BREEDING BIOLOGY AND BEHAVIOUR OF THE PIPING PLOVER (*CHARADRIUS MELODUS*) IN SOUTHERN NOVA SCOTIA.

BY

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ABSTRACT

Piping Plovers (Charadrius melodus) were studied in 1975 and 1976 in southern Nova Scotia. The birds arrived on the breeding grounds in late April and soon occupied nesting and feeding territories and initiated courtship. The various behaviours used during the reproductive season, including Horizontal Threat, Parallel Run, Courtship and Distraction Displays are generally similar to those of other plovers. Mean size of nesting territories was 4,000 m^2 and nests averaged about 52 m apart. In 1975 most clutches were initiated during the first two weeks of May and in 1976 during the last week of April and the first week of May. Of 68 clutches, 65 had 4 and 3 had 3 eggs. Most eggs were laid at approximately 48 hour intervals; the longest interval was 77 hours. Incubation averaged 28 days; one extreme of 38 days was recorded. Egg size in 50 clutches varied significantly among females but not with order of laying. Average number of young hatching per nest was 3.08 in 1975 and 2.88 in 1976. Growth rates of most chicks were higher than those reported for birds in New York, and chicks with lower growth rates had greater mortality than other chicks. The fledging period is at least 27 days. A fledging rate of about 1.3 to 2.1 young per pair per year was obtained on one remote beach, while fledging rate on eight beaches receiving recreational use was approximately .73 to 1.1 chicks per pair per year. Departure from the breeding grounds takes place during July and August. The population of Piping Plovers in Nova Scotia is estimated to be 60 to 75 pairs. In Canada east of the prairies (excluding the uncensused north shore of the Gulf of St. Lawrence) the population is probably 250 to 350 pairs, and it appears unlikely that the entire Canadian population could number more than 1000 breeding pairs.

ACKNOWLEDGEMENTS

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INTRODUCTION

The Piping Plover (Charadrius melodus Ord) is a small shorebird endemic to central and eastern North America which breeds discontinuously throughout its range where suitable habitat is found. Godfrey (1966) records the breeding range from southern Canada (Alberta to Newfoundland), southward to South Dakota, Nebraska, the southern shores of Lakes Michigan and Erie and along the Atlantic coast to Virginia. The birds winter from Massachusetts (rarely: Finch 1974) to Florida on the Atlantic coast and westward to Texas along the Gulf of Mexico. There are apparently two populations: the inland one (including birds from Ontario westward) winters on the Gulf coast while the Atlantic population winters along the Atlantic coast of the United States (Palmer in Stout 1967).

Earlier accounts of the species by Farley (1919), Robbins (1919), Pickwell (1925), Bent (1929), Cruickshank (1939), Nichols (1939) and Wilcox (1939) are largely anecdotal. A single study by Wilcox (1959) provides most of the breeding information known for the species.

The present study was undertaken to obtain baseline information on the Piping Plover and its status in Nova Scotia. Emphasis has been placed on detailing the biology and behaviour associated with the nesting cycle and on examining the relationship between nesting success and the multiple use of beaches.

HABITAT OF SPECIES

Preferred breeding habitat along the Atlantic coast is dry, light-coloured sand beach along the outer shore. Nesting may occur in the narrow sloping strip of sand between the foot of the seaward face of the dunes and the high-tide line, but relatively flat unvegetated expanses of sand are particularly favoured. Such areas occur at or in the lee of the tips of building sandspits, or where storm surges have caused wash-outs in dune chains. A scattering of fine gravel, small stones and broken sea shells often characterizes these spots. Locations on raised sand flats well above high-tide line or on the sheltered side of spit systems are presumably the more desirable because nests and small chicks in these areas face less risk from heavy wave action and high water than do their counterparts on the seaward face of the dunes.

