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NUMBERS, BREEDING SCHEDULE, AND TERRITORIALITY IN PECTORAL SANDPIPERS OF NORTHERN ALASKA

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When the spring snows on the tundra of northern Alaska recede in late May and early June, there is a floodtide of birds arriving to begin breeding activities in the short summer. The compression and even elimination of certain pre- and post-breeding stages in the schedule of events on the tundra and the synchrony of breeding effort in common species raise a number of questions regarding populational adaptations among birds of tundra ecosystems. For example, some species, or at least some of their members, appear to arrive paired. Another example is the shortness of the period of territorial behavior, which in some species may be compressed to the extent that observations in late June or later lead late-arriving observers to maintain that these species are non-territorial.

With such considerations in mind, several important questions can be posed for studies of arctic birds: What are the densities and spacing characteristics of common species? How does this spacing develop and change in time? And how does this timing relate to other events of the breeding and post-breeding seasons when the birds are still being supported by the tundra?

A striking feature of tundra communities is the number of shorebird species. They are wholly or primarily insect predators. Differences from year to year in relative abundance and amount of breeding in parts of the arctic, even in species considered in general to be common there, suggest a wide range of adjustment to a wide range of variation in the conditions of existence provided by the tundra. Because shorebirds collectively are such a conspicuous component of animal life of tundra, and because their general role in food chains is similar from species to species, information about them is basic to broader inquiries into the dynamics of tundra ecosystems. Comparative data on such characteristics as spacing and timing of breeding events is therefore needed if their role in food relations is to be analyzed and understood.

The shorebird fauna resident over the lower foothills and coastal plain of northern Alaska consists of 13 species: three plovers, a turnstone, seven sandpipers (including dowitcher and snipe) and two phalaropes. With these my colleagues and I have had sufficient experience over seven seasons of field work to regard them as regular breeders, however varying their numbers. These species are more generally distributed and common than was evident to Bailey (1948) from the specimens he examined from the area. An additional five species (four sandpipers and a godwit) also occur as breeders, but only locally or sporadically, and apparently rarely or never, so far as known now, in the numbers in which the first 13 can be found.

On the coastal flats near Barrow, seven of these thirteen are common: Pectoral Sandpiper ("*Erolia*" *melanotos*), Baird Sandpiper (*Erolia bairdii*), Red-backed Sandpiper (*Erolia alpina*), Semipalmated Sandpiper (*Ereunetes pusillus*), Golden Plover (*Pluvialis dominica*), Ruddy Turnstone (*Arenaria interpres*), and Red Phalarope (*Phalaropus fulicarius*). All but the phalarope are territorial in the classical sense, showing characteristics of advertisement, intolerance, isolation and area-attachment. Among the territorial ones, however, there is a dichotomy with regard to persistence of

the pair-bond. The members of the pair tend to remain together through the nesting season in all but the Pectoral Sandpiper. In this species, once nesting is underway, the males leave. A similar event occurs in the Red Phalarope, except that it is the females that leave. In both species the main exodus comes in the first two weeks of July. This means that a substantial fraction of the total insect predator fauna removes itself, as it were, from the scene of its replacement efforts once that replacement is started. In the Pectoral Sandpiper, males presumably move to more southern latitudes, at least into Canada and the United States, to spend the rest of the summer before migrating to their South American wintering grounds, but this interesting matter has never received any systematic study.

It is the objective of this paper to report on several population characteristics of one of the common northern Alaskan shorebirds, the Pectoral Sandpiper, and to suggest a framework within which comparisons with other shorebird species may be sought in the interests of a clear and generalized picture of their breeding ecology.

Finally, a side issue regarding the Pectoral Sandpiper needs mention in the introduction. The reader has noticed that I put its generic name in quotation marks. I have no definite views of the limits of the genus *Erolia* for lack of knowledge regarding most of its members; but it seems doubtful that *melanotos* is close to its typical members, if these are exemplified by *bairdii* and *alpina*, the two other species of the group which I know best. Europeans (British Ornithologists' Union, 1952) place the Pectoral Sandpiper in the more inclusive genus *Calidris*, which consists of *Erolia* and *Ereunetes* of the A.O.U. Check-list (1957) along with the two species of knots. My acquaintance with northern Alaskan shorebirds and their behavior has to do with six members of this complex (actually seven since "*Crocethia*" appears to be merely an *Erolia* like *bairdii* and *alpina*), and although my experience with them was acquired mainly "on the run" with other work, I would suggest that *melanotos* is not closely related to any of these seven except possibly *fuscicollis* (see discussion). Perhaps the relationships of *melanotos* within *Erolia* can be elucidated only when more information is available for Eurasian as well as American members of the eroliine complex. More studies such as the recent ones of Portenko (1957) and Gladkov (1957) are needed. One characteristic already mentioned in which *melanotos* differs from most members of *Erolia* is in the brief duration of the pair-bond. Other equally or more basic differences will be brought out in the sections to follow. It may seem far-fetched now, but I suspect that *melanotos* is related to *Philomachus*, the Ruff of Eurasia.

DEDICATION

It is a pleasure to dedicate this paper to Erwin Stresemann on the occasion of his 70th birthday.

ACKNOWLEDGMENTS

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For translation of a Russian reference, I express my thanks to Gordon H. Orians. Madame E. Kozłowa of the Zoological Institute, Leningrad, has kindly called my attention to several recent papers dealing with Eurasian species of shorebirds. Paul D. Hurd, Department of Entomology, University of California at Berkeley, identified insects from stomach contents. For comments or information helpful in the preparation of this paper, I am also indebted to P. H. Baldwin, T. J. Cade, A. H. Lachenbruch, W. J. Maher, P. A. Marler, G. H. Orians, and especially to W. J. Hamilton III, whose recent paper on the Pectoral Sandpiper (1959) was the impetus for the preparation of this one. Gene M. Christman made helpful suggestions regarding the illustrations and prepared the final versions.

METHODS

Field work in northern Alaska was conducted in five seasons, 1951 to 1953 and 1955 to 1956 and was based at the Arctic Research Laboratory near Barrow. My own records are supplemented by those of other observers also working at Barrow in the same years and in 1957 and 1958. Their names are given in the acknowledgments.

Observations of significance on local movement, habitat use, nesting, and behavior were routinely recorded in field notebooks through each summer. The bulk of the data for this paper, however, is taken from breeding-bird censuses of three plots mentioned by Pitelka, Tomich, and Treichel (1955:87). Their location with reference to Barrow is shown in figure 1 of that paper. The number of censuses for each plot and the inclusive dates are as follows:

	Plot 1 Old beach ridge 40 acres	Plot 2 Low tundra 20 acres	Plot 3 Marsh flat 86 acres
1951	8 (4), June 10–July 15	9, June 13–July 17	3, June 27–July 16
1952	10 (2), June 11–July 12	8, June 13–July 12	6, June 26–July 17
1953	10, June 5–July 8	12, June 18–July 29	5, June 19–July 26
1955	5 (1), June 10–July 12		
1956	6 (2), June 5–July 14		

The figures in parentheses under plot 1 are additional censuses of the northern half only.

On plot 1, all censuses were obtained by the writer; on plot 2 censuses were obtained by others named in the acknowledgments assisted or replaced by the writer at various times; on plot 3 the writer participated in all censuses except several of those for 1952.

On the flat grassy tundra of the Barrow region censusing is easy. Vision is unimpeded, and there as in other parts of the arctic, birds are relatively unwary. Those tending to wariness, that take flight or walk away, can be seen easily because of low ground cover and low relief. Display and nesting activities occur among virtually *all* members of the resident avifauna over a four-week period, June 5 to July 5, so that with five to ten coverages of each area within this interval, the level of accuracy in estimating numbers is high.

The estimate of breeding density in the Pectoral Sandpiper is based mainly on territorial males which occupy sites over a period of days or weeks. No claim is made for the identity of an individual occurring on a given site. Presence is noted and evidence of local residency is shown by displays, territorial chasing and fighting, and association with a female at least during part of the period of territorial occupation. From a compilation of such records on a summary map, certain characteristics

of spacing can be documented and estimates of density made. This method is in general use in population studies of birds and is discussed further by Kendeigh (1944) and Pitelka (1951).

With each census, the incidence of certain activities was routinely noted on the plot map when the record of occurrence was entered. Thus, the collective censuses provide a sampling of the incidence of these several activities, and trends of change in the relative levels of each through the breeding season can be described. This will be done for incidence of pairs, territorial occupation, display flights, and flocking of the Pectoral Sandpiper.

All records of these activities were pulled from the five seasons' census data and plotted by five-day intervals. The number of censuses in each five-day interval had to be adjusted for differences in areas of the three census plots. This adjustment is based on the fact that plot 2 is twice the size of plot 1, and plot 3 is, for practical purposes, four times the size of plot 1. Thus, the adjusted values represent the number of times that 20-acre units were censused in each interval. The distribution of all censuses in five-day intervals and the values resulting from adjustment for area are as follows:

	Number of censuses	Adjusted values
June 1-5	2	3
6-10	4	5
11-15	15	22
16-20	16	23
21-25	10	15
26-30	16	34
July 1-5	11	25
6-10	5	10
11-15	8	18
16-20	4	5
21-25	0	
26-30	2	5

The figures in the second column represent time-area units. By taking the raw frequencies for any activity, dividing by corresponding time-area factors and multiplying by 100 to avoid fractions, we get a series of index values which describe the general trend of change in incidence of that activity through the breeding season.

The validity of this procedure rests on several considerations: The special activity was noted at the time a sandpiper's occurrence was recorded. The same procedures and same areas were used in the five seasons, with the exception that plots 2 and 3 were not censused in 1955 and 1956. This merely means that the sampling of the incidence of the several activities is more limited for those two seasons than for the previous three. As the purpose of this analysis is to provide a generalized schedule of breeding-season events, this difference in sampling is not serious. Ease of censusing on flat tundra with low cover has already been mentioned. Censuses were carried out during either morning or afternoon hours, and timing varied for each plot. However, this is not considered to produce bias because the daily activity period of birds in general under circumstances of continuous light at 71° 20' N latitude is not only long but, in the Barrow region, modified frequently by changing weather so that no consistent difference in censusing conditions was necessarily to be expected between morning and afternoon hours even if one part of the day were favored. Censusing was deferred on occasion if the weather was so bad that efficiency was seriously reduced. Nevertheless, in the interests of regularity and comprehensiveness, censusing occurred under widely varying weather conditions. Thus, while censuses were taken in that part of the daily cycle when the majority of birds were active, in other respects the procedure was about as unbiased as circumstances would permit.

Local habitat differences do not appear to complicate the arguments for the procedure described above. In common species occurring with fair consistency over the mosaic of tundra habitats, there may be local variation in abundance level according to prevalence of upland versus wet marsh. In the Pectoral Sandpiper, territorial males favor upland sites; transient flocks tend to occur more frequently in low or wet tundra. As the range of habitats on the three plots collectively is typical of the area, and as no one activity is limited to a particular habitat type, it is considered that the

sampling of activities is adequately representative for purposes of a general picture. The fact is that year-to-year differences in relative abundance of the Pectoral Sandpiper and several other species are greater than local differences related to habitat observed in any one season.

The distribution of sampling effort is good for the main part of the breeding period, June 11 to July 15. While the sampling from June 1 to 10 should have been better, the main activity on a population scale occurs after June 10 anyway, and the limited data for early June are considered to reflect adequately the general trend of events.

It may be added that although much is made here of data from census plots, these are subject to evaluation on the basis of additional field experience with Pectoral Sandpipers away from the census plots in each season. Moreover, the notes of all coworkers give information which supplements and to some extent tests that of the censuses. This information was gathered as events in the field having to do with Pectoral Sandpipers struck the observers as worthy of record and as time permitted such recording, for this species was never a special subject for our research. What we have outside of census data is as much a credit to the Pectoral Sandpipers' colorful extrovertedness as to any other circumstance. Only the Red Phalarope is comparably intriguing among breeding shorebirds of the Barrow area.

