—one day after two others, and two days after the first to hatch, 26 July. Incubation period was 26 days (or almost 27 days). One egg in nest No. 2 hatched 27 days after the nest was found. Several eggs pipped two days before hatching. The eggs hatched over a two-day period, 23–24 July in nest No. 3 and 28–29 July in nest No. 2. Nest No. 4 had not hatched, but two eggs had cracked when we left on 29 July. Brandt (1943) reports an incubation period of 23 days in one instance in Alaska, but without details. Dementiev *et al.* (1951) report that the incubation period is unknown. Höhn (1957) reports the hatching of one egg 24 days after completion of the clutch on Banks Island. My experience with Killdeer suggests that the incubation period can be lengthened two days if the nest is regularly visited. The young spent one night in the scrape after all had hatched. We have no observations of parents with young away from the nest.

Reactions to humans. Black-bellied Plovers were extremely shy at

the beginning of the incubation period. I found the first nest on 30 June accidentally while studying frost features through binoculars. The male, sitting on this nest, left it as soon as we appeared, over 200 meters away, and ran very fast with head down, for 75 meters, along a frost crack. At that distance he stopped, looked up, called, and flew away. On 2 July the clutch was completed, and we saw the first distraction display—running in a crouch with the near wing lowered. The birds at nests Nos. 1, 2, and 4 would not come within 100 meters until the last week of incubation, while the male at nest No. 3 showed marked concern more than two weeks before hatching. Toward the end of the incubation period, the male left the nest when we were about 100 meters away. When the eggs pipped and cracked in nest No. 1, the parents came within two meters to display. The less-aggressive bird at all nests was markedly less full plumaged. On leaving the nest, the male usually flew to a high ridge and watched us, occasionally calling *gleee* or *keéeku-kudléah*. The usual cry from the nest was *koodléé*. If the intruder withdrew, often he returned to the vicinity of the nest and seemed to settle on eggs. The male at nest No. 3 did this three times within 30 meters of the nest while we were waiting for him to return, and at one place spent 27 minutes in rather “disinterested” preening after seeming to have settled on a nest.

For details of the several levels of intensity of distraction behavior see Table 1. The circling bird regularly came closer when behind and against the light. Occasionally he rushed in (presumably aggressively), showing a maximum of white, holding his head down, back feathers ruffled, and tail cocked and partly spread; occasionally he spread his wings wide on this run. At nest No. 3 the female stood and flapped her wings slowly (very much like the distraction display of a Golden Plover) while the male was running in close with wings spread and head thrust forward. The pair ran together in an arc, he with head lowered, she with head raised.

Reaction to jaegers. A Black-bellied Plover dashed at a Parasitic Jaeger hovering over a loon (*Gavia stellata*) nest 30 June, flying very fast, calling *kidloóeeeoó*, and chased the jaeger up the Aktineq River. In July Black-bellied Plover males Nos. 1 and 2 drove Long-tailed Jaegers away from their nests, as Brandt (1943) has described.

RINGED PLOVER

Charadrius h. hiaticula Linnaeus (Eskimo: Koódee-koodléah)

The population that we studied was part of the Old World *C. h. hiaticula*. We have indicated (Van Tyne and Drury, 1959) that we

agree with Bock (1958, 1959) that the New World population is the same species as the Old World Ringed Plover. The former, however, raises the white feathers of its throat conspicuously in threat behavior on migration, while the broad breast band of the European race seems to be emphasized by that population. This needs further study.

We found this species on gravel pavements, which the prevailing east wind kept nearly free of vegetation, on a hilltop east of the Aktineq, on gravel bars at the Aktineq and at Ooyarashukjooet, and on thinly vegetated cobbles of an old beach deeply scarred with frost cracks, 50 meters above sea level at Oonakuktooyuk. The sites agree with those reported from central Baffin Island (Wynne-Edwards, 1952), and from southern Baffin Island (Sutton and Parmelee, 1956) for *C. h. semipalmatus*.

Display flight. We saw Short-eared Owl-like flight at Ooyarashukjooet on 14 July and at Oonakuktooyuk on 20 July when we entered a territory. Many times we heard birds in the air and on the ground calling *tché-rick tché-rick* more and more rapidly until the call became a steady rattling that ended suddenly on a descending slur. Soper (1928) and Sutton and Parmelee (1956) described this as the flight song of *C. h. semipalmatus*. Simmons (1953, 1955) pointed out that flight song may be found as low-intensity distraction or hostility displays. The call is common on fall migration when birds are threatening.

Aggressive postures. The female collected 14 July showed moderate concern and was not the bird that performed the owl-like flight or that suddenly flew in close and stood with head held high, breast fluffed out (described by Edwards *et al.*, 1947, as an aggressive display). Usually the cries of birds disturbed on their territories attracted one or two neighbors that stood and called nearby, as Mason (1947), and Sutton and Parmelee (1956) reported.

Distraction display. When running, the birds seemed to try to put themselves on the side of the intruder away from the chicks, as Ledlie and Pedler (1938) suggested for the Little Ringed Plover (*Charadrius dubius*). Simmons (1952) wrote that *semipalmatus*, in areas where there is less fear of humans, direct the distraction display to, or at right angles to, the intruder; while *hiaticula* direct it away.

WHITE-RUMPED SANDPIPER

Heteropygia fuscicollis (Vieillot)

(Eskimo: *Livilivilak*)

Reasons for reinstating *Heteropygia* are given below (Behavior and Systematics).

We heard no calls that resembled *livilivilak*. Thus, the Eskimos'

name seems to be name transfer from Semipalmated (*Calidris pusillus*) and Least Sandpipers (*Calidris minutilla*), which have such a call, and are named "livilivilak" by the Eskimos of Baffin Island, Southampton Island, and Melville Peninsula. Bylot Island, together with Arctic Bay, where Shortt and Peters (1942) collected juveniles, seems to be the northeasternmost recorded breeding of White-rumped Sandpipers.

We saw no bird of this species, until the general arrival on the afternoon of 19 June.

Habitat and density. White-rumped Sandpipers nested in the mossy hummocks in marshes, or in the mossy depressions in clumps of grass and sedge in the uplands (Figure 2—wet mossy). This habitat was under snow until about 15 June and, being protected by a snow blanket, had a uniform environment where mosses survive. At least six pairs nested in our study area (mapped on Figure 2). We saw none elsewhere except at a large creek three miles north of camp on 26 June.

Territory. Sutton (1932) described most of the actions except ground display. Displays were conspicuous on the afternoon that the species arrived. In display flight the bird flew with ordinary wingbeat to a height of 15 to 25 meters, and there changed to a shallow wingbeat like that of a Spotted Sandpiper (*Actitis macularia*). The bird held its head up and neck stretched out, giving a song sounding like a fish reel running, or, as Sutton puts it, a typewriter carriage. Inserted into this song were two or three sequences, during which the bird violently extended and drew back its head. It called *ng-oik* six to 10 times in succession, sounding like a small pig; *ng* with head hunched in, and *oik* with head up and neck stretched (Figure 5). At the end of the display the bird set its wings above the horizontal and glided to the ground—silently, calling *zip-zip*, or giving the fish-reel song. As it landed, usually near another bird, it folded its wings, then slowly stretched the wing nearest the other bird straight over its head. The single-wing display was much less well developed than in Baird's Sandpiper and in the Purple Sandpiper (*Calidris maritima*) described by Keith (1938). On the other hand, flight displays strongly resemble that of Pectoral Sandpipers (*Heteropygia melanotos*), as described by Witherby *et al.* (1940) and Pitelka (1959).

On 20 June we watched for about 12 minutes two birds (presumed to be males) fight in the presence of a third (presumed female). The males rushed at each other with head lowered, back feathers ruffled, but wings not spread. They flew up 15–25 cm. (6 to 10 inches) to peck and beat each other with their wings, land, and chase, sometimes chasing each other with wings spread and tail partly cocked. Finally one flew away toward camp; the other followed to the edge of Golden Plover

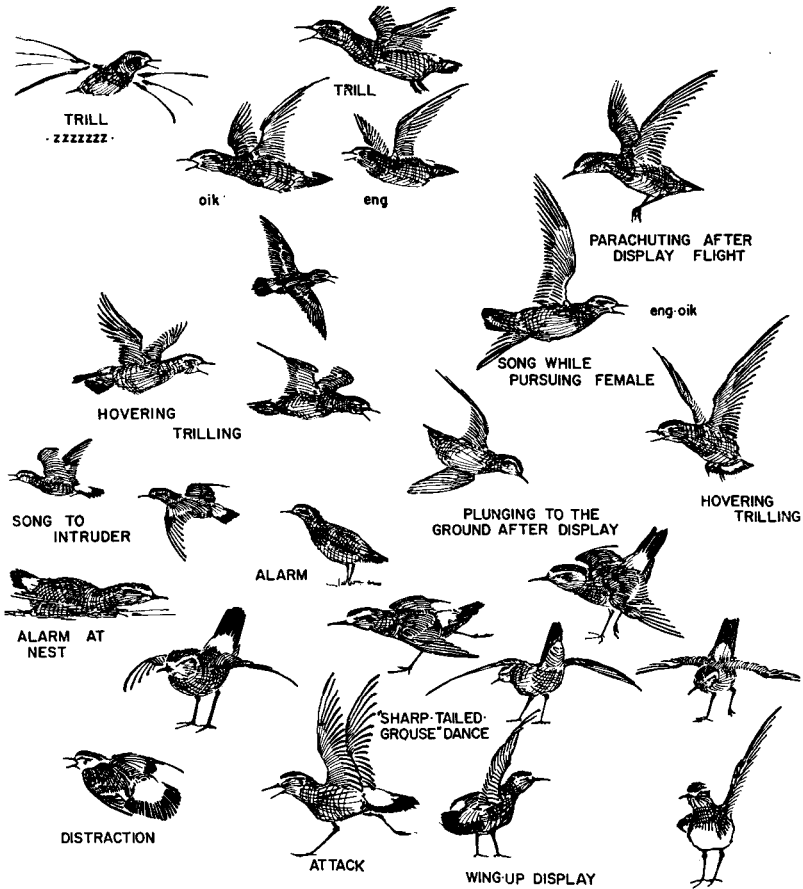


Figure 5. White-rumped Sandpiper displays.