Piping Plovers as a species have the ability to colonize newly available nesting areas fairly quickly, often within several years (Wilcox 1959). This makes them well adapted to take advantage of unstable coastal dune systems. The main factor determining the selection of new areas for occupation is probably nest site rather than food supply. This is also the case in the Ringed Plover (Charadrius hiaticula), Little Ringed Plover (C. dubius) and Kentish Plover (C. alexandrinus alexandrinus) in northern Europe (Sluiters 1954). Best nesting conditions for Piping Plovers are offered by beach systems which are either building or declining, and thereby

making available broad expanses of relatively unvegetated, raised terrain suitable for nest sites. When a given system has washed away or become vegetated, the plovers move on to another area where the dune system is in the appropriate state of decline or development.

STUDY AREA

Cadden Beach. -- The major study area is located at Cadden Beach near Port Joli in Queens County, Nova Scotia, and consists of a sandspit 1.4 km long and from about 75 to 200 m wide (Fig. 1). The broad, relatively flat expanse of unconsolidated sand is strewn with small rocks, fine gravel, clods of peat, driftwood and other debris. From the steeper seaward beach the system slopes gently down to an extensive area of tidal sand flats along an inner lagoon behind. In two areas low sand dunes form the boundary between the spit proper and the tidal flats of the lagoon. Maximum height of these poorly vegetated (*Juncus balticus* >> *Ammophila brevigulata* > *Sonchus arvensis*) dune systems is about 3 m above the general level of the beach. Across most of the spit vegetation is extremely scanty. *Arenaria peploides*, the most abundant species, occurs in scattered clumps along the margin towards the lagoon beach. *Ammophila brevigulata* is distributed sparsely across the spit, often present only as single sprigs.

Other beaches. -- In addition to Cadden Beach, eight other beaches along the eastern and southern shores of Nova Scotia where Piping