Date for breeding season were obtained from egg dates in several collections mentioned in the acknowledgments and from records obtained by my coworkers and myself. The large sample in collections for this arctic locality is mainly the result of extensive collecting in the 20's and 30's by Charles D. Brower and more recently by his sons (Bailey, 1948:40). Data on young were obtained by us in the field with the exception of three dates for downy young in museum collections from the Barrow area.

DISTRIBUTION ON THE ARCTIC SLOPE

The Pectoral Sandpiper occurs generally over the arctic slope from the foothills to the coast. How far inland and upward it occurs is not known, but it is present commonly at Umiat, at 300 to 400 feet elevation (Kessel and Cade, 1958:52) and also at East Oumalik, 280 feet (Childs, MS). It has also been recorded at the mouths of the Nuka and Etivluk rivers (Kessel and Cade, *loc. cit.*), both tributaries of the upper Colville at elevations of 1800 and 1200 feet, respectively. The species breeds along the lower Etivluk and probably also along the Nuka and other parts of the upper Colville drainage. Localities mentioned here and elsewhere in the text are shown in figure 1.

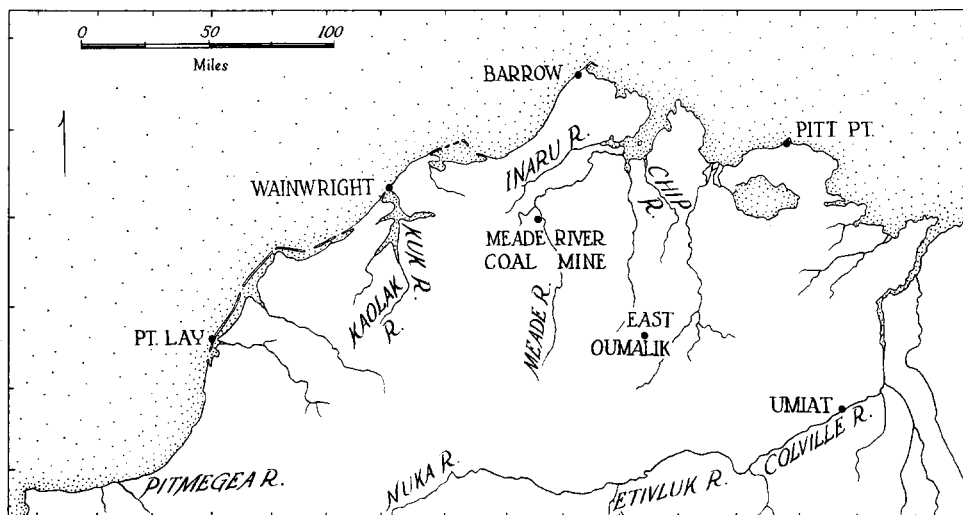


Fig. 1. Map of northern Alaska showing localities mentioned in the text.

Near Barrow, Pectoral Sandpipers usually appear in the first week of June. Our records are as follows:

Year	First day of field work	Earliest record
1951	June 7	June 7
1952	May 29	June 9
1953	May 27	June 1
1955	May 29	June 6
1956	May 29	June 6
1957	May 30	June 1

The late date for 1952 is explained by persistence of late snows which delayed arrival and onset of breeding in several species. Given a mild spring and early exposure of the tundra, Pectoral Sandpipers may appear several days ahead of our earliest record. In 1898, Pectoral Sandpipers were taken at Barrow on May 30 (Stone, 1900:26). In 1914, at Demarcation Point, to the east of Barrow and close to the Yukon border, Brooks (1915:384) recorded first arrivals on May 23, some of which were said to be associating in pairs. In 1949, at Wainwright, Rausch collected two males on May 25 and 26, respectively. In 1957, along the Meade River 60 miles south of Barrow, a male already displaying was observed on May 31 (Maher).

Nesting begins in the second week of June and continues for one month, with some nestings initiated as late as the second week of July. Small partly grown young may be seen from the second week of July through the second week of August. In the interior, and to the southwest toward Cape Lisburne, this schedule is shifted forward somewhat (see fig. 3). Flocking occurs most conspicuously (pertaining to both numbers and frequency in the last week of June and in the first half of July; it occurs irregularly until the third week of August, after which only straggling small flocks are seen. The latest dates of occurrence recorded by us are September 1 at Barrow and September 3 at Meade River.

Field experience over a series of years leads both T. J. Cade and me to regard the Pectoral Sandpiper as the most generally distributed and probably the most abundant sandpiper on the arctic slope of Alaska. In many places it is or can be, depending on the year, the commonest species.

Large year-to-year differences in relative abundance may occur. Near Barrow, for example, the species bred abundantly in 1953; but it did so sparsely and was scarce after mid-July in 1952, and apparently also in 1958 (Cade). In the interior, such variation appears to be of a lesser order, and at Umiat the Pectoral Sandpiper is common and quite consistently so. Thus, in five out of seven seasons between 1949 and 1958, it was regarded as the commonest species (Kessel and Cade, 1958; also our records). In 1957, early in the breeding season, the Pectoral Sandpiper was considered the commonest shorebird species at Meade River Coal Mine (Maher) and near the Inaru River (Cade); similarly it was the most abundant species later in June at Wainwright in 1955 (Childs) and 1958 (Brock). It was noted as one of the commonest shorebirds at Point Lay and Pitt Point in 1957 (Cade), and along the Pitmegea River in 1958 (Childs), even in mid- and late July, after males had left; at both localities frequent calling and distraction displays of females indicated presence of young scattered over the tundra.

The Pectoral Sandpiper is the commonest species in many places even though some smaller species of sandpipers associated with it, such as the Red-backed and Semipalmated, are also widely distributed and regardable as common, at least near the coast. These latter species occur more scatteredly, in pairs tending to remain intact through the breeding season, and they apparently hold territories larger than those of the Pectoral.

HABITAT

The Pectoral Sandpiper, like most bird species which breed on the coastal plain, is active over a variety of tundra habitats which are intermixed in mosaic fashion over a terrain that is flat, poorly drained, and usually wet. Near Barrow, several variants of low grass-sedge cover prevail over these habitats (Britton, 1958), and near Umiat the main habitats are grass-sedge marsh of a type similar to one at Barrow but with lusher, taller growth, and cottongrass tussock-dwarf shrub tundra of a type which becomes important about 30 miles south of Barrow. On both of these areas, shores of lakes and ponds are also visited, especially when these are on or adjacent to areas of the types just mentioned, where territorial and breeding activities take place.

Near Barrow, territorial males settle on low, flat wet marsh if there is available some promontory or raised area such as a mound, hummock, or low shelf. They settle more frequently on higher ground with a more varying microtopography as along low ridges separating marsh flats or on uplands with ponds and marshy basins of varying size. It appears that in choice of nesting area, females are not attracted to high ground, and nesting near Barrow occurs in all variants of tundra vegetation as long as there is a continuous cover of grass or sedge and the nest site is a relatively well-drained one.

This implies that members of a pair do not associate through the nesting period. Many aspects of the pair relationship in Pectoral Sandpipers require study, but there are several lines of circumstantial evidence indicating that the relationship is brief. Thus, a female with clutch completed does not associate closely with a male. Males do not share in incubation, and they leave the breeding grounds before most eggs are hatched. Females establishing nests evidently avoid the areas heavily utilized by territorial males, for, as data in ensuing sections will show, the number of females nesting on or near plot 1 was only a small fraction of the number of females observed associating with males settled on that plot. Consequently, there is reason to believe that in habitat distribution, nesting females are more widely dispersed than are territorial males. Over the five breeding seasons for which census data are shown in figure 2, there are but five instances of females nesting in the vicinity of male territorial sites; these are marked by + signs. In each instance both male and female were noted near such sites only on the last date given for the male; but in each the female remained present through the first half of July. It may be significant that these nestings near or within male territories are all relatively late.

BREEDING DENSITIES NEAR BARROW

Breeding densities of territorial males on plot 1 are shown in figure 2. This plot, 20 x 2 acres, was located along a low ridge separating extensive marshy tundra and clusters of small ponds and polygons on either side. With relatively high ground continuing along the axis of plot 1, this area provided optimal habitat for territorial males. Densities of established males in the five seasons along with numbers of nesting females remaining on their respective areas after local males left are as follows:

	1951	1952	1953	1955	1956
Males					
Two or more records	6	2	8	4	3 (4?)
One record only	1	3	4	1	2 (0?)
Females	0	0	3	2 (3?)	0

Thus, using records for territories found held on at least two dates, densities ranged from two to eight males over the plot of 40 acres; if we add single records to these, the densities ranged from 5 to 12.

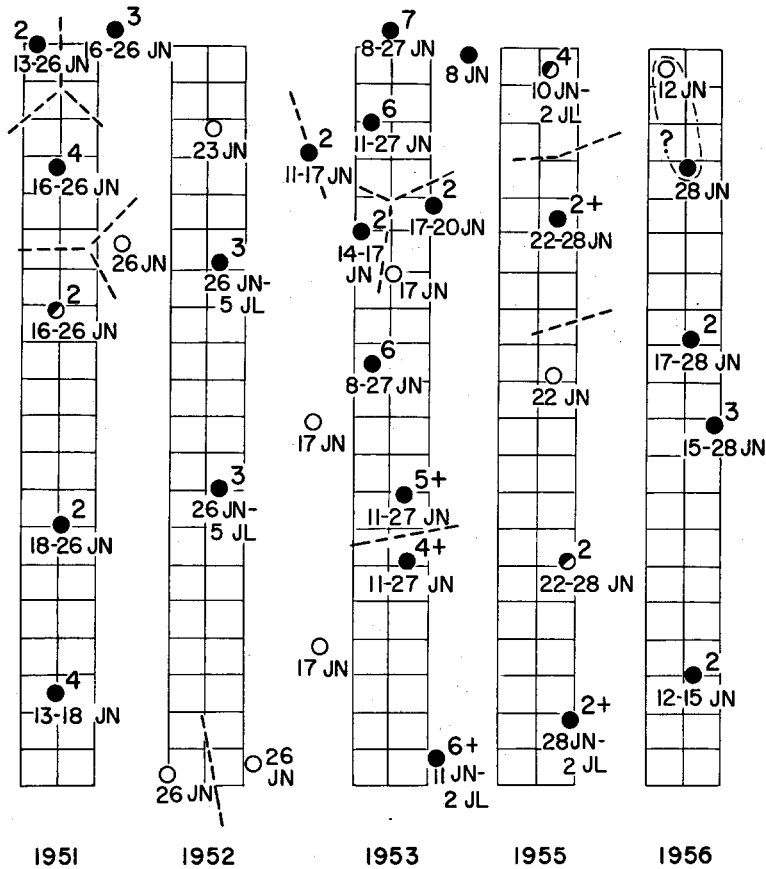


Fig. 2. Occurrence of established breeding male Pectoral Sandpipers in five summers on a census plot of 40 acres (plot 1 of text) near Barrow, Alaska. On each 20×2 -acre grid, circular symbols indicate location of settled males: a solid dot indicates a male observed associated with a female at least once; half-shaded circle, a male seen near a female at least once, but association not close and leaving doubt; open circle, male not observed with a female at any time. The interval over which a territorial site was found occupied is given below each symbol, and the number of records (separate dates) on which a male was present is given to the upper right of each symbol. A + sign indicates territorial sites near which nesting females were present in late June and July. Broken lines indicate territorial boundaries between neighboring males.