Creek where it trilled, returned, and landed abruptly near the third. We saw and heard no song displays or territorial disputes after 30 June. We saw conflicts at two territorial borders: the marsh on the upper edge of Plover Plateau; and the flat east of the mouth of Golden Plover Creek near Loon Pond on 20 June. However, by the time the young of nest No. 4 had hatched (north of Loon Pond), territories as such had been abandoned and both young and parents trespassed unmolested.

Courtship. 1. Flight. On 21 June one bird chased another, set wings like a pigeon, and glided past, calling *ng-oik*, then banked and turned sharply on set wings (Figure 5). The pursued flew on in a semicircle

from near Loon Pond up over Kungo Hill, and the pursuer repeated the action several times. Over Kungo Hill, a bird from the West Ridge joined, and the three flew together for about 15 seconds with no conflict. Then the pursuer from Loon Pond returned, and the newcomer (a second territory) displayed on canted wings, calling like a pig, and the chase went on over Plover Plateau. A third territory and route was from the Upper Phalarope Ponds, up Golden Plover Creek to the marsh at the head of Plover Plateau. The behavior of these males, when females passed through their territories, suggests modification of courtship similar to that described by Pitelka (1959) in Pectoral Sandpipers: *i.e.*, that there is no persisting pair bond and females may nest without regard for any male's territory. We found two nests where there was one male—on the two sides of the mouth of Golden Plover Creek.

2. Ground. Ground displays resemble those of the Sharp-tailed Grouse (*Pedioecetes*). The displaying bird gave a constant twitter—*bsssssssssssss*; lowered his head, cocked his furred tail straight up (making the white rump conspicuous), spread his stiffly held wings to the side, dragging their tips on the ground, and rapidly stamped his feet. (We have no proof of the sex, and possibly the role of the sexes might be reversed.) In this position the displaying bird glided around after the (presumed) female, facing her (or side to her), sidling around her in a semicircle. Every now and then he raised the wing that was toward her when he was running along beside her. Several times he raised both wings (without stretching them), and tilted and spread his tail toward her. She stood with her head up and occasionally briefly raised the wing on the side toward him. She walked nervously, but stopped if she got more than two meters away. When she moved, he stopped displaying, ran up to her side, and started to sidle around her again. The action stopped suddenly, and the two birds stood idly, or the female suddenly flew off. When she flew, he pursued her in a mad dash over the marsh and hillsides, chiefly in long, straight flights, but occasionally with sharp zigzags. Displaying was interrupted repeatedly for periods of 15 minutes to an hour, during which time the birds appeared to feed.

Nest and eggs. The nests were in a mossy clump in grasslike growth. The grasslike plants growing near the nests we found included Narrow-leaved Cotton Grass (*Eriophorum angustifolium* Roth), Grass Rush, Water Sedge (*Carex aquatilis* Wahlenb., var. *stans* [Drej] Boott), or Arctic Redtop (*Arctagrostis latifolia* [R. Br.] Griseb.). The moss was usually Bog Moss (*Aulacomnium* ? *palustre* [Hedw.] Schwaegr.), but also other Hypnaceae such as Broom Moss (*Dicranum* sp.), Twisted Moss (*Tortella* sp.), Shining Moss (*Tomenthypnum nitens* [Schreb.]

Loeske), and Gray Moss (*Rhacomitrium ? langinosum* [Hedw.] Brid.) —(Figures 2, 5). The clutch in our earliest nest must have been completed by 25 or 26 June (Table 2); so that if eggs are laid every other day, egg laying must have started two days after the species arrived. This remarkable adaptation to arrival under rapidly changing conditions, yet exactly timed for proper breeding, should be further documented. Hinde (1951) and Nisbet (1957) have commented on the accuracy of timing of shorebird migration with the breeding cycle. Clutch size was four in all nests.

TABLE 2¹
NEST DATA—WHITE-RUMPED SANDPIPER

<i>Nest No.</i>	<i>Date found and contents on that date</i>	<i>Location</i>	<i>First egg hatched</i>	<i>No. of young produced</i>
1	28 June (4 eggs)	Loon Pond	15 July	4
2	3 July (4 eggs)	Lower Plover Plateau	22 July	(1 collected) 4
3	7 July (4 eggs)	Upper Plover Plateau	20 July	4
4	12 July (4 eggs)	Phalarope Ponds	15 July	4
<i>Brood</i> 5	20 July	Northwest Tui-Tui Tabletop		4
6	25 July	Upper Phalarope Ponds	May have been Nest No. 2	2+
7	25 July	Southeast Tui-Tui Tabletop		4

¹This form of table was used by DuBois (1936, 1937); and by Sutton and Parmelee (1954, 1956, etc.) in their Baffin Island studies.

Activities during incubation. During the last two weeks of incubation, we found only one bird near the nest, and that bird reacted uniformly to intruders. Earlier, a bird loafing on the edge of the territory sang and took part in flight song on several occasions. In our nest-checking rounds we found no birds on the nest in 3 of 16 visits to nest No. 1; in 3 of 12 visits to nest No. 2; in 3 of 9 visits to nest No. 3. These suggest that birds spent 20 to 30 per cent of the time away from the eggs during the day when we made our rounds. When we waited for the parent to return, it came back fast and directly, not as if it had been frightened from the nest by our approach. Alternatively, the bird of one sex may have been frightened by us at a great distance and the other sex was returning hurriedly, having responded at meeting that

bird. Sutton's (1932) evidence from collected birds indicates that only the female incubates. We presumed that the "loafing" individual was the male. Pitelka (1959) found that male Pectoral Sandpipers take no part in incubation, and Portenko (1959) reported the same in the male Curlew Sandpiper (*Calidris ferruginea*). When the bird returned, it entered the scrape with head down and, often, back feathers slightly ruffled. Then, with exaggerated fluffing of belly feathers, and sidewise movements that became faster and faster, then a wriggle, it pressed itself onto the eggs. In doing so it thrust its head far forward so that it rested along the ground.

Hatching and care of nestlings. One egg pipped four days before it hatched (Table 2), but usually the first egg pipped 24–18 hours before the nest was empty. The young spent the first night in the nest if they hatched in the afternoon, but did not return once they left. Two birds (equally solicitous) accompanied the young from nest No. 4 into the marshes around Loon Pond on 17 July. But in four other cases we saw only one parent with a brood of four, as did Sutton (1932). When alarmed, the young ran very fast and even swam well, but they returned to shore at the first opportunity. At nest No. 3 two birds fluttered to within three feet of our faces in "frantic" distraction, 11 days before the eggs hatched.

Reactions to intruders. The incubating bird was very tame; she sat until the intruder was within two or three meters. Once she had been put off the nest, she ran around nervously and occasionally stopped and pecked at the ground in a stiff, mechanical way unlike her deep probing when feeding. When with young, White-rumps, like Baird's, began to display when the intruder was as much as 75 meters away, but their concern did not reach the maximum shown at the nest until the intruder was at a similar distance (5 meters) from the young. The distraction display involved no fluttering unless a young one was captured and held. We saw no wing-up displays in distraction behavior.

Feeding behavior. Unlike the Baird's Sandpiper, which fed by picking from the surface in dry places, White-rumped Sandpipers fed by probing deeply in moss and wet vegetation. They usually made two or three quick probes (from half to the full bill length), then ran several inches and repeated. The young fed in thick, soft, wet mosses, probing deeply like their parents.

Dr. George W. Byers identified the stomach contents of two adults:

1. Three larvae of cranefly (Fam. Tipulidae, Gen. *Tipula*); 19 larvae of cranefly (Fam. Tipulidae, Subfam. Limoniinae); 3 spiders; 1 adult cranefly (Fam. Tipulidae, Gen. *Tipula*)—wing only.

disputes. As the displaying bird landed, it held one wing fully stretched straight over its head, and ran along the ground for about one meter (Figure 6). Occasionally it opened the other wing partly, but did not spread it, or spread both wings fully over its back. Sometimes it ran with one wing spread high over its back, then folded the wing, ran on, and spread and stretched the wing again. The raised and stretched wing was almost always the one toward the other bird. Sometimes the bird sang the trill on the ground, running or standing up very straight.

The female at nest No. 3 crouched, stretched her head forward, and called *coi-it* (Figure 6) when the male lighted from a song flight and ran with wings stretched above his calling *drrrrrr*.