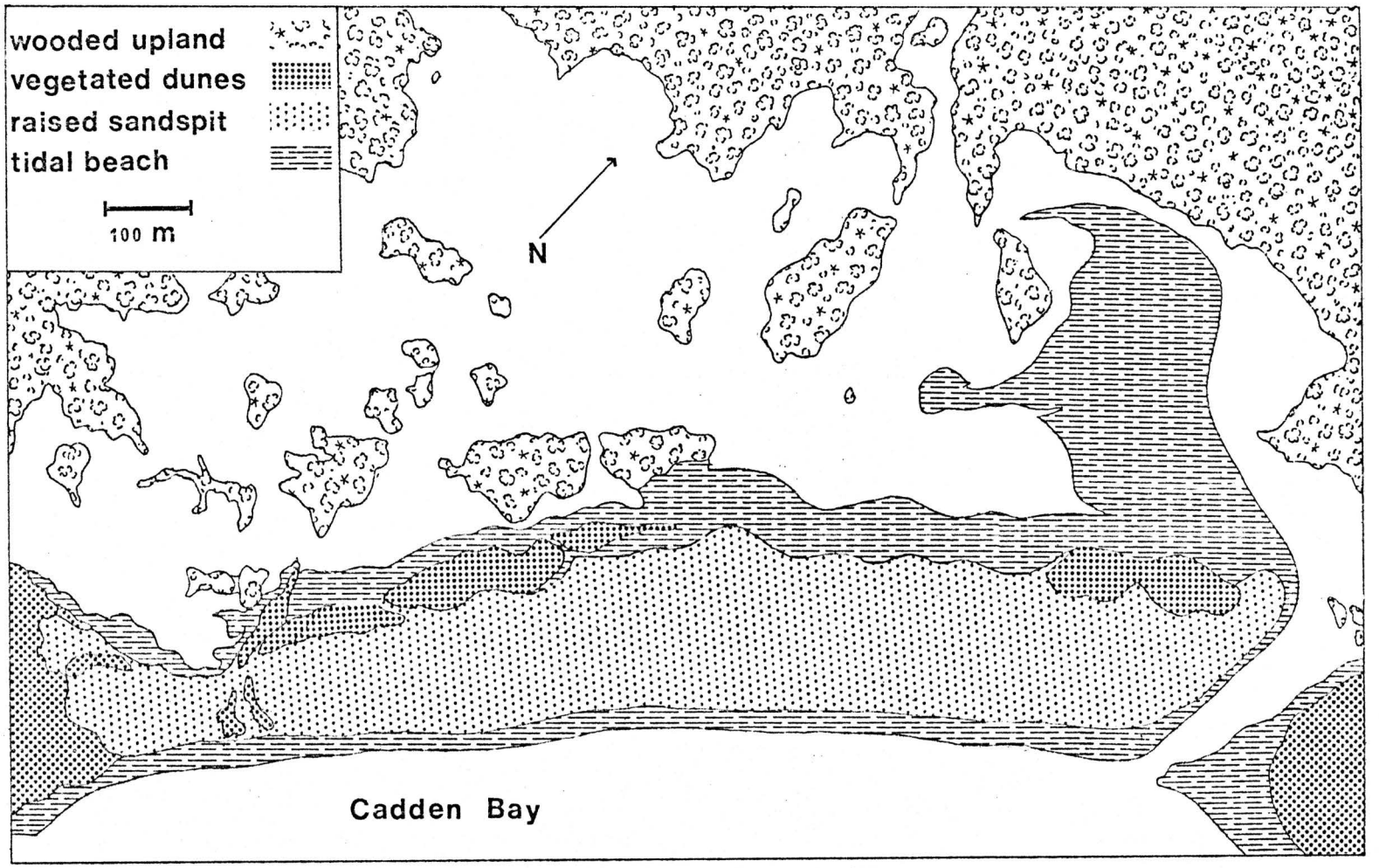

Fig. 1. Map of study area showing features of topography and vegetation.

Plovers breed were visted on a regular basis, usually at 2 to 3 week intervals. These were Conrad's Beach in Halifax County, Cherry Hill in Lunenburg County, Summerville and Sandy Cove in Queens County and Little Port Le Hebert, Louis Head, Baccaro and Cape Sable Island Beaches in Shelburne County. On two beaches (Conrad's Beach and Summerville) nests were located on raised areas of unvegetated sand, while on the remaining beaches they were placed between the seaward base of dunes and high-tide line.

MATERIALS AND METHODS

Piping Plovers were observed on Cadden Beach from May 1 to August 15, 1975 and from April 22 to August 10, 1976. Visits to eight other breeding beaches in Nova Scotia were made between May and August of 1976. Adults were captured on their nests using a drop trap (1975) or a circular walk-in trap (1976). The drop trap was 60 cm on the side and 10 cm high, and was made of 1 cm mesh wire screen supported by light wooden slats. It was propped on a stick and activated by a rope running to an observer lying prone at some distance. (For further details see Wilcox 1959). The circular walk-in trap was formed by standing a 50 cm x 120 cm strip of wire screen (mesh 0.5 cm) on its long edge in a roughly circular shape with ends bent inward to create a funnel effect. The top was loosely filled in with picture wire.

Both methods of trapping had drawbacks. A number of birds were unwilling to approach the traps closely and when they did so seemed

unable to recognize eggs within or beneath a trap. Typically, after I erected a trap and withdrew, the bird returned to the vicinity of the nest, and wandered around within several metres of the trap as if searching for the eggs. If it did not discover the nest within 5 to 10 minutes it withdrew from the area and approached from a different direction, this time ranging its wanderings more widely about the nest. After 30 to 60 minutes of repeated wanderings and approaches from various directions the bird often departed from the nesting territory. Some birds which did recognize eggs in the trap were unable or unwilling to enter and sit on the nest. Instead they would move along the sides or the rear of the trap peering in at the spot nearest to the eggs and would generally finish by settling down with breasts pressed against the outside of the trap as if incubating. The walk-in trap had the further disadvantage of a constant opening and some birds which had entered it left again as I approached from the side containing the opening. When trapped birds realized their plight they often ran about fluttering erratically within the trap. Several eggs were cracked in this manner.

Adults were banded with aluminum and coloured leg bands and were also colour marked. Chicks were banded as they hatched or when first encountered. In 1975 14 adults and 53 chicks were banded and in 1976 11 adults and 91 chicks received bands. Nineteen adults in 1975 and four in 1976 were colour marked. After hatching, chicks were recaptured as often as possible. In 1976 all captured birds were weighed and measurements of culmen, tarsus, wing and tail were taken.

It was possible to determine sex of adults of some pairs from colouration of the neck ring and the band across the forehead; within a given pair the male usually had the darker markings if there was a detectable difference.