These figures, however, must be lowered to get closer to true density because they include individuals whose territories were only partly contained within plot 1. From the spacing of males shown in figure 2, and taking into account evidence on territorial chases and evidence for boundaries on all plots censused, territory size is estimated to be from 10 to 15 acres. In 1953, in the densest population recorded, territories averaged smaller, some being no more than 6 to 8 acres. In that year, more use was made of the lower portions of the gentle slopes bordering plot 1 along its long axis; more males were also established on the neighboring low wet marsh of plot 3 (see beyond).

On plot 2, although the habitat averaged lower and wetter, the overall mosaic included islands of high ground, and breeding densities did not differ significantly from plot 1. On plot 3, however, breeding densities were lower because of the extensive flats of

low marsh. Nevertheless, these additional plots reflected the differences between 1951, 1952, and 1953 found on plot 1, as the following tabulation of occupied territories shows:

	1951	1952	1953
Plot 3 (86 acres)	2 (4?)	0 (2?)	7
Plot 2 (20 acres)	2 (3?)	2	4
Plot 1 (40 acres)	6 (7?)	2 (5?)	8 (12?)
Totals	10	4	19

From these data, maximal densities on varied tundra providing sufficient islands of relatively high ground may be estimated at 10 to 15 breeding males per 100 acres. The lowest density observed, in 1952, was three per 100 acres. Five or six per 100 acres is probably more usual or "average."

The figures indicate number of territories of which at least parts were included with the area of the given plot, and those in parentheses give the number of territories if we include birds recorded in territorial display and/or paired and apparently attached to an area on but one date. The totals indicate better the magnitude of differences in local breeding numbers among the three years than do the data for plot 1 alone. This difference is three- to five-fold depending on whether or not one takes into account the maxima indicated in the parentheses.

BREEDING SEASON

A total of 76 egg dates is available for the Barrow area (fig. 3). Included are a few from localities along the coast to the east as far as the Colville River. An additional 29 are available for inland localities to the south and southeast of Barrow, along the Meade and Chipp rivers (fig. 3). These localities are 60 miles south to 75 miles southeast of Barrow, within the belt of the first low hills in the direction of the Brooks Range.

The distribution of dates for complete clutches shown in figure 3 are based on dates on which the clutches were taken; that is, no adjustment has been made to bring them forward within some modal interval assumed to represent the main period of laying. Nevertheless it appears that near Barrow most clutches are laid in the interval from June 21 to 30. All known clutches consisted of four eggs. The incubation period is at least 23 days (Conover, 1926:308), and the period when most young are seen near Barrow is from July 16 to 25. When allowance is made for a few days spent in or near the nest by young just hatched or hatching, the interval between modal periods of egg laying and of young recently hatched but already moving over the tundra freely is about right.

Clutches can be started as late as July 8. Thus, Bee (1958:187) reports taking a female on July 9, 1952, which had an egg in its oviduct plus two enlarged ova with diameters of 20 and 10 mm. probably representing the third and fourth eggs of a clutch. One complete set obtained along the Chipp River on July 15, 1933, was labelled "eggs fresh"; another, "perfectly fresh," was taken at Barrow on July 6, 1883 (Murdoch, 1885:112).

Prior to June 15, near Barrow, the incidence of first eggs is probably low. Most of the dates in figure 3 are based on sets taken in the years from 1926 to 1938, and of the eight sets taken prior to June 21, all but three of those in the interval 16 to 20 were obtained near Barrow in one season, 1938. Early records for 1938 suggest that the summer might have started especially warm that year, but temperature records of the Weather Bureau for Barrow do not bear this out.

There is other evidence to support the statement just made regarding infrequency of clutches started prior to the 15th. Murdoch and his coworkers (1885) obtained 18

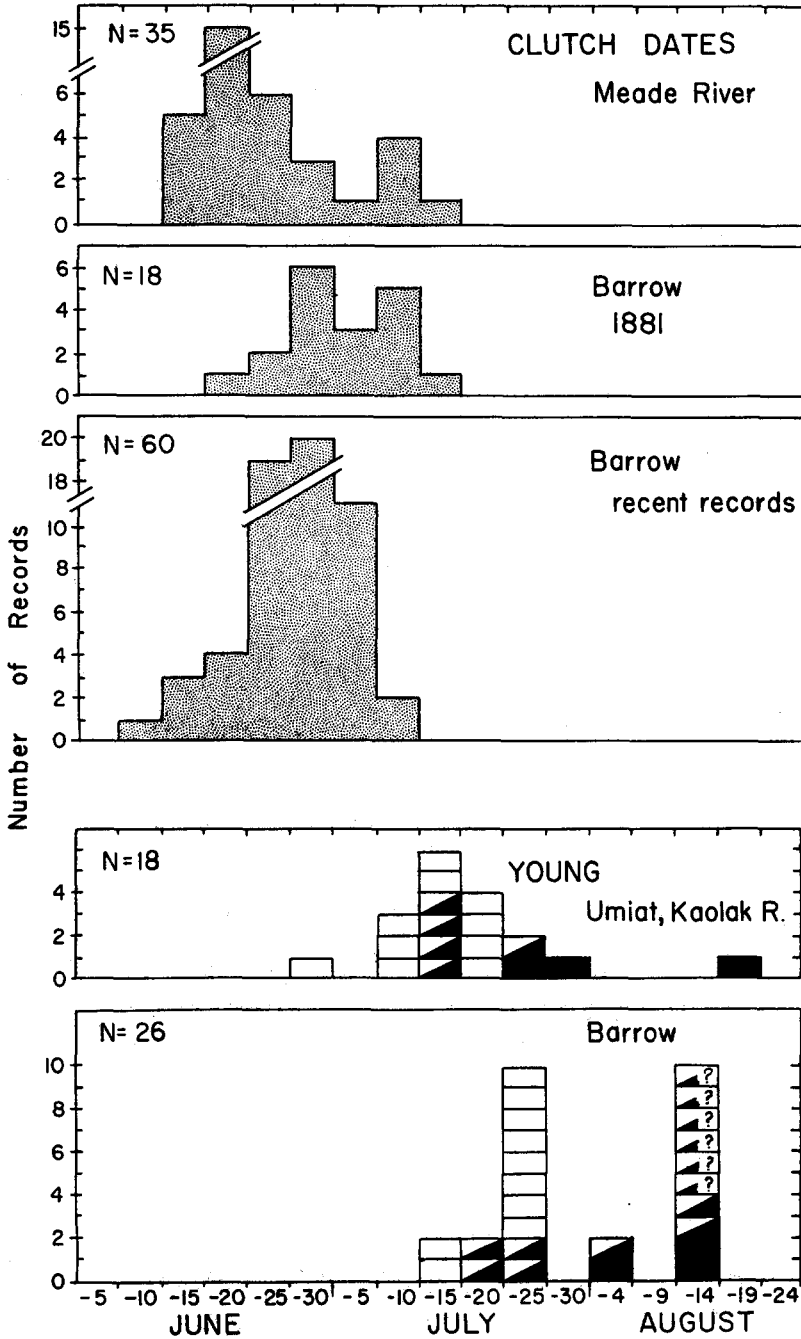


Fig. 3. Breeding season of the Pectoral Sandpiper in northern Alaska shown by distribution of dates for clutches of eggs and for young observed or collected. Dates are grouped in five-day intervals: June 1-5, 6-10, etc. Open blocks indicate young recently hatched; partly shaded blocks, partly grown young; solid blocks, young fully grown or almost so. For recently hatched young, each record represents one individual or, if two or more siblings were observed, one family group. (The year "1881" should read 1883.)

clutches in 1883, a sample from one season and one locality now in the United States National Museum and not bettered as a single-season sample by any data I have from all the egg collecting in northern Alaska since then. The earliest collection date was June 20, although earliest actual laying on the basis of large embryos in one set taken June 28 was about June 10; the latest collection date is July 12 (*op. cit.*:112). [Murdoch (*loc. cit.*) states "most of the eggs obtained were collected in 1883," but according to records sent to me from Washington, the 18 sets discussed here were all taken in that year.]

Thus, the breeding season in 1883 (see fig. 3) was evidently somewhat delayed over the normal timing, but as ensuing sections will show, such variation is probably not unusual. Seasons in which breeding near Barrow averages earlier than shown by the distribution of recent records in figure 3 must be rare.

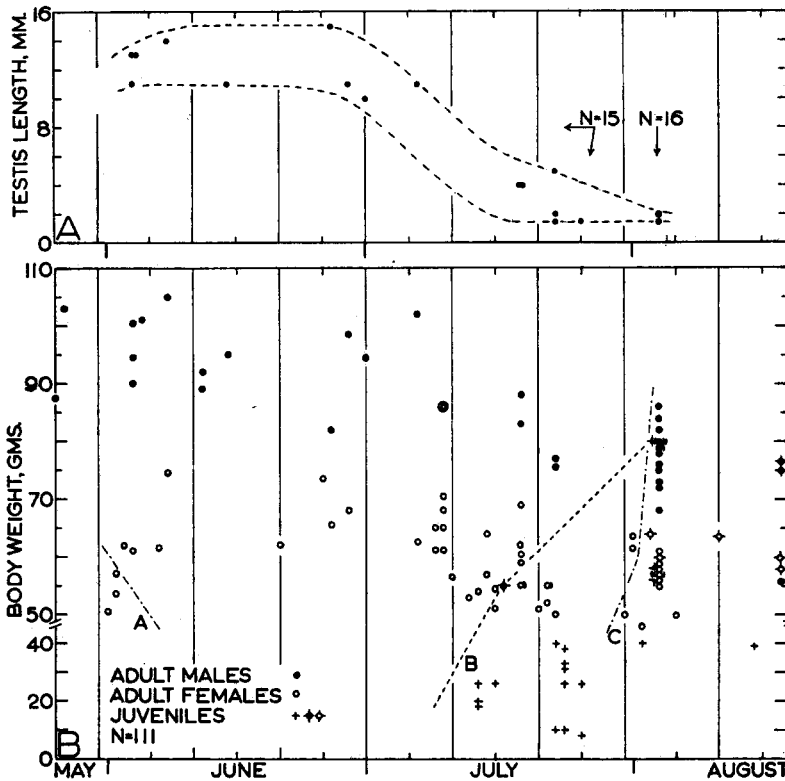


Fig. 4. A, seasonal change in testis size (length of left testis) of Pectoral Sandpipers. Measurements from the sample of 16 for early August include both adult and juvenal individuals, but none exceeded 2 mm.; all other males were known adults.

B, variation in body weight showing gradual decline for adults through the summer. One exceptionally heavy female, in egg-laying stage (July 9), shown by a double circle; all other adult females in pre- or post-laying stages. All weights taken from specimens collected on breeding grounds from foothill districts (Umiat, Kaolak River) north to coast, except three females to left of line A taken at Anaktuvak Pass (see text). Line B shows the approximate trend of appearance of earliest young at successive weight levels; hence all records of juveniles fall on this line or to the right. Line C: to the left, adults and juveniles are separated; to the right, all known juveniles (12) are indicated by symbol, but the remainder (28) includes both adults and juveniles not aged satisfactorily when collected. Note change in scale at 50 grams.

Taken in body, the data indicate that near Barrow egg laying may begin as early as June 5 or 6 (earliest completed clutch taken June 9), but that most clutches are started between the 15th and 25th of June, while latest clutches may be started as late as July 5 to 10. While known dates of laying would be required to establish the maximal interval over which clutches can be started in any one year, from the data at hand it seems reasonable to guess that this period is about 30 days.

Over this period plus a week or so in early June, males may breed, as is shown by data on seasonal change in testis size summarized in figure 4A. They arrive on the breeding grounds with testes fully developed or almost so. Testicular regression begins in early or mid-July and is completed in about a month's time, prior to or during the first laps of migratory movement.