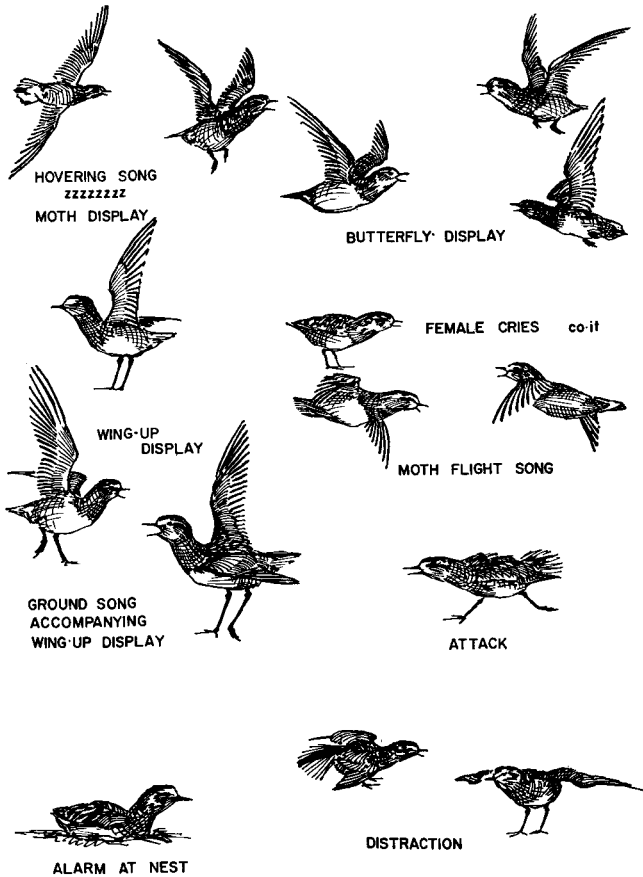


Figure 6. Baird's Sandpiper displays.

An aggressive bird rushed at another with head down, bill thrust forward, and back feathers conspicuously ruffled. Most action on the ground consisted of running along with head lowered, wings barely spread, tail spread and cocked up a little (Figure 6). When two displaying birds came together, they used the wing or wings-up display (Figure 6) and kept up a continual whining cry, *dree-dree* or *túi-túí* or rarely *drree-dree-dree*.

From 15–20 June, during the time of the most vigorous and continual displaying, eight to 10 Baird's Sandpipers fed together on the wet, sedgy, recently exposed crowns of the Bluffs west of camp. As the snow left, these groups dissipated. Occasionally they showed hostility, and sang, but we saw no prolonged disputes. These birds were presumably new arrivals that were not yet territorial. We found neither nests nor parents in that area later. Keith reported (1938) that Purple Sandpipers had common feeding grounds. Other than this suggestion of one, which soon dissipated, we found none.

Baird's Sandpipers were singing in the evening of 12 June and continued to sing, especially in the evenings and mornings through egg laying; then singing decreased sharply as incubation started 23 June. We heard songs sporadically until 29 June and again for several days after 5 July, when the first young had hatched, both as part of display to an intruder and in the morning and evening, when we were not intruding. The actions at that time were the same as those during early territorial activities.

Courtship. On 17 June, on a wet, bare, stony area on the edge of the snow, we watched a pair of Baird's Sandpipers in vigorous display for about 20 minutes. At first the male made several twittering and trilling song flights along the edge and out over the snow, singing both while he flew and while he glided. He spread one wing high over his head, underside toward the female, immediately after he landed and repeatedly afterward. Most of the time one bird crouched with head stretched toward the other, which stood erect and still. He ruffled his back feathers and flew at the other, and the two fluttered up like game cocks, equally aggressively. After a flurry of fighting, both crouched, facing each other, with heads down and forward. Next the male flew at the female and pounced on her back while she stood still. He stood on her back about 15 to 20 seconds, pulling out of her crown some feathers that we could see float away in the wind. She stretched her head forward and spread her tail while they copulated; occasionally she stretched one wing as if to keep balance. He got off, and stood stiffly with breast and head raised while she stayed crouched. She lowered her head and started to run, at which he pounced, pecked at

her head, and they copulated again. This happened three times; then she flew about 40 meters down the edge of the snow bank and he did not follow. Without 8X binoculars at 20 meters we would have thought this was a fight.

Nest and eggs. Nearly all the nests were associated with a low hummock. The typical area consisted of coarse pebbles and black, dead mosses, over which were scattered clumps of Gray Lichen, foliose and fruticose lichens (*Cetrarias*, especially *cucullata* [Bell.] Ach. and *Parmelias*, *Thamnolia vermicularis* [Sw.] Ach., *Alectoria nigricans* [Ach.] Nyl., and *A. ochroleuca* [Ehrh.] Nyl.), tufts of Grass Rush, Arctic Bluegrass (*Poa rigens* Hartm.), Poppies, Purple Saxifrage, Bell Heather, and Arctic Willow. Sites were often marked with frost cracks, where mosses, sedges, and mat plants (Avens, Bell Heather, and Arctic Willow) were more conspicuous in the low places. The earliest nests—Nos. 1, 5, 6, and 11—were placed on especially wind-blown and south-facing areas. We concluded that nests Nos. 2 and 6 were displaced by our making camp on the beaches where the Baird's Sandpipers were trilling on 13 June; but incubation must have started in nest No. 6 the day after we arrived (hatched 3 July). On 19 June, the first day of incubation, we watched the bird on nest No. 2 (Table 3) while it sat and added to the nest. It reached out to the front and sides, picked up sprigs of moss, Grass Rush, or Bell Heather and, sweeping its head down and backward as if brushing its breast feathers, carried the sprig back to the fold of the wing or all the way back to the base of the tail and beyond to drop it. Birds at nests No. 2 and 3 (before the clutch was complete) spent as much as half an hour on the nest—"building," frequently leaving and returning. The bird at nest No. 3 used Arctic Willow leaves. At nest No. 3 and nest No. 2, an egg was laid every other day. The earliest egg in our study area was probably laid 6 June (nest No. 6). The last egg in our study area, in nest No. 14, was laid on 28 June. Clutch size in all nests was four. For data on nests see Table 3.

Activities during incubation. At 10 nests we found a bird incubating at nearly every visit, but at two we found the parent missing relatively frequently. Several times during incubation we saw both parents at a nest; and we noticed a marked day-to-day difference in the aggressiveness of the incubating birds (see below—Reactions to Intruders). The less-solicitous parent was at the nest on approximately 20 per cent of our daytime nest-checking rounds at the 10 nests mentioned. The more-solicitous parent taken with young on 21 July was a male. When the bird ran in and settled on the nest, it usually first put its bill down among the eggs (not seeming to arrange them), and then vigorously

TABLE 3
NEST DATA—BAIRD'S SANDPIPER

<i>Nest No.</i>	<i>Date found and contents on that date</i>	<i>First egg hatched</i>	<i>No. of young produced</i>
1	16 June (4 eggs)	7 July	4
2	18 June (3 eggs)	10 July	4
3	17 June (2 eggs) ¹	—	—
4	22 June (4 eggs)	11 July	4 (no egg left)
5	26 June (4 eggs)	7 July	4 "
6	26 June (4 eggs)	3 July	3 "
7	28 June (4 eggs)	13 or 14 July	? "
8	30 June (4 eggs)	8 July	3 "
9	3 July (4 eggs)	12 July	4 "
10	3 July (4 eggs)	(not revisited)	
11	5 July (4 young)	4 or 5 July	4
12	5 July (4 eggs)	19 July	3 (1 did not hatch; left in scrape)

¹ Clutch size four in all 12 nests. Nest No. 3 destroyed by a dog.

shuffled from side to side and squirmed more and more rapidly down onto the eggs. It held its head in on its shoulders and did not thrust its head as far down and forward as did the White-rump. Incubation period at nest No. 2 (found before completion of the clutch) was 21 days. This seems to have been unrecorded previously.

Hatching and care of nestlings. Eggs hatched between 3 and 19 July, but the eggs of seven nests hatched between 7 and 13 July. All but one egg pipped the day before hatching; that egg pipped two days before hatching. In several nests one, two, or three eggs hatched in one day; and in every case the young left the nest the following day. We have no indication that the young returned to the nest after the last egg hatched. After hatching, the young often stayed several days in the vicinity of the nest, accompanied by both parents, and then moved to wind-blown, well-drained soils of frost-patterned areas and old beaches, or to muddy pond shores thinly scattered with sedges. The parents leading young gave a new alarm call—*drrrreeee* or *drrrreeeeet*—not so low as the call note on migration, nor so mellow as the *tii-tii*. The young were slow and clumsy for three days after hatching. Either parent's song or the *drrrreee* alarm made the young "freeze" the first day and for at least two weeks after hatching. We saw no pooling of young into flocks, but when young were disturbed, parents from nearby broods showed alarm and sometimes joined in distraction.

Reaction to intruders. Until the clutch was complete, parents showed little concern at the nest. With the start of incubation, the parents became solicitous, sat very close and, when disturbed, fluttered at an

intruder and performed distraction displays. The birds were markedly more solicitous in cold weather than in warm. The parents were secretive and seemed anxious to get the intruder away and then get back to the nest. Some birds returned to the nest if we sat down, as close as two to three meters. When we left they followed some 40 meters, calling; then, with head down and feathers smoothed, they ran back to the nest, stopping two or three times to look and call. In comparison with White-rumped Sandpipers, Baird's left the nest more readily, which made Baird's nests much easier to find.