POPULATION ESTIMATE

During 1976, 66 of the 75 chicks hatched from the 26 known nests on Cadden Beach were banded. Fifty-one chicks were captured at least once after leaving the nest. Forty of these were chicks from known nests while the remaining 11 were considered to be chicks from unknown nests since, based on comparison with growth curves for known aged chicks, none of them could be referred to the 9 unbanded chicks from known nests. Since all recaptures occurred in similar habitat and since brood size and age should be similar for known and unknown chicks, it has been assumed that the chicks caught represent an unbiased sample of the chicks present on the beach. Using this assumption and the following proportion an estimate of the total number of nests can be obtained.

$$\frac{\text{no. of unknown chicks}}{\text{no. of known chicks}} = \frac{\text{no. of unknown nests}}{\text{no. of known nests}}$$

The estimated total of unknown nests (with binomial 95% C.I. rounded to the nearest larger and smaller integers above and below the mean) is 7(3-13) nests (based on 11[5-17] chicks being the estimated number

of unknown chicks per 51 chicks recaptured), which when added to the 26 known nests yields 33 (28-39) as the estimated total number of nests.

The actual number of Piping Plover pairs is probably somewhat lower than the number of nests, since renesting routinely follows early loss of nest or brood. At least 3 and probably several more (judging from late hatching dates) of the 26 known nests were renests. I therefore consider that there were actually about 27-29 pairs on Cadden Beach.

In addition to breeding pairs, a proportion of the summering adults appeared to be either unmated or unsuccessful in producing a clutch. Somewhat arbitrarily I have estimated about 10 birds to be in this category.

An estimate of the number of chicks hatched on Cadden Beach in 1976 was obtained from the proportion:

$$\frac{\text{no. of known chicks recaptured}}{\text{no. of known chicks}} = \frac{\text{no. of unknown chicks recaptured}}{\text{no. of unknown chicks}}$$

This yields an estimate of 21 unknown chicks which when added to the 75 known chicks gives a total estimate of 96 chicks hatched.

EARLY SEASON ACTIVITY

Arrival in Nova Scotia. -- Most of the Piping Plovers breeding along Nova Scotia's beaches arrive from mid to late April. In 1975 the earliest sighting in the province occurred at Yarmouth on April 4 (Dobson 1975) while the first 1976 report was from Cape Sable Island on March 28 (Mills 1976).

Due to difficulties in distinguishing the sex of unpaired birds I do not know the relative proportions of males and females present among these early arrivals. Male Little Ringed Plovers according to Simmons (1956) and Lapwings (Vanellus vanellus) according to Klomp (1946) tend to return before females, which may also be true of Piping Plovers. A few Piping Plovers may return already paired but most apparently pair on the breeding grounds.

Flocking. -- Upon arrival unpaired birds tend to gather in small flocks on neutral (i.e. not claimed or defended as part of any pair's territory) feeding areas. Aggressive interactions are numerous in these assemblages, with much threat posturing and chasing in evidence. I have not observed aerial or ground courtship activity to originate in these early flocks although often birds engaged in courtship flights that were initiated elsewhere along the spit, fly in to land in these areas.

A number of other plover species also show flocking behaviour on arrival on the breeding grounds, as has been noted by Laven (1940) in Ringed Plover, Tomkins (1944) in Wilson's Plover (Charadrius wilsonia), Phillips (1972) in Killdeer (C. vociferus), Graul (1973b) in Mountain Plover (C. montanus) and Hall (1964) in Blacksmith Plover (Hoplopterus armatus). In some species (Ringed, Wilson's, Mountain and Blacksmith Plovers) courtship and copulation may occur in early season gatherings, and in Mountain Plovers aggressive hostility is also shown. Although details are incomplete for the various species it seems possible that initial flocking by plovers on the breeding grounds, by placing birds

of both sexes in close proximity, may generally stimulate the development of behaviour associated with territoral establishment and courtship.