In the interior, snow melt and onset of spring is earlier, and as a result some differences in timing of breeding occur between there and the coast. Figure 3 shows no significant difference in the total period over which clutches were found, but the modal period for egg laying in the population as a whole is evidently earlier. The median date for 29 clutches from the interior falls in the interval from June 15 to 20, whereas for the two Barrow distributions, the median dates fall in the interval from June 26 to 30. A similar difference appears in a comparison of the dates on which young have been seen or collected (fig. 3). There is thus probably as much as a week's difference in the population timing of breeding activities between the tundra bordering the arctic coast near Barrow and that 50 to 100 miles inland.

SUMMER WEIGHTS

Weights from northern Alaskan specimens are graphed against time in figure 4B. For both sexes, it appears that maximal weights occur through June and that there is a gradual decline in average weights through the summer. Females in egg-laying stage would be substantially heavier than those comprising the sample discussed here. One such female weighed 86 grams; the recorded maximum otherwise, for June females, is 75. The trend in summer weights is summarized as follows:

Sex	Time interval	Sample size	Range	Mean with standard error
Males	June	11 adults	82-105 gms.	94.6±1.9 gms.
	July	5 adults	75-102	85.0±4.9
	August 1-5	16 ads. & juvs. ¹	68-86	78.2±1.0
Females	June	8 adults	61-75	65.9±2.0
	July 1-15	14 adults	51-71	60.2±1.2
	July 15-31	13 adults	50-69	57.5±1.6
	August 1-5	13 ads. & juvs. ²	46-64	56.7±1.3

¹ Males weighing less than 65 grams excluded; these are assumed or known to be juveniles incompletely grown, some possibly also missexed.

² Females as low as 46 grams included in this distribution because known adults of this sex weighed as low as 50 grams in late July.

Three low weights from females taken at Anaktuvak Pass in the first days of June and almost certainly in migration are not considered to be significant exceptions to the earlier comments about June maxima since it is likely that migrants heading for the coastal plain have ample opportunity to gain weight in the days or perhaps even weeks when they are already in Alaska, advancing northward as weather permits.

Also shown in figure 4B are weights of juveniles at various stages of growth. From these data it is seen that the main growth period for the population of young is the latter half of July and early August and that by the first of August, some young have already entered the weight ranges for the adults then present.

The data give no indication of premigratory weight gain in adults or young through late July and August. To whatever degree such gains occur, they evidently do so south of the breeding grounds. This is supported by weights of Pectoral Sandpipers collected on August 5, 1957, in southern Manitoba, at Delta (just north of 50° N lat.). All were adults.

	N	Range	Mean
Males	8	99.5-141.0	117.6 gms.
Females	3	56.0- 99.5	71.2

On the basis of July weights for males and late July weights for females given above, these southern Manitoba records yield estimates of weight gains of 38 and 24 per cent, respectively.

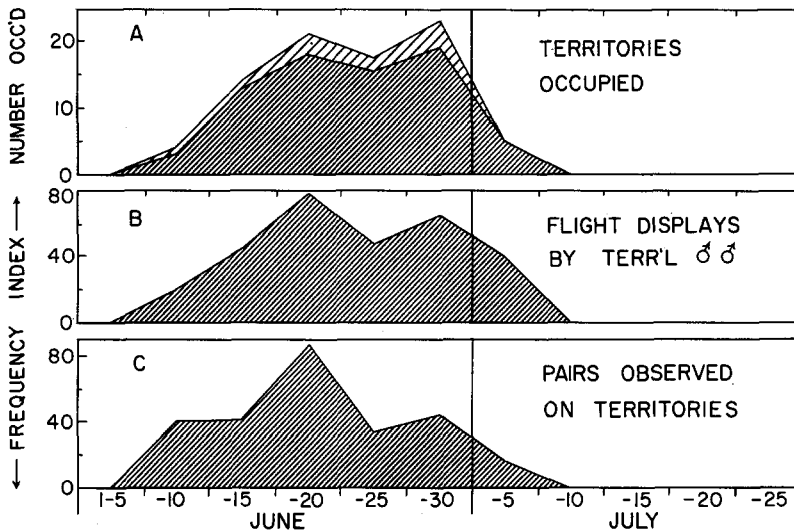


Fig. 5. Timing of certain breeding activities of the Pectoral Sandpiper near Barrow, Alaska.

A, change in number of territories occupied, based on a summing of all records from census plots for five years. Each territory or locally settled male is represented by only one entry in any five-day interval; those males or sites for which there are two or more records in a given breeding season fall within the densely barred portion of the graph, while males for which there is but one record in a given breeding season are shown by the lightly barred band.

B, change in frequency of flight displays of territorial males, based on records from census plots adjusted for varying amounts of sampling effort (see text).

C, change in incidence of pairs observed on territories occupied earlier or later (or both) by males; data obtained as for graph B.

SEASONAL TREND IN NUMBERS IN RELATION TO BREEDING SCHEDULE

Numbers increase through June, but the data (figs. 5 and 6) suggest two waves of arriving birds—not literally “waves,” but rather statistical modalities in numbers recorded indicating the chief periods of change in local abundance. The bulk of the breeding population settles down in the course of the first three weeks. With the second “wave,” there appears to be additional breeding effort, but it is not clear to what degree such effort is the first for the season as against reneating. To varying degree between

years, this second wave apparently also includes nonbreeders. These questions will be considered further after the normal schedule is described.

In the first weeks of June, the arriving members of the breeding population spread inconspicuously, there usually being no large flocks or local concentrations preceding dispersal for breeding such as characterize the Red Phalarope. Early arrivals may concentrate on islands of exposed tundra along the coast (Murdoch, 1885:111); but the main movement of sandpipers along the coast eastward and their spread over the tundra for breeding stations occurs by more or less continuing drift, weather permitting, of single individuals and small flocks that rarely exceed a dozen individuals, and usually number around six.

By the end of the first week of June territorial males are displaying and pairing starts. There is typically an interval of at least a few days between arrival and onset of these activities. With poor weather, only a fraction of the males display early and then relatively infrequently. With warm weather, and especially by mid-June, one gains the impression that males still on the move and encountering already settled and aggressive males are ready themselves to settle down given suitable sites. The seasonal build-up of display and pairing is shown in figure 5. On the basis of area-related samples taken in the course of five years' census work (see methods), the numbers of males settled on territories is shown to increase until the 15th, and the amount of display activity reaches a peak near the same date. This interval of maximal display correlates with both the end of the main period of territorial establishment and maximal frequency of pairs observed as such on occupied territories (fig. 5). Such pairs were also recorded in the interval from June 8 to 15, and some nests do get started in that interval in at least some years; but pairs were observed most frequently in the interval from June 16 to 20 just prior to the main period of egg laying (fig. 3). This evidence suggests arrival of females somewhat later on the average than that of males; it may be added that a few small flocks consisting only of females and evidently in transit were noted on June 9 and later over the several years. Females may, however, arrive as early as males (Stone, 1900; Brooks, 1914).

After June 15, territorially stationed males prevail over the tundra until the last days of June. The two latest records of territorial chase or conflict are June 27 and July 1. The latest record of both territorial occupation and display is July 5. Near the end of June and in the first week of July, males leave rather abruptly. Flocking of males then ensues, but without conspicuous local waves or concentration, and the bulk of them is gone by the 15th. In both 1955 and 1956, when the departure of males was particularly watched, on a population basis they were in effect gone by the 11th. Males may be present scatteredly until the first days of August; our latest specimen record of an adult male is July 22, but Bee (1958:187) took at least one near Teshekpuk Lake as late as August 3.

Thus, after July 5, the dispersed members of the breeding population consist only of incubating females, and this is a period of relative quiet. Eggs hatch mainly in the second and third weeks of July, and young are seen most frequently in the last half of July. Partly grown young may still be seen, however, in the middle of August. By the end of July local females that have earlier attended young are leaving, and most of them depart before the 10th of August. Much of this exodus, as Murdoch (1885:111) noted, occurs without flocking; they "slip quietly away." Males in transit in mid-July are joined by females whose nesting failed or was completed early so that mixed flocks may be seen then, and such flocks are most frequent in the second and third weeks of July. They usually consist of less than 20 individuals, but occasionally they reach 50.

Juveniles still on the breeding grounds in late July and August comprise at first the

bulk and later virtually the whole of such flocks as are seen. Near Barrow, these flocks occur, but only irregularly. If they are present, they remain locally only for a day or two, if that long, and in some seasons, no major movements or local concentrations are noticed at all. In part this may be because over the Barrow area, which projects northward in one sense as a broad-based peninsula, there is not the concentrating or funneling effect on birds in fall migratory passage such as occurs in the spring, and anyway, the main migratory paths may be overland, through passes of the Brooks Range, rather than coastwise. The late summer arrival, in Manitoba, of adults in late July and juveniles in late August (Hamilton, 1959) in general agrees with the chronology on the breeding grounds.

As is shown in figure 5, virtually no flocking occurs in the interval from June 21 to 25. On census plots none was recorded at any time in the five years of study, and there is but one mention otherwise of flocks in this interval in notebook records of any observer. This was a flock of seven males noted on June 25, 1955, the earliest such record. After the 25th, flocking is resumed and reaches a minor peak in the interval from July 6 to 10 which indicates the main exodus of males. There is an interval of relative quiet as nesting females are completing incubating or attending young. Flocking becomes commonplace from mid-July onward. Censusing stopped after July 20, but were data available over a period of years, the index of numbers of birds in flocks would tend to be high, but varying widely from year to year, not only in level of abundance but also as to the intervals of the last six weeks of the summer in which such flocks were witnessed.

Thus, for the effective breeders there are six populational phases: (1) the early summer rise in numbers of settled birds, preceded by only a low level of flocking (June 1-15); (2) the interval of relative stability, when territories are occupied in greatest number, pairing occurs and most nesting is started (June 15-30); (3) the desertion of territories by males when flocks may be seen which consist only or mainly of males (June 25-July 10); (4) the completion of incubation by females now alone and the care of young (chiefly July 10-31, occasional ones so occupied to a later date); (5) the departure of adult females, accompanied in varying degree by late occurring males and later by juveniles already flying (July 15-August 5); and (6) the exodus of juveniles (July 25-September 1). From dates for breeding events given in various reports from arctic Siberia, it is clear that the schedule is similar there. The only exception is that fall departure may be later. Thus, Pleske (1928:249) writes of "*Heteropygia maculata*" [= *E. melanotos*] migrating past the Kolyma delta until September 22, with some late birds seen on October 3.

Against all this 1952 stands as an exception. Snows persisted and the summer began a week to ten days late. Although the first Pectoral Sandpiper was observed on June 9 and the first display on the 12th, no locally settled male was seen on the census areas until the 23rd, and the majority arrived after that date. The amount of flocking in the interval from June 26 to 30 was of the same order as in the other four years, but in 1952 this represented the bulk of the arriving birds from which only some established breeding territories. Thus, four of the five territorial sites used in 1952 were first occupied in that interval (fig. 2). Only two of these were found occupied more than once. All records from plots 2 and 3 also fall or start in the interval from June 26 to 30 and not earlier. The overall record for the five years (fig. 5) shows that of 29 territorial sites found occupied in two or more censuses, for 80 per cent of them the occupation began before June 20. Thus, not only were breeding numbers lowest in 1952, but such breeding as occurred began late. Interference of breeding by weather is known for various arctic birds, for example in *Calidris temmincki* (Southern and Lewis, 1938).

There then ensued an amount of flocking, from July 1 to 10, which was three to six times that witnessed in the same interval in other years, and considerably more than that witnessed in any other interval within the part of the summer when censuses were taken. After the 10th, however, the bulk of the birds left, and after the 15th they were scarce. In the interval from August 11 to 15, the first recently hatched young were observed, again showing lateness in such breeding as occurred. On August 19, Pectoral Sandpipers appeared in numbers—they were recorded as “common on the tundra today”; but after that date, only scattered small flocks were seen, the last on September 1.