Rarely, calls of *túi-túi* at the nest attracted a second bird, which stood in the background, calling occasionally. We saw no aggressive behavior toward the second bird. One parent at nest No. 4 left before we were 75 meters away, and did not return until we were 50 meters or more away. The other parent let the observer get within 20 meters without an outcry; then flew at him. In contrast, both parents at nests Nos. 6 and 7 were much wilder.

When the eggs were pipping and hatching, and when parents were escorting young, aggressiveness and distance at which they started attention getting (advertising display) increased markedly (to as much as 300 meters), and several neighbors entered the territory of a bird that was displaying. The adults made themselves conspicuous as if to keep the eyes of the intruder up and away from the young. When we got in among the young and they broke out of hiding, the parents quickly flew toward us and started creeping over the ground, flapping both wings, and crying *péew, péew*. There was a call that made the young break out of hiding and run to the parents, but I do not distinguish it in my notes. On 5 and 21 July parents sang in the air before performing vigorous distraction display, and again when we had moved off about 60 meters.

Feeding behavior. The dry surfaces of Baird's habitat were suitable for their technique of picking food off the surface.

The stomach contents of three adults were identified for us by Dr. George W. Byers:

1. Fragments of two beetles of same species (Fam. Carabidae); one spider; one small crustacean (leg only); one beetle larva (Fam. Carabidae); and miscellaneous plant fragments, including moss leaves and stems.
2. One fungus gnat (Fam. Mycetophilidae—wing only); three beetles of two species (both Fam. Carabidae); one adult crane-fly, male (Fam. Tipulidae, Gen. *Tipula*).

TABLE 4
SUMMARY COMPARISON OF THE SANDPIPERS

<i>White-rumped Sandpiper</i> (<i>Heteropygia</i>)	<i>Baird's Sandpiper</i> (<i>Calidris</i>)
Nesting Site	
Well-vegetated sites among clumps in carpet of vegetation, in a moss base. Nest in clump of vegetation, on moss and plant foundation.	Wind-blown, lichen-strewn, early snow-free areas, with many bare patches. Nest on bare soil; scrape made in natural depression.
Excitement	
Raises head and sleeks plumage before flight display.	Raises head and sleeks plumage before flight display.
Aggression	
(a) Head thrust forward, back feathers ruffled, wings spread to sides, tail slightly cocked; crouching run.	(a) Head thrust forward, back feathers ruffled, wings spread at the sides, tail partly fanned; crouching run.
(b) At the end of "Sharp-tailed dance," head is raised and near wing often stretched over the head.	(b) Runs in front with head raised and near wing stretched over back showing under wing.
Appeasement	
Stands with head raised.	Stands with head raised.
Action of Companion during Display	
During "Sharp-tailed dance," several times raised head and then near wing.	At end of song flight, crouched, thrust head forward and called <i>co-it</i> . Both actions similar in ground displays.
Alarm Call—Advertisement	
None heard.	<i>Toówee-toówee</i> .
Courtship Display	
<i>Ground display</i>	
Varied and ritualized.	Similar to aggression.
(a) Runs to companion in aggressive posture or	(a) Runs to companion in aggressive posture or
(b) Performs dance with wings stiffly spread, tail cocked straight up and furred, head thrust forward, calling <i>bessszip</i> .	(b) At end of flight display, stops and stretches near wing up, occasionally calls <i>toówee-toówee</i> or trills as in flight song.
(c) Stands before companion with tilted tail and raised wings.	

TABLE 4
(Continued)

<i>White-rumped Sandpiper</i> (<i>Heteropygia</i>)	<i>Baird's Sandpiper</i> (<i>Calidris</i>)
<i>Display flight</i>	
<p>Flies up to about 15-25 meters where hovers or sails, calling:</p> <p>(a) Trill like a fish reel, sometimes ends with <i>zip-zip</i> call as floats down.</p> <p>(b) Call of <i>ng-oik</i>, bobbing head, then sails down on set wings.</p> <p>Display flight occasionally given with two or three birds in the air, seemingly both male and female; one did not posture in flight. Flight sweeping over large area.</p>	<p>Flies up to about 15 meters where hovers or sails, calling a rapidly repeated alarm or trill.</p> <p>Display flight only seen to be given by a single bird. Flight localized over small territory.</p>
<i>Flight song</i>	
<p>Clearly differentiated from ground song, and of two types: "small pig" and "fish reel." Decreased with start of incubation; last heard 30 June.</p>	<p>Given on the ground and in air: <i>toówee-toówee</i>, rapidly repeated; grades into trill. Decreased sharply with start of incubation; reappeared after young hatched.</p>
Distraction Display	
<i>Aggression</i>	
<p>(a) Flight songs of both types given at start of incubation period.</p> <p>(b) Stands with head raised, feathers sleeked and silent; runs rapidly, crouching, head thrust down and forward, back feathers ruffled, wings usually barely spread, tail fanned and tilted, squeaking and twittering constantly, occasionally crouching in a depression.</p> <p>(c) Flutters into intruder's face, squeaking and twittering. Sat close using concealment.</p>	<p>(a) Flight song at start and end of incubation period.</p> <p>(b) Stands with head raised, feathers sleeked, calling <i>toówee-toówee</i>; runs rapidly with head thrust forward, back feathers ruffled, wings partly to almost fully spread (more widely spread than by White-rump), and head held out stiffly, tail fanned and tilted; stops to cry <i>toówee-toówee</i>, or twitters (low grating <i>peccw-peccw</i>) while running. Comes closer (2-4 meters) when behind observer.</p> <p>(c) Flutters at intruder's face, and when alighting stretches one wing high over back, and may present one wing, in a posture similar to the one-wing display.</p> <p>Showed aggressive actions at greater distance, presumably as demonstration display.</p>

TABLE 4
(Continued)

<i>White-rumped Sandpiper</i> (<i>Heterophygia</i>)	<i>Baird's Sandpiper</i> (<i>Calidris</i>)
<i>Leading away</i>	
Runs along in crouch, about 4 meters from intruder, wings held at the sides or tips across rump, partly open; tail fanned and tilted down, head thrust forward, squeaking; zigzags and starts and stops. If ignored, (b) and (c) above. Displacement feeding. Occasionally crouched briefly in hollow with head forward as if onto eggs. Leads about 10 meters from nest, then runs around to the side, back to the nest, with short nervous runs. Leading away is a clearly expressed action.	Runs in crouch, at an angle to intruder, wings partly open and lowered, the near wing dragged, tail occasionally fanned and tilted, head thrust forward; stops and raises head to cry <i>toówee-toówee</i> , starts and stops. Leads about 10 meters from nest. Leading away is much less well developed.
At Nest	
Clutches completed 25 June–2 July. Only one sex seems to incubate; in at least one case, both parents accompanied young; in four others, only one parent was seen with young. Concern at the nest increased just before and after young hatched.	Clutches completed 12–28 June. Both sexes seem to incubate and show concern; both sexes accompany young. Concern at the nest greatly increased just before and after young hatched.
Feeding	
Feeds by deep probing; stomach contents were larvae.	Feeds on the surface; stomach contents were adult and flying insects.
Territories	
Six nests in one square mile of our study area; arrived after the snow had left the lowlands—19 June. Territories large and complex; two nests 35 meters apart suggests polygamy.	Twenty-five territories in one square mile of our study area; were on territory when we arrived. Territories averaged 50 meters across, simply organized.
Young	
Hatched 15–22 July. Strongly buffy below.	Hatched 3–19 July. Grayish-white below.
Eggs	
Greenish-brown background color with darker spots and splotches. Females 1 and 4 laid two days after arrival.	Tan to chocolate-brown background color with darker spots and splotches. Incubation period 21 days.
Calls	
Mouselike squeak. "Fish reel." "Small pig" <i>ng-oik</i> .	<i>Dreet</i> or <i>toówee-toówee</i> . Trill.

3. Two beetles of same species (Fam. Carabidae); two muscoid flies (probably Fam. Anthomyiidae); one adult crane fly, male (Fam. Tipulidae, Subfam. Limoniinae, *Limnophila* sp.); many crane fly eggs and leg segments (Fam. Tipulidae, Gen. *Tipula*); and many segments of legs from a slender-legged arthropod, perhaps a phalangid.

All of these animals could have been picked from the surface.

Migrants. Nonbreeding birds gave the *túí-túí* calls, but we heard the hoarse *drrrrceet* of birds on migration first on 30 June. We saw the first flock 7 July; five on 11 July; then 16, seven, and five on the walk to Oonakuktooyuk on 20 July.

SANDERLING

Calidris alba (Pallas)

(Eskimo: Idlouk and his family had no name for this species)

The reasons for including *alba* in *Calidris* are given below (Behavior and Systematics).

We saw one bird in distraction display on the dry uplands near Oonakuktooyuk. It ran with head low and neck thrust forward, calling *drreeet* or *tweeet*, *tweeet*, bobbing occasionally like a Spotted Sandpiper. Then it flew, alternating periods of ordinary flight with periods of rapid, shallow wingbeats, again like a Spotted Sandpiper.