FIDELITY TO NESTING AREA

At least some adults returned to their territories a second year. Two of the three previously banded adults caught on nests on Cadden Beach in 1976 were females captured on the same territories they had occupied in 1975. Both nested within 20 m of their nest sites of the previous year. The third bird, a male, occupied a 1976 nesting territory that was about 1 km from the site of the nest from which he had hatched in 1975. At least five other previously banded adults were present on Cadden Beach in 1976 but unfortunately none of these could be captured and positively identified. In addition one banded adult was observed on each of Cherry Hill and Summerville Beaches in 1976.

Since to my knowledge no one has previously banded Piping Plovers in the Maritimes and, since no previously banded birds of this species were observed in the province in 1975, I am persuaded that all previously banded Piping Plovers observed in Nova Scotia in 1976 were banded by me as adults or chicks on Cadden Beach in 1975. I therefore feel it reasonable to conclude that of the 67 birds banded in 1975 a minimum of 10 (or 15%) returned to the province in 1976.

Wilcox (1959) found that 39% of banded adult Piping Plovers in Long Island returned to the same nesting area in succeeding years. The tendency to return to the same breeding area (and sometimes nesting

territory as well) after nesting has occurred there once has been reported for a number of other plover species including Ringed Plover (Laven 1940, and Bub 1962), Killdeer (Lenington and Mace 1975), Kentish Plover (Rittinghaus 1956), Mountain Plover (Graul 1973b) and Lapwing (Spencer 1953).

The percentage of first year birds returning to breed in the area of hatching appears to be relatively low for Charadrius plovers. The values in the vicinity of 5% cited by Lenington and Mace (1975) for Ringed, Piping and Kentish Plovers may reflect both an increased likelihood of wandering and higher mortality among first year birds than adults.

TERRITORIAL BEHAVIOUR

Horizontal threat display. -- The horizontal threat display is of primary importance in the establishment of territory. Most horizontal threat displays originate on the ground when the bird is moving and take the form of a charge. In assuming the horizontal threat posture the bird leans forward on slightly bent legs with head drawn well back into the body (Fig. 2). The neck ring becomes prominent and with increasing intensity the wings are slightly raised and the feathers of the breast, sides and upper back are puffed. At still higher intensity the tail is fanned open and depressed, while the feathers of the back, sides and upper breast are raised to the extent