The large numbers in the first ten days of July greatly exceeded numbers of males

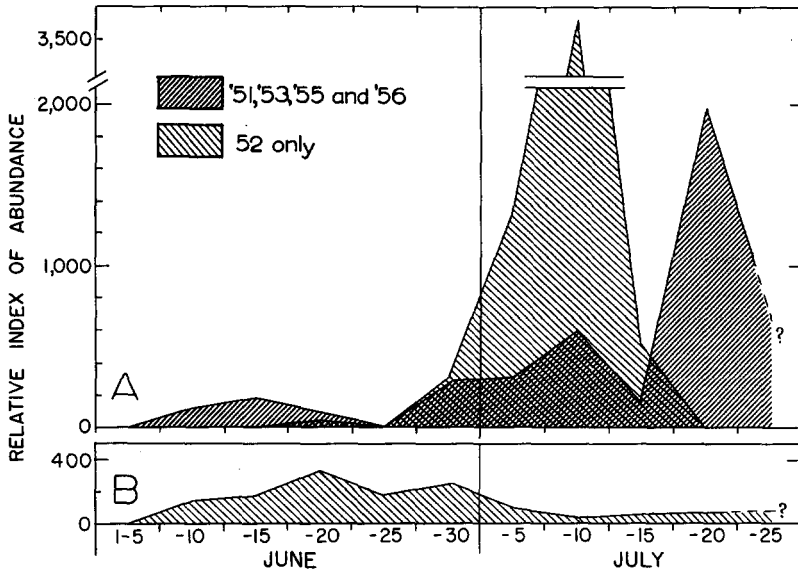


Fig. 6. A, changes in amount of flocking of Pectoral Sandpipers on their breeding grounds, based on records from census plots, (see text for explanation). The usual trend is shown by the combined records for four seasons; an exceptional year (1952) is shown separately.

B, change in relative numbers of settled breeding birds, also based on records from census plots and graphed similarly so that change in proportion of settled, spaced breeders to individuals in flocks (A) may be seen.

when these desert territories in this interval in typical years, and they occurred at a time when females are attached to nests; hence, they can be considered to have consisted mainly of nonbreeders. Supporting this conclusion are the facts that the late snows delayed onset of breeding, that breeding densities over the five-year period were lowest in 1952, and that postbreeding numbers were low.

The ingress, in 1952, of large numbers in late June and early July may be an extreme manifestation of a sequence of events which occurs to lesser degrees in other years. Thus, in each of the other four years, flocking occurred in the interval from June 26 to July 10, significantly ahead of the time, even in the compressed schedule of the arctic summer, when Pectoral Sandpipers left their territories and breeding was concluded. The membership of such flocks probably includes mainly nonbreeders and others whose earlier efforts may have failed, but some at least evidently begin breeding as late as did the majority in 1952. This last point is supported by the following lines of evidence: (1) Over 50 per cent of the clutches are normally completed before June 25, an estimate

based on numbers of clutches produced by the 25th plus half of those found in the interval from June 26 to 30 (fig. 3). Yet territorial occupation continues through the last week of June without decline in anticipation, as it were, of the change to come in the first days of July. (2) Frequency of display and incidence of pairs observed on occupied territories also remained moderately high through the interval from July 1 to 5, after which neither display nor pairs were observed. The data for the trends in these several behavior patterns even show slight rises for the interval from June 26 to 30 or July 1 to 5 over the levels just preceding, individually insignificant but collectively perhaps significant. (3) The only specimen evidence lending support to this interpretation of late entrants into the breeding effort is a female collected on June 28, 1956, which lacked a brood patch and which had ova up to 8 mm.; it was probably in pre-breeding state. Murdoch reports taking "perfectly fresh eggs" on July 6. The female mentioned on page 241, taken with an egg in its oviduct on July 9, 1952, may also have been an individual which had not bred earlier.

Although no statistical significance can be attributed to the slight late upswing in breeding activities shown in figure 5 without more and better samples of such events, I do think it justifiable to say at least that the incidence of these events remained at a high enough level into the first week of July so that one concludes that some breeding is not initiated until quite late. A question remains, however, as to the degree that such late breeding effort is significant populationally or even characteristic of the Pectoral Sandpiper in general over its northern Alaskan breeding distribution. Clutch dates from the interior (fig. 3) suggest that some breeding is initiated as late as it is along the coast; but because weather usually permits the onset of breeding earlier in the interior, late breeding may not be so important on a populational scale as it is near the coast. Such importance may derive not only from wider variation in weather affecting breeding success of the population already there, but also from late arrivals which, if they settle at all and breed, probably do so more along the coast than in the interior because drifting of late birds tends to occur most in the coastal belt where seashore, deltas, lake margins and marshes provide maximal habitat for flocks.

DISPLAYS AND CALLS

In our observations of the Pectoral Sandpiper, no attempt was made in the field to study behavior *per se*, and therefore we have no record of the repertoire of display actions and the usual vocalizations accompanying any of them. We can, however, describe the commonest actions in territorial behavior forced upon our attention in the course of censusing and other field work. Several displays which figure in courtship, recorded several times by the author and his associates, are also worth describing so far as our brief notes permit. This information falls short of the standards demanded by modern ethology, but on the other hand, we do seem to have a great deal more information about the Pectoral Sandpiper on its breeding grounds than has been available heretofore. The account of displays in Witherby *et al.* (1940) and Dementiev *et al.* (1951), for example, are only approximately correct, and then only from a qualitative standpoint as they are not developed from any sustained experience with the species over a series of seasons.

Routine call-notes are described by Bent (1927:176) and Witherby *et al.* (1940:260). We have nothing to add to these accounts with the exception of a threat note used by territorial males which is described in the section on territoriality (page 253).

Those displays recorded in our notes several times and in most instances witnessed many more are described below, but only in enough detail to show their more conspicuous features. Variants recorded as isolated instances are identified as such.

1. The most frequent display of the territorial male is given in flight on a course merely a few feet above the ground and over distances of 400 to 500 feet. The flight speed is slow, the wing beat usually shallow and broken, high over the body. There may be brief glides. The chest area is swollen so that the streaked bib stands forward of the white under parts. During flight, the male hoots regularly, two to three times per second. The note is a double *who-u, who-u, who-u*, usually given ten to twenty times in a single series, and occasionally as many as 28 (2 records). The wing beats may be deep and slow by comparison with normal flight, suggesting a butterfly. Then they are synchronized with the hoots, which are given at the slower tempo of about two per second, so that, apparently, the main hoot is given with a downstroke, the second syllable with an upstroke. With each downstroke, the head bobs up. In its strongest and loudest form, the display includes this type of wing beat. Toward the end of a display flight, the note may become just a single-syllabled hoot, and then the bobbing of the head weakens or stops. The double-parted hoot may also be given in gliding flight, or in a glide broken intermittently by quivering of wings, and here also the head will bob with the notes, but not so strongly as when the deep wing beat is used. The hoot is a low, loud, far-carrying note, although in windy weather the sound may be lost easily. The tempo is usually sustained; sometimes it increases slightly as the flight proceeds. The flight may be ended with a direct drop to the ground, or with the wings set horizontally, the bird soaring up slightly in a glide, then setting down. This display has been witnessed at Barrow as early as June 9 and as late as July 5. It is observed earlier in the interior and along the arctic coast at lower latitudes (May 31 at Meade River; May 30 at Pitmegea River). Nelson (1884) and Buturlin (1907), in describing the flight display, state that the male rises high, 30 feet above the ground or more, and hoots during a gently gliding descent. This was not the style of flight we found usual in northern Alaska.

2. A ground display in which the same note is used appears to be the usual courtship display. Typically the male is about six or eight inches behind the female and to one side of her. His chest is inflated, his wings are dropped slightly, and his tail is held vertically so that the lateral white feathers show. As he follows her, usually in short runs, less frequently at a slow sustained pace, he hoots regularly. The hoots are usually softer than those given on wing, but with chest swelled and inflated periodically as in the flight display. Instead of short runs the male may prance intermittently and even sway. In this and more terminal parts of the display (see beyond), the prance appears to be a ritualized short chase and occurs when the female is standing or when she pauses, thus frustrating the periodic advance of the male toward her. This entire performance has been likened to that of a Prairie Chicken (*Tympanuchus cupido*). Nothing like it has been witnessed in any *Erolia* or near-*Erolia* observed by us in northern Alaska.

It is stated by Nelson (1884), and this is still the latest authority for more recent statements such as those of Witherby *et al.* (1940:260), that the chest expansion is the result of inflation of the esophagus. To whatever degree esophageal inflation figures, it is not the only mechanism expanding the chest. In the breeding male, there is a striking amount of subcutaneous lobular tissue, as Nelson himself also noted, and it appears that this acts to raise the chest to varying degree by congestion with lymph or possibly even blood. Sutton (1932:135) comments on subcutaneous "glands" of *melanotos* and their occurrence also in the White-rump, *E. fuscicollis*, noting that these had a rich blood supply. Thus, in *melanotos*, the chest may remain partly "expanded" for prolonged periods of time. A male resting on a mound will appear heavy chested, the lower edge of the streaked bib will stand forth from the white of the adjacent underparts, and he will show no sign of heavy breathing nor will he be making any sounds. The morphological basis of this display should be re-examined carefully.

3. What may be a terminal phase of pairing occurs when male and female fly instead of walk, the male displaying as in 2. The male follows the female about one foot behind and to one side of her, hooting periodically. The flight continues over 100 feet or more. Both sexes beat their wings shallowly in a quiver above the level of the body.

4. In a ground display which may be merely a variant of display 2, the female, standing still, is approached by the male with his chest inflated, hooting. When a foot or so away from her, he turns to one side with the tail then raised and almost vertical and with lateral rectrices and undertail coverts showing conspicuously. He gives a cough-like note, *craw, craw, ki-li-li*, the head bobbing with the first two notes which are harsh. As the notes are given, the male runs away from the female. The latter showed no response in those displays witnessed.

A variant between displays 2 and 4 suggests that the display actions after approach by the male depend on the reaction of the female. Thus, a male approaches, as in display 4, and in addition may lower and dip the body forward slightly so that the displayed tail is the more conspicuous. The female moves away. The harsh *craw* note is then given two or three times, followed by hoots alternated with short advances toward the female. After a pause, such a sequence may be repeated. In one instance it occurred three times and a vigorous chase followed.

The *craw* note was observed on one occasion to be given three times by a male as he flew to a grassy mound and chased a male longspur from it. This suggests an aggressive component to the displays combined here under 4 as against 2, in which the action of the male is more solicitous and if any notes precede the hooting, they are weak and rather high-pitched. In the frequently windy weather of the Barrow region, soft notes are difficult to hear.

5. At the close of a display, the male may compress his plumage and raise his head and body rather abruptly becoming tall and slim. In this stance, the tail is in normal position. One record suggests a partial transition, the male slimming somewhat but still holding his tail up, prancing his feet and holding his bill open (sound, if any, not heard). In this instance the female took wing and the male followed.

6. A flight display without vocal accompaniment is given by the male when he flies low over his territory, in a straight line or in a semicircle, intermittently fluttering his wings shallowly and producing a *whirr*-ing sound. In this performance he may fly up slightly, then glide, thus following an undulating path. The few records we have of this behavior suggest that such flights alternate with hooting flights as a male crosses his territory or when he is returning to his favorite mound-post after a hooting flight. Also, it appears that this flight-glide alternation is peculiar to males on territories.