The vegetation of the site was like that described for the nesting of this species in Greenland (Salomonsen, 1950–1951), streaked with alternate lines of vegetation (mosses, Avens, Arctic Willow, and some sedges) and almost barren soil, so regular as to seem ploughed.

II. BEHAVIOR AND SYSTEMATICS

Heinroth (1911), Lorenz (*e.g.*, 1941), and Mayr (1942 and 1958) have emphasized the importance of behavior in systematics. In this paper an attempt is made to use behavior to help define genera of plovers and sandpipers.

Our observations indicate that the courtship displays of the plovers (Ringed, Golden, and Black-bellied) contained similar elements, while the displays of the sandpipers were varied. The actions of the Baird's Sandpiper were simple and generalized. The similarity of actions (rushing, displaying of wings, and fluttering) that preceded copulation, to those seen in aggressive situations and in the presence of a human intruder, suggests that ritualization has not advanced very far, either to rigidity of the individual actions or to separation into several dif-

ferent actions. However, the song flight and dance of the White-rumped Sandpiper do not grade into any of its other activities, and thus are more "derived" or "less probable," as Lorenz (1935) says. On this purely behavioral basis, the sandpipers are less closely related than the plovers. Yet nearly all students place the White-rumped and Baird's sandpipers in the same genus, while putting each of the three plovers in a separate genus. This may only show the danger of making comparisons between subfamilies, based on one taxonomic character (behavior in this case).

Plovers. Displays, nesting sites, eggs, nestling and adult plumages, and skeletal features show that Golden Plover and Black-bellied Plover (Table 1) are very closely related and, in fact, do not justify separate generic status (Van Tyne and Drury, 1955 and 1959). Although we found the behavior of these two species similar, many behavior characteristics are uniform for all the plovers, and to use these as the only basis of classification would produce results as unsatisfactory as has the use of only morphological features. Lowe (1922) pointed out a morphological separation: presence of rudimentary hind toe and two cervicodorsal vertebrae with free ribs in the Black-bellied Plover, in contrast to lack of rudimentary hind toe and presence of three cervicodorsal vertebrae with free ribs in the Golden Plover. Lowe also listed nestling plumage and features of the osteology of the skull. We found the presence of the white collar—uninterrupted in the Black-bellied Plover and interrupted in the Golden Plover—but this is not without exception (see photograph in Van Tyne and Drury, 1959).

The differences in the skull, described by Lowe as conspicuous, are dictated by the habitats of the two species, as Ernst Mayr suggested to me in 1954: the Black-bellied Plover is marine and the Golden Plover largely fresh water in the nonbreeding season. Nasal glands, correlated with the marine habitat, have by their size and pressure suppressed the formation of bones and modified the region at the base of the bill, complicating embryological processes and degree of ossification in the Black-bellied Plover. Bock (1958) discusses this problem in detail, especially the structure of the skulls, and reviews the confused history of the classification of plovers based on (1) functional characters (plumage color and skulls), and (2) the presence or absence of a hind toe. The last character comes and goes without relation to other taxonomic features. Mayr (1945) and Delacour (1951) show the superficiality of the hind toe as a generic character, both in plovers and in sandpipers.

Fänge, Schmidt-Nielsen, and Osaki (1958) and Schmidt-Nielsen (1959) show that the nasal glands have a salt-excreting function in species that drink salt water. This explains the taxonomic distribution

of these glands according to species habitat and why they are so important that skull modifications appear to accommodate them. Features directly selected by habitat are not of generic value.

The ground displays, especially of aggression (Table 1), appear indistinguishable between Golden and Black-bellied plovers, but differ in detail from those of the *Charadrius* plovers that I have seen in Killdeer, Semipalmated Plover, and Piping Plover (*Charadrius melodus*) and that Edwards *et al.* (1947), Laven (1940), and Mason (1947) have described for Ringed Plover; Ledlie and Pedler (1938), Dathe (1953), and Simmons (1953) for the Little Ringed Plover; and Simmons (1953) for the Kentish Plover (*Charadrius alexandrinus*): *e.g.*, (1) the raising of wings (correlated with colored axillars) in aggressive situations appears in the *Pluvialis* plovers, not in *Charadrius*; (2) the ruffling of back feathers and lowering of head (correlated with brightly patterned back) in aggressive situations is emphasized by *Pluvialis* plovers, while *Charadrius* plovers emphasize the throat and breast (correlated with contrasting dark and white rings) and the fanned tail. Furthermore, (3) head-bobbing displacement activity (raising head, neck, and forward end of the body while lowering the tail) is absent in *Pluvialis* plovers, and universally present in *Charadrius* plovers.

In distraction display, the two *Pluvialis* species seem to differ, but actually the differences are in degree only. Golden Plovers stood up and faced the intruder and approached directly. When running away, Golden Plovers did not crouch as low as the Black-bellied, nor did they throw themselves into a depression. Their more upright posture in running and beating wings created the illusion of a four-footed animal—"the rodent run." Black-bellied Plovers spread their wings more fully, thrust their heads down and forward, and crouched lower; they approached the intruder diagonally and stood at an angle. Both male and female Golden Plovers distracted, whereas only male Black-bellied Plovers did. Actually the distraction by the female Black-bellied Plover at nest No. 4 was similar to that of the Golden Plover. It will be important for comparison to have more details of the distraction displays of female Black-bellied Plovers and male Golden Plovers from other areas in order to see whether there is geographical variation and to see whether the differences that we observed are species specific or sexual. In these displays, both of the *Pluvialis* plovers use their wings in unison.

In contrast, the distraction display of *Charadrius* plovers (*e.g.*, Ringed Plover, Little Ringed Plover, Kentish Plover [described by: Armstrong (1952), Dathe (1953), Edwards *et al.* (1947), England *et al.* (1944), Ledlie and Pedler (1938), Mitchell (1935), Simmons

(1952, 1955), Sutton and Parmelee (1955), and Williamson (1947)], Killdeer and Piping Plover) are alike in those features that differ from the display of the *Pluvialis* plovers: e.g., wriggling along the ground, leaning on one side and waving one or both wings in an uncoordinated way (broken wing act)—see illustrations of Killdeer (Deane, 1944) and Little Ringed Plover (Dathe, 1953; Simmons, 1955). In the *Charadrius* group, one wing seems to wave independently of the other. Ringed Plovers, Little Ringed Plovers, and Killdeer may turn on an intruder and approach with wings raised and spread (see illustrations in Simmons, 1955, which also show a Kentish Plover sprawled in a posture very like that of a Black-bellied Plover). The tail is fanned and quivered in *Charadrius*, and I have not seen the tail cocked up in this context. Both Black-bellied and Golden plovers may tilt and cock their tails when bowing before an intruder. We never saw *hiaticula* run with head lowered and back feathers ruffled as in Black-bellied and Golden plovers. They ran either with heads pulled in onto their shoulders (crouch run, Simmons, 1955) or with head raised and body feathers sleeked, as Golden Plovers did or Black-bellied Plovers did when “ridden off” by Golden. When *Charadrius* plovers crouch, they seem to try to hide; when *Pluvialis* plovers crouch, they “pretend” to settle on a nest.

Sandpipers. The relationships within the sandpipers are more complex. Skins show that the young of Baird's and White-rumped sandpipers are similar to the other species of “*Erolia*,” to which the young of *Calidris (Ereunetes) pusilla* are also very similar. This led Van Tyne to agree with Witherby *et al.* (1940) that *pusilla* be included in the same genus with *bairdii*, *alpina*, and *minutilla*. The behavior of these species, as described by various authors, agrees. Many fragmental and some fairly complete descriptions are available—e.g., quotations in translations of Birula and Suschkin in Pleske (1928), Brandt (1943), Brown (1938), Haviland (1915 and 1916), Keith (1938), Portenko (1959), and Sutton (1932). In aerial song, aggressive action, and distraction behavior, Knot (*Calidris canutus*), Sanderling (“*Crocethia*” *alba*), Dunlin (*alpina*), Purple Sandpiper (*maritima*), Semipalmated Sandpiper (*pusilla*), Western Sandpiper (*mauri*), Least Sandpiper (*minutilla*), Temminck's Stint (*temminckii*), and Curlew Sandpiper (*ferruginea*) are similar in noncomplex actions, little ritualized from hostility postures. Their trilling song is given while hovering or in butterflylike flight. The song grades into a characteristic scold note. In fact, behavior indicates that Knot and Sanderling (both using wing-up threat action—Birula in Pleske, 1928) are closer to most of the members of *Calidris* than are *fuscicollis* and *melanotos*. The Knot's

song departs from the usual trill to a call *kou-hi*, not unlike a Baird's *toóooowee*. According to Sutton (1932) *fuscicollis* resembles *melanotos* in the presence of throat or pectoral sacs. The reproductive behavior of these two: flight song, "sharp-tailed grouse" display and failure of the male to take part in incubation suggest that *melanotos* and *fuscicollis* are at a different level of ritualization from that of the rest. The male Curlew Sandpiper, otherwise closely resembling the other *Calidris*, is reported by Haviland (1915) and Portenko (1959) to take no part in incubation. The spring plumage changes in Knot, Curlew Sandpiper, Sanderling, and Dunlin form a series with the Least and Semipalmated Sandpiper and Stint type of spring plumage.