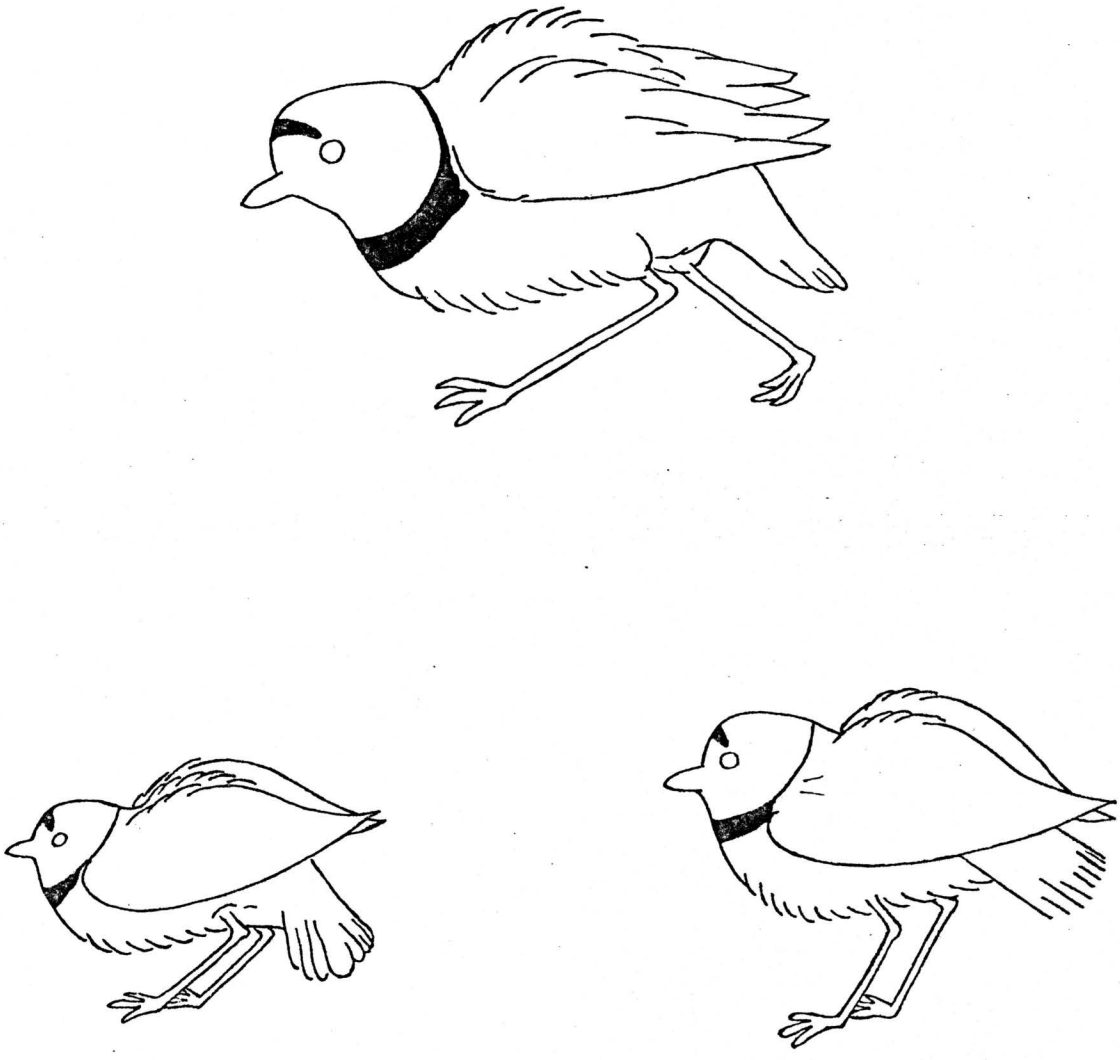

Fig. 2. Some postures used during horizontal threat display.

that the bird acquires a very frayed and ragged appearance. The less intense form of the display is more frequent when at least several birds are present and is performed during low gliding runs directed towards the various individuals at close range. In such situations charging birds usually swerve aside before reaching the target bird so that actual chases and fights seldom ensue. Within small flocks several birds may at times simultaneously perform horizontal threat charges, continually swerving aside and redirecting their displays towards other individuals to create a melee of scurrying bodies. Such deflections of horizontal threat seem clearly related to the presence of alternative "targets", but whether because the initial target bird is more reluctant to flee in the presence of conspecifics or because the alternative target birds distract the attacking bird, cannot be said.

Encounters between two individual birds more often lead to high intensity display and chases of 30 m or more. Typically the charging bird begins with a low-intensity threat display posture. The low glide then becomes a fast run which changes into a normally postured run before the bird finally slows to a walk. High intensity charges between two birds at close quarters rarely terminate in brief fights. The partners may initially face each other in horizontal threat display and then jump and fly towards each other at close range, seemingly directing the bill and wings toward the head, neck and upper back regions of the opponent. Most threat skirmishes subside within several minutes as the birds gradually move apart, often vigourously pecking

the ground in displacement feeding, or running with abrupt stops and starts. There is not normally an obvious winner in these encounters.

Vocalizations with horizontal threat display involve a series of low, rattling bec-bec-bec calls which become increasingly rapid and take on a whirring throaty undertone as the display progresses.

Parallel run display. -- After territorial boundaries have become fairly well defined parallel run displays become increasingly important. Typically the birds run in parallel along a line, sometimes wherever two birds meet, but usually near a territorial boundary.