7. A raised-wing display is given by individuals on the ground, when scattered in small loose groups and not yet territorially dispersed. One or both wings may be raised in address to another individual. In a particularly strong expression of the display, both wings may be held up while the bird moves a short distance toward another individual. The records are too few and brief for comment on sexes and sizes of groups or details of actions. But it may be added that this display was observed only a few times and only in the first half of June (latest record, June 16). From comments on this type of display by Armstrong (1947) and by authors he cites, it appears that it is a mild challenge display, but it may become more vigorous, with both wings used, in aggressive supplanting as described by Hamilton (1959:167). Our observations along with those of Buturlin (1907) suggest that in *melanotos* the raised-wing display is used in the early part of the courtship period. In some shorebirds, raised-wing actions are also incorporated into ritualized displays, in pairing and mating, for example, in *Calidris*

temmincki (Southern and Lewis, 1938); but none of us has ever witnessed this in the Pectoral Sandpiper. This may perhaps be correlated in part with the circumstance of short-term pair relation in *melanotos* by comparison with species of *Erolia* in which the pair unit persists and in which raised-wing displays ("greeting signals") occur more frequently. Our finding raised-wing display rare in *melanotos* is worth special emphasis because the summary by Witherby *et al.* (1940) suggests that raised wings may figure in usual displays as they do in smaller species of *Calidris* (*Erolia* and *Ereunetes* of Americans' usage), but this does not appear to be true.

8. A strong distraction display is given by the female near a nest or near young. This has been observed many times. No such action has been seen by us in males.

TERRITORIALITY

Territoriality of the Pectoral Sandpiper is based on the male who isolates himself on an area used for pairing and probably mating and for feeding and roosting by the male and also by the female in the interval of their association. Nesting typically occurs away from male territories; if it occurs on an area used by a territorial male, the occurrence appears incidental to the presence of the territorial male somewhere in the vicinity, as the female goes about her routines alone.

Over large areas of upland tundra such as occur south of Barrow, where territorial males are established one next to the other and their hooting on quiet days in the middle of June may be heard everywhere, it seems certain the territories are self-contained except for marginal areas where local topography or positioning of water bodies buffer them so that overlap in use of feeding areas may result. But this matter requires further study, as in some situations it appears that males may feed on low marshy flats adjacent to their territories which are not included within the defended domain of any neighbor.

Densities of territorial males on census plots have already been discussed. Territory size was estimated at 10 to 15 acres; in 1953, however, with a significantly denser population, territories were smaller. Spacing of males, intervals of territorial occupation and other data from plot 1 are summarized in figure 2. Where encounters between two neighbors showed a boundary to occur, this is drawn on the map as a broken line.

Territories are held certainly over periods of days and probably even over periods of a few weeks, at least by some individuals. But the latter point requires testing with marked birds. In summarizing occupation of territories, I have done this by using the span of dates over which each area was held (see fig. 2), and deriving the total number of such records for each five-day interval.

The general timing of territorial occupation for the population as a whole along with incidence of hooting displays on territories is shown in figure 5. Territorial activity reaches a peak in the third week of June, and correlated with this is a markedly higher incidence of pairs seen on occupied territories. The data for all three series of events, in conjunction with evidence on numbers and incidence of flocks discussed, suggest a second, but weak peaking of breeding activity in the last days of June and early July as stated earlier.

Evidence from plot 1 indicates that the females in general nest in areas other than those used heavily by territorial males. Thus, presence of a female in association with a male was noted on many more territories than the numbers of females remaining on plot 1 to nest (see tabular summary, page 239). It may be that this results from the special circumstance of a continuous axial upland (beach ridge) providing particularly choice sites for territories; that is, where the mosaic of tundra habitats provides a better interspersed of the main types, males may be more widely spaced and the females occur among them more frequently. Further aspects of the pair relationship

will be discussed later. It may added here, however, that at no time was any territorial aggression, even suggestively such, observed in females.

On their territories, males announce by flight displays, challenge neighbors and intruders with such displays, repulse intruders by chase, and maintain conspicuous positions on certain favored mound-posts; that is, all features of classical territoriality emphasized by students of birds are present in the Pectoral Sandpiper. I may add, however, without extended discussion here, that territory should be defined as an exclusive area, not merely a "defended" one. Armstrong (1947:273) states that "the essential feature of territory is defence . . .," and a number of authors preoccupied with territoriality in birds, before and since 1947, have pushed a similar view. This is to be noted particularly for Hinde (1956), who, in the latest review of the subject of territoriality, remarked that in its essentials, the concept of territory had not undergone any significant change since Howard (1920). The fundamental importance of territory lies not in the mechanism (overt defense or any other action) by which the territory becomes identified with its occupant, but in the degree to which it is in fact used exclusively by its occupant. This places proper emphasis on the degree to which a population partitions available habitat among its members, at density levels presumably leading to most effective reproduction. It may be claimed, therefore, that functionally territory is primarily an ecological phenomenon and not a behavioristic one, the special antics of birds and the crowds of people studying them having warped the emphasis too much and too long. It is for this reason that data on spacing and the discussion of exclusiveness of occupied territories in the Pectoral Sandpiper have been placed in the first paragraphs of this section, ahead of observations on actions used in maintaining that spacing.

The site of a settled territorial male, once found occupied, can be relocated with a male present again and again. After the breeding season is well started, and in poor weather generally, he will spend many hours quietly on his territory, resting much of the time on one mound or one of several such mounds favored as territorial posts. There he stands as conspicuously as the local terrain permits, and from there he watches his territory. He may be seen napping on such a mound. Feeding occurs in various parts of the territory, and in some instances evidently outside of it, also (see above). At times of chasing or courtship, the male may be seen on his post standing with chest raised and feathers of the back somewhat raised, alert to what is going on around him. I have, however, heard only the routine alarm note from a male on his territorial post, and that only occasionally. There is no vocal announcement from the ground by a territorial male, and special notes which might be significant in a territorial or courtship context have been recorded only rarely.

A male, whether alone on his territory or in association with a female, will take wing to chase an intruder and continue such a chase over as much as 200 yards before turning back. The height of such flights is usually no more than 10 to 15 feet. Observations of a sequence of such chases and turn-backs show that the boundary is a definite one, respected similarly by each of two neighbors, and that the chase rarely continues outside of the territory of the chaser. Encounters indicating fairly definite boundaries were seen on plot 1 but not on plot 3; on the latter, with extensive low wet marsh between areas preferred by males it is likely that the territories were buffered, and chases witnessed took place only occasionally between apparent neighbors.

In situations of territorial aggression, males give a special note which is a harsh, protracted swishing. It is flatulent and loud, seeming best described sometimes as a jabber, at others as a gurgle. This note is rarely given other than in territorial chase on wing. Once, after a male displayed twice on the ground following a female, he chased

her on foot a distance of several feet and gave the jabber note during this chase. It is heard most frequently in the first half of the breeding season in two sorts of situations: (1) when one or several males are closely chasing a female and are chased in turn by a male over whose territory they fly, and (2) when newly arriving birds in small flocks fly over or come to rest scatteredly on an occupied area; in the latter situation the established male may chase several members in succession, reacting similarly to males and females.

In routine announcement, the male takes wing and flies a few feet above the ground, hooting as he courses along one main axis of the territory, then dropping to the ground at the end of the flight. The display typically follows a straight line. He takes wing again and returns to his favorite resting mound. In the course of this return flight, what was described earlier under display number 6 may occur.

In challenges, the hooting display is used when an intruding male flies overhead and the occupant rises and flies beneath him, hooting as the two advance together. Or, the occupant may hoot and threaten (jabber) alternately. Here the occupant drops back to the ground as he reaches the margin of his territory, while the intruder continues his flight, perhaps changing direction when challenge occurs. If a chase occurs and the occupant turns near his boundary to return to his mound, he may display on the return flight.

The flight display is used more or less similarly by neighboring males challenging each other along boundaries or over area not yet partitioned. Two males fly parallel to each other, a few feet or even a few inches apart, and continue thus for a distance of several hundred feet with occasional sidewise movement of one toward the other, hooting most of the way. At the end of the flight they separate, apparently returning to their respective territories. At the beginning of the season when territorial limits are not settled, such challenge displays may occur successively between one male and first one, then another of his neighbors or prospective neighbors. Display challenging with one male coming over the territory of a neighbor only to be chased with display by the latter has been recorded as late as June 26.

Males may also challenge each other on the ground along a boundary. In the best recorded example (June 22, 1955), two males walked side by side, bodies bent forward, chests expanded, bowing every few seconds as they moved, but not giving any calls. They moved back and forth along the "boundary," with mild chase of one by the other intermittently. A short flight occurred to another position on the boundary, the display on foot was resumed, and this was repeated several times through a distance of about 50 feet until they moved well to one side, when a short chase ensued. They then separated and flew in opposite directions, each about 300 feet, and set down on their respective territories. During the alternation of ground display with short flight, one or both males would land on snow patches, thus becoming more conspicuous. This tactic is used in territorial conflict by several other species of sandpipers and by longspurs.

Actual physical conflict is rare among territorial males and was noted but once (June 11, 1953) between a male who alighted on a large snowbank and a second male which immediately approached from the opposite direction. A short fight ensued, whereupon they returned to their respective areas.

THE PAIR RELATIONSHIP

Observations reported here lead one to infer that the male Pectoral Sandpiper may be polygamous or that he establishes a short-term pair-bond but can repeat this several times through a season. The latter now seems to be more likely. Certain relevant observations have already been mentioned (page 239)—the responsibility of the female

alone in nesting, the avoidance generally of male-favored habitat by breeding females, and the departure of males before eggs are hatched. It may be added that males on their territories are observed alone much more frequently than in association with a female. Most of the records of pairs are based on observations over one to three dates, mostly closely successive, so that one infers that the association represents the courtship and egg-laying intervals of a single pairing. At no time was a male seen with more than one female on a territory so that at least for the period required by mating and egg laying, there is now no evidence that the male is any more than monogamous. While marked birds are obviously required to settle this point, it seems likely that were more than one female associating with a male in one interval of time, we would have witnessed this in the field at least a few times.

For five males from the five seasons' data for plot 1 there are records of associations with females two or three times separated by intervals allowing for successful completion of a clutch. This leaves unexcluded the possibility that the small proportion of males providing these records may have been associated with renesting females.

Regarding renesting, this is a moot point. As it is known to occur in the high arctic in such species as the Lapland Longspur (Pitelka MS) and Pomarine Jaeger (Pitelka *et al.*, 1955; Maher MS), it is possible likewise for shorebirds, but we have no bona fide instance in any species from northern Alaska.

Another line of circumstantial evidence which supports the view of a short-term pair-bond is the behavior of males toward females known to be tending nests. Conover (1926:307) mentions that a male may join a female driven from a nest, whereupon he begins courtship display and chases her. I have witnessed this also near Barrow. In such chases, a male will leave his territory and thus encounter other males who may join in the chase or challenge the intruders. In one particular instance of a female known to have a nest with four eggs on plot 1 in 1955, her movements evidently made her particularly vulnerable to local males. On June 28, after I disturbed her, she was chased by three; on July 2 she was chased by six, and within the hour on the same area and presumably involving the same female, a chase with eight males was seen. Size dimorphism facilitates distinction of sexes when they are observed closely in a group. Thus, this behavior also supports the view that males may seek a succession of mates through one season.

Another implication of these observations is that in some situations males may tolerate each other and evidently dispense with territorial isolation while still able to pursue a female. Perhaps it is significant that these observations were made in the last week of the breeding season (earliest record, June 27). If the males can mate without strong territory attachment, even in just a part of the season, the point, while highly conjectural, is of interest in that it suggests an incipency of conditions which, evolutionarily, may lead to lek organization and to promiscuity as seen in the Ruff.