The feeding habits do not clarify the classification. The two major techniques: (1) quivering, probing action characteristic of *fuscicollis* and (2) a stabbing peck—*bairdii*—cut across the taxonomic features. Earlier authors (Hartert, 1912–1921, and Witherby *et al.*, 1940) included all these species in *Calidris* (excluding *alba*). Mayr (Delacour and Mayr, 1945) included *alba* in *Calidris*, and I agree. The place of the Stilt Sandpiper (*Micropalama himantopus*) needs clarification by behavior study.

If any species are taken out of the genus *Calidris*, *fuscicollis* and *melanotos* should be the first. Pitelka suggests relationship of these to the Ruff (*Philomachus pugnax*). The members of *Calidris* (*s.l.*) are sufficiently different from *melanotos* to justify its separation even as a monotypic genus. Now the questions arise whether *fuscicollis* (1) lies outside the extremes of variation represented by the other *Calidris* (*s.l.*); (2) is different enough to justify a monotypic genus; (3) is close enough to *melanotos* to justify inclusion with it; (4) is closer to the other peep that have a white rump and decurved bill (*ferruginea* males do not incubate; even *himantopus* shows sexual size differences that are suggestive). Present knowledge suggests that *fuscicollis* behavior is beyond the limits of variation known within the rest of *Calidris* (*s.l.*) and has moved in the direction of *melanotos* although not as far. Because of this, I suggest reinstating Coues' (1861) genus *Heteropygia*, of which *fuscicollis* is the type and about which there is no nomenclatural doubt. Portenko (1959) retains *Heteropygia* for *melanotos*. Species included in this genus by Sharpe (1899) are *melanotos* ("maculata"), *fuscicollis* ("Bonaparte"), and *acuminata*; and, in addition, *bairdii*. My studies exclude *bairdii* from the genus *Heteropygia*, as here, and show its relation to *Calidris*.

III. ECOLOGICAL INTERACTIONS OF CLOSELY RELATED SPECIES

What mechanisms in these six shorebirds allow sympatry without interbreeding or ecological interference (competition)? Darwin (1859) established that closely related species tend to compete for habitat and food necessities. Recently several studies (Gibb, 1954; Hartley, 1953; MacArthur, 1958) have examined the segregation of habitat or food that prevents direct competition between closely related species. Shorebirds are especially favorable subjects for this type of study. On migration they might be able to take advantage of what Lack (1954) calls a superabundant food supply, but actually we can assume that they do not because of observably different feeding techniques. Our studies of shorebirds on Bylot Island show that these species are subject to the classic rules of ecological competition and segregation.

Interaction of plovers. We found habitat segregation between Golden and Black-bellied plovers, but the segregation was not clear nor did it seem effective, because we also found conflict between the two. Armstrong (1952) described conflict between Little Ringed and Ringed plovers where these two largely allopatric species overlap as a result of recent changes in range. The two *Pluvialis* plovers survive sympatrically here, but over most of North America their breeding ranges do not overlap. Because we should expect that there will be geographic variation in the mechanisms allowing sympatry, it will be interesting to study interspecific relationships in other parts of their overlap, *e.g.*, Alaska and Siberia.

Dementiev *et al.* (1951) state that in the Soviet Union the European Golden Plover nests in the marshy and wetter parts of the tundra, while the Black-bellied Plover avoids these and selects the higher, dry tundra. Gladkov (in Dementiev *et al.*, 1951) says that *squatarola* and *apricaria* mutually exclude each other, but the authors comment only that *dominica* is more numerous on the Taimyr Peninsula where it shares the dry biotope with *squatarola*. Black-bellied Plovers began to lay later than Golden Plovers, when most of the uplands were free of snow, yet chose restricted areas—the most barren. They fed on dry places in contrast to the wet, often marshy places where Golden Plovers fed. The late arrival and laying, and exposed habitat, allows Black-bellied Plovers to be High Arctic breeders. In contrast, the calendar and the vegetation of their habitat suits Golden Plovers to the Low Arctic. Where Golden and Black-bellied plovers occur together, displacement (character displacement of Brown and Wilson, 1956) can be expected to exaggerate the site-preference differences. This habitat displacement must depend on the local nature of the vegetation and must be a re-

versible process, depending upon ability of one species to appropriate nesting sites of its choice.

Conflict between Golden Plover and Black-bellied Plover. On 8 and 9 July, at Golden Plover nest No. 2, a male Black-bellied Plover, which persisted in approaching too close, was repeatedly attacked and driven off. Whenever the Black-bellied approached, one or both Golden ran at him (Figure 3), calling *pwit-pwit-pwit*, sometimes attacking in a flying dive, and the Black-bellied Plover, retreating, flew up, wheeled, and dove at one of the Golden. The Golden stood its ground but crouched, spreading one wing momentarily (Figure 3), as the Black-bellied passed over and settled. Occasionally one of the Golden cried *ka-sweéooowit*, bobbing its head violently. The Black-bellied Plover held its neck stretched up (appeasement) and occasionally called *kleeeee*. The Golden Plovers did all the aggressive displaying.

When we approached, the female Golden ran up to us with head partly lowered, breast feathers fluffed out, and scolded *pwit-pwit-pwit*.

On 12 and 14 July we watched Golden Plovers pursuing female Black-bellied Plovers in three different places on the uplands and at the mouth of the river at Ooyarashukjooet (Figure 3). Pursuits, scarcely 20 meters at Aktineq, were 100 meters to half a mile at Ooyarashukjooet.

Our notes indicate that most trespassers were females. The conflicts increased toward the end of the incubation period, perhaps because the longer time gave the Black-bellied Plovers more opportunities to find nests. Unsatisfied incubation drives may be the behavioral basis of the trespassing because both species should respond to the similar eggs of the other. I would expect the incubation drive of a bird to decrease as the incubation period passed, if she were not incubating eggs to reinforce the drive.

Our few observations do not allow us to say whether there were interspecies territorial struggles or not. But Golden Plovers laid eggs about two weeks before the Black-bellied Plovers in "neighboring" territories, and the periods during which territorial aggression is evident must differ.

These conflicts expose the eggs of Golden Plover to greater danger from cold and predators, but we found no lessened nesting success. The species that harries another while incubating its own eggs can be expected to hold the breeding ground. It will be interesting to see the expression that the competition takes farther south, where Golden Plovers replace Black-bellied Plovers.

The third plover (Ringed Plover) occupied the especially barren or vegetation-free habitat of active sea beaches and abandoned river bars.

Differences of habitat, size, and displays (voice and patterns of plumage) separated this population so that there was no problem of overlap or competition.

Interaction of sandpipers. The three species of sandpipers ignored each other. Baird's Sandpipers arrived, probably by 1 June, and occupied the most barren places to nest and feed on surface-living insects. White-rumped Sandpipers arrived on 19 June and occupied vegetated, relatively sheltered areas. They fed by probing deeply into the moss. We found Sanderlings on dry, frost-lined uplands where we saw neither of the other species. Baird's is adapted to High Arctic breeding grounds, while the White-rump is adapted to the mossy bogs of the Low Arctic. I have no data on the feeding of the High Arctic Sanderling on its breeding grounds, but on migration it probes shallowly and frequently uses a turnstonelike technique in seaweed.

In the two plovers and the two sandpipers that we studied in detail, territorial boundaries were universally ignored by the time the young had hatched and left the nests. Parents and their young readily crossed territories and gathered in favored feeding places. This argues against any direct food function of territory unless in the realm of a "non-proximate" influence of preventing aggregation of breeding pairs beyond a "certain concentration." This concentration will be very hard to establish, because territories are highly compressible, especially under conditions that lead to crowding, *e.g.*, a late spring. Such conditions do not vary with the food supply at the time when the young have hatched and are learning to find food—one of the critical times of food pressure.

IV. ETHOLOGY OF DISTRACTION DISPLAYS

Although I recognize the fundamental value of the scheme of "conflict of drives" proposed by Hinde and Tinbergen (1951), I think that to classify all displays as the result of the relative strengths of the conflicting drives is to oversimplify. Is it not possible that many displays have been selected for themselves and their present function, without concern for their basic motivation? Is it not possible, too, that the original motivation may itself have become lost, transferred, or ritualized? Furthermore, if the immediate motivational context exists, as that theory suggests, why is there the great difference in specificity between distraction and courtship displays?

Distraction displays are selected to function as a whole. I endorse Simmons' (1955) abandonment of his earlier classification, which separated "static" and "mobile" lures, because such classifications (see also Armstrong, 1949) suggest uniformity in what is actually a spectrum of

intensity, as Simmons pointed out. He also pointed out that the use of the word "displacement" activity, as it applies to aggressive and brooding drives, is misleading in distraction displays, and he emphasized the importance of the aggressive motivation.

The explanation of distraction displays, on the basis of a conflict situation, suggests a basis for the gradation and variation seen during a series of encounters; but I agree with Simmons that distraction displays are not expressions of drives thwarted *at present*, and are clearly ritualized into a specific action of survival value. It is also obvious (Skutch, 1955) that there cannot be impairment of coordination. In the conflicts between Golden and Black-bellied plovers, all distraction displays were absent—even nest-defense postures. Deane (1944) reported a marked difference in distraction displays of Killdeer, when directed to cow or horse, or to man—yet the same conflicts of drives were present. Clearly, then, these postures are not an expression only of conflict of attack and flee drives, but are separately ritualized. At present, although there is gradation in the intensity of display, each stage in the gradation is uniform. If present conflicts of drives were responsible for impeded actions, one would expect different forms and combinations of actions from each individual at each visit. Instead, the whole distraction action is ritualized and selected as a unit.

Plovers. Males of both Black-bellied and Golden plovers showed aggression to the intruder (head lowered and back feathers ruffled) and occasionally came very close in a conspicuously aggressive posture. The aggressive rush was more evident in Black-bellied than in Golden action, perhaps because the male did most of the distraction. The butterflylike display flight in distraction of Ringed Plovers must be largely motivated by hostility, as it is in its intraspecies context. This grades into a demonstration display, which is even more conspicuous in other species: Baird's Sandpiper and Lesser Yellowlegs (*Totanus flavipes*)—(in my experience); godwits (*Limosa*); Redshank (*Totanus totanus*)—(Simmons, 1955).

The gradation of each action into most of the others must be emphasized. As the drives of aggression, flight, brooding, fear, and concealment rise and fall, the bird approaches and threatens, settles into a hollow, flattens itself on the ground, and spreads its wings—yet stamps its feet and beats its wings. Any movement stimulates fleeing, and the bird runs off, flopping or shuffling. The aggressive actions, the standing and calling ("static lure"), and the flight over the ground ("mobile lure" or "rodent run"), all serve, in present practice, functions different from their "original" conflict of motives. They now serve to attract attention and lead the intruder off. As such, the actions are ritualized,

but this does not mean that the basic "tendencies" are totally removed.

It has been generally accepted that a movement can become ritualized—thus stereotyped, modified, and removed from its original context. Is it not possible that a posture can become ritualized and removed from its original motivational context, too? Meyerriecks (1959) documents the emancipation from the attack-flee-sex motivational conflict of crest raising in Green Heron (*Butorides virescens*). I suggest that distraction displays must be considered separate from their original motivations and that the whole act has become ritualized, including its motivation. The concept of conflict of drives is an excellent ground work for understanding, but it is dangerous to explain all postures, and especially the highly ritualized ones, on the basis of their elements of hostility, sex, and fleeing. An action such as distraction display may itself become a unified "uneasiness action" or "displacement activity." Once this has happened, interpretation of the elements of the posture according to the meaning of the components in an "original" conflict situation will produce either nonsense or an unnecessarily complex "dissection." The action is an element in itself, no longer compound. In this context, the elements of attack, flee, and sex exist as motivations—but also, so do distraction, nest defense, alarm, response to predator, and probably many others.

Sandpipers. The sandpiper species varied in the amount of calling during distraction, and in aggressiveness. It may not be coincidence that Baird's dancing, wing-quivering distraction was not present in the White-rump. In White-rumped Sandpipers, a similar act is part of the courtship ceremony! The brooding or nest-defense posture, conspicuous in the plovers' actions, was not conspicuous in those of the sandpipers. The brooding drive was stronger in sandpipers than in plovers, however, because the parent sat closer. The difference may be associated with difference in size and color.

Comparison distraction and courtship displays. Why are similar distraction displays so widespread and courtship actions so specific? The similar series of actions in the distraction of plovers and sandpipers may be "old actions" or the result of convergence in the tundra habitat, but they do not occur in the other families we observed. In contrast, the well-known tameness of tundra species is probably convergence, because of the distances a parent can be seen once it leaves the nest. This visibility requires that parents abandon early or sit tight.

The uniformity of distraction display in the plovers and sandpipers, even to the point of retaining the broad intergradations of action, is shown by the uniformity of actions at different nest sites, and it contrasts with the differences in courtship and hostility displays. This is

to be expected from the "purpose" of these actions. *Distraction* has a shotgun effect, and the selective action of species-specific differentiation serves no purpose. In contrast, in *courtship*, selective advantage, where species overlap, has ritualized certain actions and emphasized differences that provide the species with isolating mechanisms (Brown and Wilson, 1956). In the courtship displays there is uniformity in detail, presumably because of the one male to one female relation in pair formation, in contrast to the one to "anyone" in distraction. Both types of ceremony are uniform, but in the one, each specific act is important; and in the other, only the whole effect is important, and it must be generalized enough to attract attention of several kinds of predators. Because of this ritualization, the original motivations are not clear in distraction, and only comparative studies can clarify them. For example, the nest-defense posture is modified in Golden Plover to a bow, with beating wings (Figure 3), and is nearly unrecognizable as defense in Black-bellied Plover, where it has become a helpless bird prostrate on the ground—but prostrate only in hollows (Figure 4) that hold a "nest" when the drives are of lower intensity.

LITERATURE CITED

- ALLEN, A. A. 1934. The Golden Plover. *Bird-Lore*, **36** (5): 321-332.
- AMERICAN ORNITHOLOGISTS' UNION. 1957. Check-list of North American birds (fifth edition). Baltimore, Md. 691 pp.
- ARMSTRONG, E. A. 1947. Bird display and behaviour. Oxford Univ. Press. New York. 430 pp.
- ARMSTRONG, E. A. 1949. Diversionary display. *Ibis*, **91**: 88-97, 179-188.
- ARMSTRONG, E. A. 1952. The distraction displays of the Little Ringed Plover and territorial competition with the Ringed Plover. *Brit. Birds*, **45**: 55-59.
- BIRULA, A. A. 1907. Ocherki iz zhizni pits poliarnavo poberezhia Sibiri. [Information on the life of the birds of the polar coast of Siberia.] *Memoires de l'Academie Imp. des Sciences de St. Petersbourg, Cl. physiomathém*, **18**: 75-80.
- BOCK, W. 1958. A generic revision of the plovers (Charadriinae, Aves). *Bull. Mus. Comp. Zool.*, **118** (2): 27-97.
- BOCK, W. 1959. The status of the Semipalmated Plover. *Auk*, **76**: 98-100.
- BRANDT, H. 1943. Alaska bird trails. Bird Research Foundation, Cleveland. 464 pp.
- BROWN, R. H. 1938. Breeding habits of the Dunlin. *Brit. Birds*, **31**: 362-366.
- BROWN, W. L., JR., and E. O. WILSON. 1956. Character displacement. *Systematic Zool.*, **5** (2): 49-64.
- COUES, E. 1861. A monograph of the Tringae of North America. *Proc. Acad. Nat. Sci. Phila.*, **1861**: 170-205.
- DARWIN, C. 1859. The origin of species by means of natural selection. Modern Library, New York. 386 pp.

- DATHE, H. 1953. Der Flussregenpfeifer. Die Neue Brehm-Bücherei. Leipzig, 1-38.
- DEANE, C. D. 1944. The broken wing behavior of the Killdeer. *Auk*, **61**: 243-246.
- DELACOUR, J. 1951. The significance of the number of toes in some woodpeckers and kingfishers. *Auk*, **68**: 49-51.
- DEMENTIEV, G. P., N. A. GLADKOV, and E. P. SPANGENBERG. 1951. Ptitsy Sovyet Soyuza. [The birds of the Soviet Union.] State Publishing House "Soviet Science," Moscow. Vol. 3. 680 pp.
- DRURY, W. H., JR., and M. C. DRURY. 1955. The Bylot Island expedition. Bull. Mass. Aud. Soc., **39** (6) : 259-265.
- DUBOIS, A. D. 1936. Habits and nest life of the Desert Horned Lark. *Condor*, **38**: 49-56.
- DUBOIS, A. D. 1937. The McCown's Longspurs of a Montana prairie. *Condor*, **39**: 233-238.
- EDWARDS, G., E. HOSKING, and S. SMITH. 1947. Aggressive display of the Ringed Plover. *Brit. Birds*, **40**: 12-19, pls. 1-8.
- ENGLAND, M. D., E. O. HÖHN, E. G. PEDLER, and B. W. TUCKER. 1944. The breeding of the Little Ringed Plover in England in 1944. *Brit Birds*, **38** (6) : 102-111.
- FÄNGE, R., K. SCHMIDT-NIELSEN, and H. OSAKI. 1958. The salt gland of the Herring Gull. *Biol. Bull.*, **115**: 162-171.
- GIBB, J. 1954. Feeding ecology of tits, with notes on tree creeper and goldcrest. *Ibis*, **96**: 513-543.
- HARBER, D. D. 1955. The birds of the Soviet Union (a review of Vol. 3). *Brit. Birds*, **48**: 313-319.
- HARTERT, E. 1912-1921. Die Vögel der Paläarktischen Fauna. Berlin.
- HARTLEY, P. H. T. 1953. An ecological study of the feeding habits of the English titmice. *Jour. of Animal Ecol.*, **22**: 261-288.
- HAVILAND, M. D. 1915a. Notes on the breeding habits of the Curlew Sandpiper. *Brit. Birds*, **8**: 178-183.
- HAVILAND, M. D. 1915b. Notes on the Grey Plover on the Yenesei. *Brit. Birds*, **9**: 162-166.
- HAVILAND, M. D. 1916. Notes on the breeding habits of Temminck's Stint. *Brit. Birds*, **10**: 157-165.
- HEINROTH, O. 1911. Beiträge zur Biologie, namentlich Ethologie und Psychologie der Anatiden. *Verhandl. V. Int. Ornith. Kongr.*, Berlin, **1910**: 589-702.
- HINDE, R. A. 1951. Further report on the inland migration of waders and terns. *Brit. Birds*, **44**: 329-346.
- HINDE, R. A. 1953. The conflict between drives in the courtship and copulation of the Chaffinch. *Behaviour* **5**: 1-31.
- HÖHN, E. O. 1957. Observations on display and other forms of behavior of certain arctic birds. *Auk*, **74** (2) : 203-214.
- HØRRING, R. 1937. Birds collected on the fifth Thule expedition. *Rept. 5th Thule exped. 1921-24* (Dan. Exped. Arctic N. Amer. in charge of Knud Rasmussen), 2, Nos. 6 (Zool.: Birds) : 134 pp., folding map.
- KEITH, D. B. 1938. Observations on the Purple Sandpiper in Northeastland. *Proc. Zool. Soc. London*, **108A**: 185-194.