Finally, a fact entirely consonant with what has been said thus far regarding the pair-relationship in the Pectoral Sandpiper is the degree of sexual dimorphism in size. As figure 4B and table 1 show, males are significantly larger than females. In this respect, *melanotos* resembles the Ruff and not other members of the genus *Calidris*, *sensu lato*, for which it is stated (Witherby *et al.*, 1940:227) that "females mostly [have] longer bills and sometimes [are] generally larger than males." Suffice it to say that dimorphism in size, color, or other features of structure, or any combination of these, typically occurs in species or groups of species in which the pair relation is brief or limited to mere mating (Sibley, 1957). Thus, on this count also, the Pectoral Sandpiper could represent a stage of evolution which may be antecedent to the more elaborate and specialized stage seen in the Ruff.

Table 1
Sexual Size Dimorphism in the Pectoral Sandpiper

	Males			Females			Size of females expressed as per cent of males using means
	N	Range	Mean	N	Range	Mean	
Wing chord ¹	12	135-143	139.4 ± 0.8	11	120-131	125.8 ± 0.8	90.2
Bill length ¹	11	28.0-31.7	29.46 ± 0.30	11	25.1-28.5	27.40 ± 0.33	93.0
Tarsus length ¹	12	28.0-30.4	29.60 ± 0.20	11	26.1-29.1	27.40 ± 0.26	92.5
Weights ²	11	82-105	94.6 ± 1.9	8	61-75	65.9 ± 2.0	69.6

¹ Based on adult specimens collected in late spring and summer in western and northern Alaska, northeastern Siberia, Yukon and British Columbia.

² Based entirely on June specimens collected in northern Alaska.

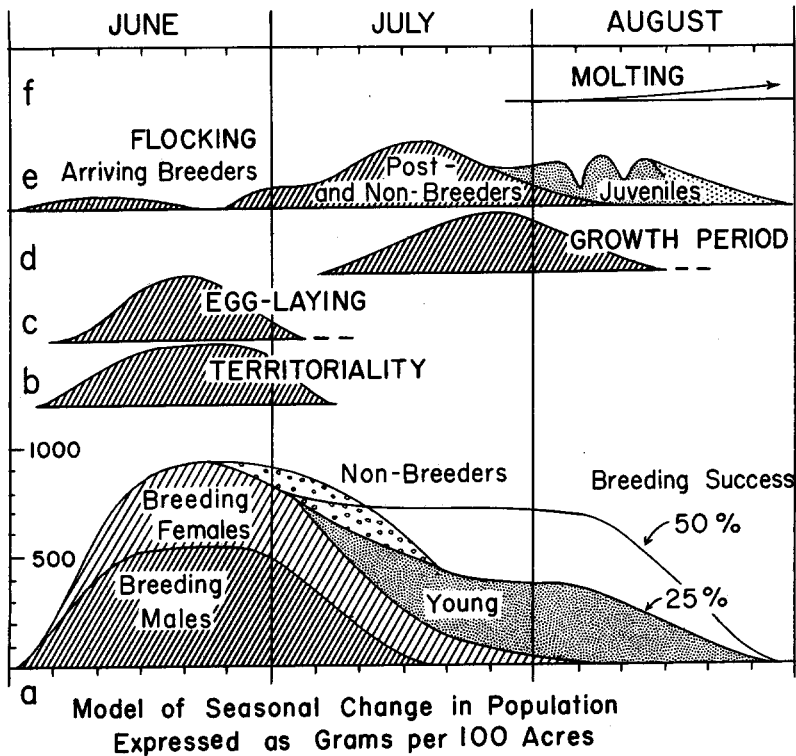


Fig. 7. A generalized schedule of population changes and breeding activities for the Pectoral Sandpiper in northern Alaska.

DISCUSSION

Timing of populational events on the breeding grounds.—Because of the strong size dimorphism between sexes of the Pectoral Sandpiper coupled with the departure of males before nesting is concluded, it is desirable to examine the timing of the main events on the breeding grounds to see whether this will throw any light on populational adaptation. To assist in this, figure 7 has been prepared.

In the Pectoral Sandpiper, unlike the Red-back and other tundra species, most or all of the annual molt occurs well to the south of the breeding grounds. Wetmore (1926:154) records two adult females in which molt had not yet started when they were collected in early September in Paraguay. But in some adults, at least, and in

both sexes on the basis of collected specimens, body molt can begin in the last days of July while they are still on their summering grounds. I say "summering" instead of "breeding" because of the possibility that early inception of molt could be limited to nonbreeders. However, two of three postbreeding adult females (brood patches still evident) collected on August 6, 1925, in Alberta are in early stages of body molt, also. Evidently the main molt period is winter; Wetmore (*loc. cit.*) records two specimens in terminal stages of molt taken in Uruguay in early February. The timing of the onset of molt on the breeding grounds is shown in part of figure 7.

Certain features of timing in breeding behavior have already been discussed in previous sections, and they are included in figure 7 in generalized and summary form. This is done for territoriality (part b), egg laying (c), and flocking (e). The latter part of the flocking curve shows the shift in flock composition from primarily adults to primarily young of the year, and the irregularities in the part of the curve which concerns young suggest the wide variation in their presence in the Barrow area while the regional exodus takes place in the latter part of the summer.

The growth period for young of the year as a group is also shown in figure 7. The latter is based on compiled weight records shown in figure 4B and on dates when young were observed in the field. The combined evidence indicates that the growth period for the bulk of surviving young comes in the latter half of July. With late breeding, as in 1952, the modality would presumably come in early August, but in such years the numbers of young would be only a fraction of what they are in a year that is "average" or at least good from a production standpoint.

The timing of the growth period takes on greater interest when it is made part of a picture of seasonal change in the composition of the population as a whole. We will assume for the moment that the number of territorial males on a large sample area of diversified breeding habitat is about the same as the number of breeding females. There is no marked unbalance in sex ratio in the breeding population, for the number of breeding females observed never left the impression there were or could be significantly more of them than males. If, now, using information on density discussed earlier, we set up a breeding population of six males and six females per 100 acres, and if we express changes which ensue in grams per 100 acres, we arrive at the picture shown in the lowest part (a) of figure 7. Thus, weight of breeding adults exploiting the tundra is highest in the latter half of June. By the end of June, exodus of males begins. Moreover, a nest may have failed, or females may drop out for this or other reasons. Thus, by early July, the biomass of breeders starts to decline, but the presence of nonbreeders, or postbreeders (unsuccessful) may keep the populational total up through the first part of July. By the third week of July, however, most of the adults are gone, and there remain only females still attending nests or young plus the growing young.

While we have no figures on nest success in this species, the incidence of mortality suffered by young sandpipers generally can be expected to be high, and we can regard an estimate of 25 per cent success as closer to the truth than 50 per cent or any higher figure. The trend of total population biomass when young are added is shown in figure 7. Also a line is inserted to show what the trend would be if success were 50 per cent. The decline starting in early August denotes the migratory departure of surviving young.

This schedule shows that the population bulks in the early part of the summer and that even if we invoke a moderately high level of breeding success (50 per cent), we cannot shift this peak to a later part of the summer. Even if we allow a few more females than six per six males on 100 acres, this shift will not occur without assumptions that run counter to the facts. And, if we have erred in the assumptions behind the model, it is in not allowing for enough failures of nests in the egg stage and for the downward

trend of adult weights shown in figure 4B. In other words, even if we examine certain variables that could shift the peaking of biomass, the pattern remains essentially the same, with the highest weights being supported in late June and early July.

It seems possible that this feature of timing may explain part of the success of the Pectoral Sandpiper as a tundra shorebird, both in its wide distribution over northern Alaska and in its relative abundance in foothill as well as coastal zones. Similar analyses should be made of data on other shorebirds before this interpretation is pursued further. But the picture in another common species, the Red Phalarope, will be similar. Here the females (larger than males) leave and hence the biomass curve may be expected to hump in the latter half of June as it does for the Pectoral Sandpiper. Although the Red Phalarope breeds commonly only on the coastal plain, its numbers there on a given area can exceed severalfold those of any other shorebird species.

It therefore seems to be significant that in two species which are both more common and of larger body size than several other shorebird species with which they co-exist, there is this feature of populational contraction after June. This raises questions of the relation of this contraction to available food.

Preble and McAtee (1923:72) show that dipterous insects comprise more than half of the food of the Pectoral Sandpiper in certain arctic areas. They also note that seeds and algae may be taken, but these must be relatively minor items of diet. Our information on food is summarized in tables 2 and 3. Insects of the groups Diptera, Trichoptera and Coleoptera, and small spiders are taken most frequently, but again the overwhelming importance of Diptera is shown. Most of the dipterous species important as food overwinter and enter the summer as larvae, passing through pupal, adult, and egg stages rapidly through the middle of the summer. There is thus a marked dip in the supply of larvae occurring through late June and the first half of July, in which period the bulk of adult flies emerge. Hence, it appears, first, that the period when most Pectoral Sandpipers and Red Phalaropes are present is the period when insect larvae and pupae are abundant in the wet marshes and pond margins where they mainly feed; and, second, that early departure of adults of the larger sex is in part related to the early July decline of the larval supply.

While Lack's (1954) postulate regarding timing of breeding was developed mainly from studies of altricial birds, even in precocial ones maximal survival may be expected if young grow mainly when food is maximally available. Whether these two periods in fact coincide in the Pectoral Sandpiper remains to be shown. Sampling of surface insects in three habitats through two summers (1952 and 1953) showed a peak in mid-July (Hurd and Pitelka, MS), and it now appears that growth of young Pectoral Sandpipers occurs mainly after this peak of overall food availability. Possibly they exploit particular food items whose supply is not correctly reflected in the overall trend of insect numbers; thus, they may be taking dipterous larvae of the new year-class appearing around August 1. Nevertheless, it is argued (1) that on a population-wide basis, food demands are higher at a time other than that when young are growing most rapidly; (2) that the latter situation is eased by the departure of more than half of the biomass of breeding adults before the young make their chief demands; and (3) that the weights of adults, declining through the summer (fig. 4B), suggest that the food situation does not improve for them through July apart from questions of the welfare of the young. Another point is that the amounts of insect food may be expected to fluctuate widely from year to year because of widely varying weather conditions, and a species which adjusts to this by such populational timing as occurs in the Pectoral Sandpiper and the Red Phalarope gains an advantage over other, even smaller species, both sexes of which remain on the breeding grounds through the summer.

Table 2
Food of the Pectoral Sandpiper at Barrow, Alaska¹

Animal group	7 stomachs July 6-12, 1952		2 stomachs July 31, 1952	
	Number of individuals ²	Per cent	Number of individuals ²	Per cent
Spiders				
Linyphiidae, primarily <i>Erigone</i> spp.	105 (5) ³	10.8		
Diptera				
Tipulidae (all <i>Prionocera</i> <i>Gracilistyla</i> Alex).				
pupae	71 (4)	7.3		
adults			7 (2)	3.0
Chironomidae				
larvae	275 ⁴ (3)	28.4		
adults	400 (2)	41.3		
Muscidae, pupae	50 (1)	5.1		
Coleoptera				
Dytiscidae (all <i>Agabus moestus</i> Curtis), adults	3 (1)	0.3		
Staphylinidae (<i>Micralymna brevilinque</i> Schjødte), adults	40 (2)	4.1		
Carabidae, adults	25 (2)	2.3		
Trichoptera [all <i>Grensia praeterita</i> (Walker)] adults			230 (2)	97.0
	969		237	

¹ For the data summarized in tables 2 and 3, special thanks are given to Dr. Paul D. Hurd, Department of Entomology, University of California, Berkeley.

² Numbers in excess of 10 are estimates only.

³ Figures in parentheses indicate number of stomachs in which item was found.

⁴ Total for chironomid larvae probably too low because of difficulty in estimating number from a mass of semi-macerated material; it may have been as high as 400. From one stomach, the mass of chironomid larvae weighing 1.3 grams contained 200-300 individuals.

If these arguments are valid, it is evident that Pectoral Sandpipers time their breeding and migratory movements as parts of a total schedule adapted to the arctic summer. Elsewhere (Pitelka, 1958), I have maintained that in some species timing of breeding in relation to food may be compromised by the energy needs of molt. Here we have another set of conditions involving compromises. In the Pectoral Sandpiper, food available to growing young is presumably augmented to a significant degree by the arrangement that males leave in the first half of July, and females leave later but before the young. Hence any analysis of the timing of breeding must take into account this adaptation. Evolutionary compromises in timing may be expected because of various pressures to which the population is subject simultaneously, serially, or both; that the Pectoral Sandpiper and Red Phalarope have met such pressures with success is strongly indicated by their abundance.

An alternative view regarding the timing shown by breeding populations of Pectoral Sandpipers is that it is an adaptation reducing impact of predation. Near Barrow, the important predators depend on lemmings (Pitelka, Tomich, and Treichel, 1955), and in the absence of the latter, predators are present in such low numbers that any take of Pectoral Sandpipers would be insignificant. When Pomarine Jaegers are nesting, they may turn to shorebirds as alternative prey but they do not do this on a sustained basis (Maher, MS).

It is probable, however, that farther inland, where foxes are present through the summer and where both these and weasels occur more consistently than they do near the coast, predation becomes more important. It is even probable that predation can

be a critical factor in the welfare of foothill populations of the Pectoral Sandpiper. From interior sectors of the Colville River, Cade (MS) reports only low frequency percentages of this species in prey samples of the two breeding falcons (*Falco peregrinus* and *F. rusticolus*), about two per cent by items and less than one per cent by weight. However, in areas where jaegers, particularly *Stercorarius parasiticus*, nest, predation may become more significant. Moreover, on the Kaolak (Maher) and Meade rivers, carcasses of both adult and young Pectoral Sandpipers have been found at fox dens.

Hence, some evidence supports the suggestion that predation may have been a factor in the evolution of the population timing now characterizing the species. The negligible amount of predation in the Barrow region would not itself be an argument against this view if predation does in fact act in a more sustained manner over inland and larger parts of the species' breeding range where the predator fauna is larger and more diversified.

I do not, however, subscribe to the role of predation acting on a population as an alternate to the interpretation given above, and in my opinion, it is not possible to invoke predation strongly in these and other examples (as in the Kittiwake; see Cullen, 1957) when interpreting phylogenetic trends without examining attendant relations between prey and its own food supply. Timing evolves as changes in food supply, in time and space, bring forth adjustments in the annual cycle and behavior of the species such that survival of young is maximal and the population continues at least to main-

Table 3
Food of the Pectoral Sandpiper at Hooper Bay, Alaska¹

Animal group	8 stomachs May 21-29, 1924	3 stomachs June 6-21, 1924	1 stomach August 30, 1924
Spiders			
Linyphiidae, primarily <i>Erigone</i> spp.	3 (2) ²	3 (1) ²	
Lycosidae, <i>Tarentula</i>	2 (2)	2 (1)	
Diptera			
Tipulidae			
<i>Prionocera</i> sp., larvae	74 (6)	24 (2)	4
<i>Tipula carinifrons</i> , adults		12 (1)	
Chironomidae, larvae	25 (4)	1 (1)	32
Muscidae, pupae	1 (1)		
Anthomyiidae, adults		1 (1)	
Coleoptera			
Dytiscidae, <i>Agabus</i> sp., adults	5 (5)	2 (2)	
larvae	5 (4)		
Carabidae, adults, primarily <i>Amara</i> sp.	16 (6)	7 (2)	fragments
Chrysomelidae, <i>Chrysomela</i> sp., adults	3 (3)	1 (1)	
larvae		1 (1)	
Hemiptera			
Saldidae, <i>Chiloxanthus</i> sp.	3 (1)	1 (1)	
Trichoptera, <i>Micrasaema</i> sp., larval cases	4 (2)	1 (1)	
Hymenoptera			
Ichneumonidae, adult		1 (1)	
Gastropoda, small snail	1 (1)		
Other contents:			
Seeds	94 (6)	12 (2)	
Gravel, pieces	20 (5)		
Plant remains	1 (1)	1 (1)	

¹ Data summarized here were obtained from stomachs originally in the collections of the Fish and Wildlife Service and kindly donated for this study by W. J. Hamilton III.

² Figures in parentheses indicate number of stomachs in which each item was found.

tain itself. The predation view implies that were the adults of the Pectoral Sandpiper to remain on the breeding grounds to the end of the summer, the species would be less common or absent. If the timing arrangement characteristic of Pectoral Sandpipers and Red Phalaropes is the chief reason for their abundance as tundra shorebirds, then it is possible that predation could have assisted the evolutionary transition since escape from predators by early departing breeders would be one source of improved survival. But surely the change in the food situation would be a more potent source of improved survival for their young. The question really remaining is whether the modifying effect of reduced predation could of itself account for the abundance of these two shorebird species. A critical test of this and other aspects of the problem would be information on kind of food eaten by young sandpipers, on their survival in relation to available food, and on changing techniques in food hunting as they grow.

Generic relationships.—Among the members of the genus *Erolia*, the only species for which the available information clearly suggests relationship with *melanotos* is *fuscicollis*, the White-rumped Sandpiper. This small *Erolia*, surprisingly enough, appears to parallel *melanotos* in several respects, according to the observations reported by Sutton (1932). Thus, the female alone incubates. The males gather in flocks and leave the breeding grounds before appearance of young. Lastly, and perhaps most significantly, the males show swelling of the neck and upper chest as a part of their display and also give a "guttural rattle" that may be equivalent to the aggressive note of territorial Pectoral Sandpipers. In certain details of flight display given by Sutton, however, the White-rump appears to resemble other erolias. Also, it does not show the marked size dimorphism between sexes seen in *melanotos*. In the White-rump, therefore, we may have a species which is more or less intermediate between *melanotos* and less specialized members of *Erolia* (or *Calidris*) such as *bairdii* and *alpina*. However, Sutton is the only observer who describes breeding behavior of *fuscicollis* in any detail, and additional observations are needed. If his are confirmed, then Witherby *et al.* (1940:269) are in error when they say that the habits and behavior of *fuscicollis* "seem to be almost exactly like Dunlin's" (*E. alpina*).

The Sharp-tailed or "Siberian Pectoral" Sandpiper, *Erolia acuminata*, cannot be drawn into this brief discussion as no information is available regarding its breeding biology and displays (Dementiev *et al.*, 1951). However, the weak size dimorphism of the sexes combined with certain features of coloration and pattern lead me to doubt that it is as close to *melanotos* as has been thought heretofore.

The possibility that *melanotos* may be linked with *Philomachus* (or "*Machetes*," a generic name used earlier) has been mentioned in the introduction and elsewhere in the foregoing text. After the writing of most of this paper was completed, it was found that Dementiev *et al.* (1951) likewise say of *melanotos* that its habits and external appearance remind one of the Ruff. The relationship of the Ruff to *Erolia* (or *Calidris*) was shown some time ago by Lowe (1915a, b) on the basis of characters of plumage pattern and skull morphology. Ridgway's (1919) synopses of generic characters for "*Machetes*" and "*Pisobia*" (the latter presently included in *Erolia*) also suggest similarities. And finally, what Witherby *et al.* (1940) and Armstrong (1947) alone have to say regarding display behavior of the Ruff suggests still additional similarities. However, without comparative studies, these suggestions cannot be pursued further; for, as Portenko (1957) states, *Erolia* is evidently a heterogeneous assemblage, and this should be even more true of the more inclusive genus *Calidris*.

With these remarks I do not wish to alarm any conservative by a prospect that *Philomachus* and some part of *Calidris* might be lumped. In the former, the sternum has only one pair of incisions; in *melanotos* and other members of the latter, there are

two. Such differences combined with the high degree of dimorphism and the special features of behavior associated with it indicate that *Philomachus pugnax* may well remain in a monotypic genus. The point now is that *melanotos* may fall as close or closer to such a member of the calidrine complex as it does to other members of the A.O.U. Check-list's genus *Erolia*. Thus, in this view, shared by F. S. Andersen (1951), *pugnax* would be one endpoint in the evolutionary diversification of the calidrine sandpipers in which arena display and associated features of breeding behavior are evolved to a degree unmatched by other members of the group, and *melanotos* could represent a stage in that evolution. The interest attached to behavioral parallelism between the Ruff and other lek birds such as grouse (Armstrong, 1947) emphasizes the opportunity afforded by the Calidrinae, and comparative study of *melanotos* and its relatives may reveal something about evolutionary origins of lek behavior in this group.

SUMMARY

Several population characteristics of the Pectoral Sandpiper (*Erolia melanotos*) on its breeding grounds in northern Alaska are described, especially numbers, breeding schedule, and territoriality. Unlike any other shorebird species occurring on the arctic Alaskan slope, the Pectoral Sandpiper is common in both coastal and foothill zones, but at least near the coast, large year-to-year differences in relative abundance may occur. In the breeding season, the species is dispersed generally over coastal tundra, the males occupying territories where low promontories are available, the females nesting in virtually all habitats providing grassy cover. They are primarily insect predators; in early July, near Barrow, dipterous insects comprised at least 75 per cent of the prey.

From data gathered on census plots for five seasons (1951-53, 1955-56), usual or "average" densities were estimated at 5 to 6 breeding territories of males per 100 acres. The minimal density observed was 3 per 100 acres, in 1952, the maximum, 10-15 per 100 acres, in 1953. Numbers of breeding males in 1953 was four or five times that for 1952, the densities for the other three years falling in between. Numbers of females were about the same. Nests are placed without direct relation to territories of males and usually away from them. The pair-bond is short, and once nesting is started, females are independent of males.

Eggs may be laid over a period as long as a month, from early June to early July. Near Barrow most eggs are laid in the last ten days of June. In the interior the period is probably of the same length, but the modal interval falls about a week earlier. Testis size is maximal for about five weeks from early June to early July; testes regress over about three weeks in July and early August.

The seasonal trend in numbers in relation to breeding schedule can be divided into six phases: (1) early summer rise in numbers of settled birds; (2) interval of relative stability when territories are occupied and when most eggs are laid; (3) desertion of territories by males, in late June and early July; (4) completion of incubation by females and care of recently hatched young; (5) departure of females in late July and early August; and (6) departure of juveniles from late July to the first days of September. Flocking is most conspicuous in July when the numbers of both breeders and non-breeders moving about in early stages of migratory departure are greatest. A striking amount of flocking in 1952 in conjunction with the low breeding densities of that year indicates that near the coast, at least, this was not a productive year.

The flight display of territorial males and seven other displays are described briefly. Males isolate themselves on areas used for pairing (and probably mating), feeding, and roosting. These areas support females similarly during their short period of association with the male. Territory size is estimated at 10 to 15 acres. The period of territorial

occupation is about a month long, from early June to early July; number of established males reaches a peak in the third week of June. With respect to patterns of space occupation and aggressive behavior as well as other features, the behavior of the male Pectoral Sandpiper is analogous to that of other well-known "classically" territorial species. There is no evidence for territoriality in females.

A model of the seasonal schedule of biomass per unit area for Pectoral Sandpipers shows that the peak is reached in the early part of the summer, in late June. The main populational contraction occurs during July. This appears to be an adaptation which acts to improve the food situation for young and hence for their survival; that is, it is a populational timing mechanism superimposed on any relation between periods of active growth in young and of maximal food supply for them. This interpretation of the mid-summer contraction in numbers is preferred over the alternate view that the contraction has been selected evolutionarily because it reduces losses to predation.

The question of generic limits in sandpipers is discussed briefly because of the evidence that "*Erolia melanotos*" is not closely related to many of its congeners. Certain features of breeding organization in the Pectoral Sandpiper suggest antecedents to the lek behavior of the Ruff.

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