- LACK, D. 1954. The natural regulation of animal numbers. Oxford University Press, London. 342 pp.
- LAVEN, H. 1940. Beiträge zur Biologie des Sandregenpfeifers (*Charadrius hiaticula* L.). Jour. f. Ornith., **88**: 183-287.
- LEDLIE, R. C. B., and E. G. PEDLER. 1938. Nesting of the Little Ringed Plover in Hertfordshire. Brit. Birds, **32**: 90-102, pls. 3, 4.
- LORENZ, K. 1935. Der Kumpan in der Umwelt der Vogel. Jour. f. Ornith., **83**: 137-213, 289-413.
- LORENZ, K. 1941. Vergleichende Bewegungsstudien an Anatinen. Jour. f. Ornith., **89**, Sonderheft, 194-293.
- LOWE, P. R. 1922. On the significance of certain characters in some Charadriine genera, with a provisional classification of the order Charadriiformes. Ibis, **1922**: 475-494, pl. 6.
- LOWE, P. R. 1933. Structural diversity in Charadriine genera correlated with differences in colour-pattern. Ibis, **1933** (1): 112-129, pls. 4-5. (See also Apr. (2): 351-352.)
- MACARTHUR, R. H. 1958. Population ecology of some warblers of northeastern coniferous forests. Ecology, **39**: 599-619.
- MASON, A. G. 1947. Territory in the Ringed Plover. Brit. Birds, **40**: 66-70.
- MAYR, E. 1942. Systematics and the origin of species. Columbia University Press, New York. 334 pp.
- MAYR, E. 1958. Behavior and systematics. Chapter 16, behavior and evolution, pp. 341-362. Yale University Press, New Haven.
- MAYR, E., and J. DELACOUR. 1945. Notes on the taxonomy of the birds of the Philippines. Zoologica, **30**: 106-107.
- MEYERRECKS, A. J. 1959. Comparative breeding behavior of four species of North American herons. Publications of the Nuttall Orn. Club, No. 2. 158 pp. + 15 pl. Cambridge, Mass.
- MILLER, R. S. 1955. A survey of the mammals of Bylot Island, Northwest Territories. Arctic, **8** (3): 166-176.
- MITCHELL, M. 1935. Injury feigning movements of Ringed Plover. Brit. Birds, **29**: 61.
- MOYNIHAN, M. 1955. Some aspects of reproductive behaviour in the Black-headed Gull (*Larus ridibundus ridibundus* L.) and related species. Behaviour, Supplement No. 4, 201 pp. Leiden.
- NISBET, I. C. T. 1957. Wader migration at Cambridge sewage farm. Bird Study, **4**: 131-147.
- PICKWELL, G. B. 1942. *Otocoris alpestris praticola*. Prairie Horned Lark. In Bent, Life Histories, U.S. Nat'l Mus. Bull. No. 179, pp. 342-356.
- PITELKA, F. A. 1959. Numbers, breeding schedule, and territoriality in Pectoral Sandpipers of northern Alaska. Condor, **61**: 233-264.
- PLESKE, T. D. 1928. Birds of the Eurasian tundra. Mem. Boston Soc. Nat. History, **6**: 111-485, 37 plates.
- PORTENKO, L. A. 1959. Studien an einigen seltenen Limicolen aus dem nördlichen und östlichen Sibirien II—Der Sichelstrandläufer—*Erolia ferruginea* (Pontopp.). Jour. f. Ornith., **100**: 141-172.
- RIDGWAY, R. 1919. The birds of North and Middle America. U.S. Nat'l Mus. Bull. No. 50, Part 8. 852 pp.

- SALOMONSEN, F. 1950-51. The birds of Greenland. Munksgaard, Copenhagen. 608 pp.
- SCHERMAN, K. 1956. Spring on an arctic island. Little, Brown and Co., Boston. 323 pp.
- SCHMIDT-NIELSEN, K. 1959. Salt glands. *Scientific American*, **200** (1): 109-116.
- SEEBOHM, H., and J. A. HARVIE-BROWN. 1876. Notes on the birds of the lower Petchora. *Ibis*, **1876**: 105-126, 215-230, 289-311, 434-456; col. pls. 5, 7.
- SHARPE, R. B. 1899. A hand-list of the genera and species of birds. Vol. 1. London.
- SHORTT, T. M., and H. S. PETERS. 1942. Some recent bird records from Canada's Eastern Arctic. *Can. Jour. Res.*, **D20**: 338-348.
- SIMMONS, K. E. L. 1952. The nature of the predator-reactions of breeding birds. *Behaviour*, **4**: 161-171, 3 figs., pls. 5, 6.
- SIMMONS, K. E. L. 1953. Some aspects of the aggressive behaviour of three closely related plovers (*Charadrius*). *Ibis*, **95**: 115-127, 4 figs.
- SIMMONS, K. E. L. 1955. The nature of the predator-reactions of waders towards humans; with special reference to the role of the aggressive-, escape-, and brooding drives. *Behaviour*, **8**: 130-173, pls. 1-10.
- SKUTCH, A. 1955. The parental stratagems of birds. *Ibis*, **97**: 118-142.
- SOPER, J. D. 1928. A faunal investigation of southern Baffin Island. *Nat'l Mus. Canada Bull. No. 53* (Biol. Ser., No. 15). 143 pp. (incl. 7 pls.), map.
- SUSCHKIN, P. P. 1908. Ptitsy Srednei Kirgizskoi stepi (Turgaiskaia Oblast i vostochnaia chast Ural'skoi). [The birds of the mid-Kirgiz Steppe.] *Mat. k posnauiju fauny i flory Ross. Imp. Wyp.*, **8**: 151-154.
- SUTTON, G. M. 1932. The birds of Southampton Island. *Mem. Carnegie Mus.* 12 (Part II, sect. 2). Pittsburgh, 275 pp.
- SUTTON, G. M. 1954. Nesting of the Snow Bunting on Baffin Island. *Wilson Bull.*, **66** (3): 159-179.
- SUTTON, G. M., and D. F. PARMELEE. 1955. Breeding of the Semipalmated Plover on Baffin Island. *Bird-Banding*, **26**: 137-147.
- SUTTON, G. M., and D. F. PARMELEE. 1956. On certain Charadriiform birds of Baffin Island. *Wilson Bull.*, **68** (3): 210-223.
- TINBERGEN, N. 1951. The study of instinct. Oxford Univ. Press, New York and London, 228 pp.
- TUCK, L. M., and L. LEMIEUX. 1959. The avifauna of Bylot Island. *Dansk. Orn. Foren. Tid.*, **53**: 137-154.
- VAN TYNE, J., and W. H. DRURY, JR. 1955. A study of breeding shorebirds in the High Arctic. Abstracts of papers at the A.O.U. 73rd Stated Meeting, Oct. 25-30, 1955.
- VAN TYNE, J., and W. H. DRURY, JR. 1959. The birds of southern Bylot Island, 1954. *Occasional Papers of the Mus. Zool. Univ. Mich.*, No. 615: 1-37.
- WAGNER, H. O. 1930. Über Jahres- und Tagesrhythmus bei Zugvögeln. (I. Mitteilung). *Zeits. vergl. Physiol.*, **12**: 703-724.
- WALKINSHAW, L. H. 1948. Nestings of some shorebirds in western Alaska. *Condor*, **50**: 220-223.
- WASHBURN, A. L. 1956. Classification of patterned ground and a review of suggested origins. *Bull. Geol. Soc. Amer.*, **27**: 823-866.

- WILLIAMSON, K. 1947. The distraction display of the Ringed Plover, *Charadrius hiaticula hiaticula* L. *Ibis*, **89**: 511-513.
- WILLIAMSON, K. 1948. Field notes on nidification and distraction display in the Golden Plover. *Ibis*, **90** (1): 90-98.
- WITHERBY, H. F., F. C. R. JOURDAIN, N. F. TICEHURST, and B. W. TUCKER. 1933, 1940. The handbook of British birds, Vol. IV. Witherby, London. 461 pp.
- WYNNE-EDWARDS, V. C. 1952. Zoology of the Baird expedition (1950). 1. The birds observed in central and southeast Baffin Island. *Auk*, **69** (4): 353-392.

Contribution No. 18 from the Hatheway School of Conservation Education, Massachusetts Audubon Society, South Lincoln, Massachusetts.