The parallel run display is usually performed by two birds, but a pair may give it together toward a third bird. In such cases one member of the pair usually soon withdraws voluntarily, or rarely may be driven off by its mate. When carrying out the display both birds adopt very erect postures with heads and necks stretched upward and breast feathers puffed smoothly, so that the dark sides of the neck and the neck ring (if there is one) show sharply against the gleaming white (Fig. 3). After facing each other and head-bobbing, one bird turns at right angles and runs rapidly for some distance along the disputed line. In the same manner the second bird runs past the first, often arcing into its territory to do so, and stops abruptly either just ahead of the first bird or at some distance further along the line. The birds move by alternate turns and cover distances of from 1 to 10 m at a spurt. Each spurt is terminated as the bird draws abruptly to a halt and pulls into a more sharply erect posture, most often with a slight turning of the body so that the tail lies directed towards the

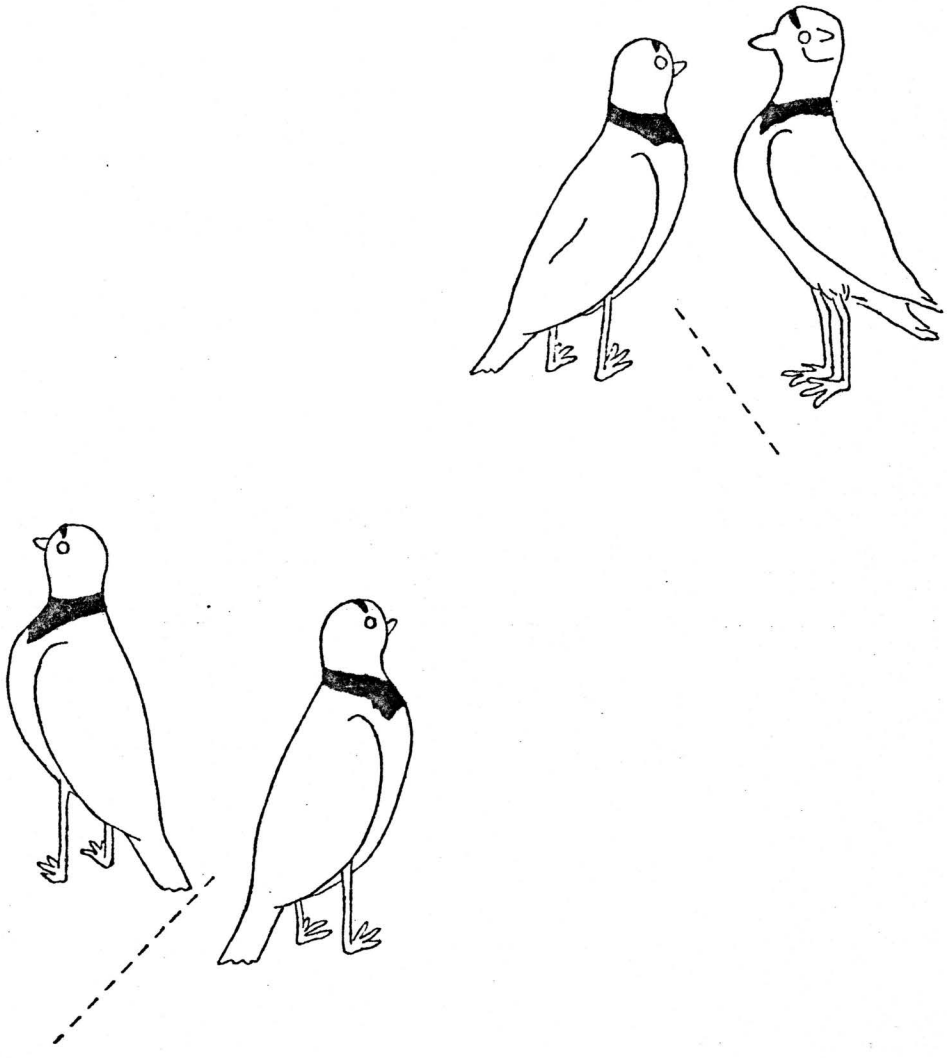

Fig. 3. Upright postures used during parallel run displays along a common boundary.

line, but sometimes with body and tail both parallel to the line or with tail pointed away from the line. If the birds are close together the stop is usually punctuated by several head-bobs directed toward the opponent while each tries to maintain as tall a profile as possible.

In more intense encounters the running spurts are sometimes characterized by violent pecking of the ground, presumably a displacement activity. The birds may also engage in bouts of head-bobbing alternated with very short rapid runs and will sometimes face across the line and shove one another shoulder to shoulder or breast to breast. During very intense parallel run encounters, horizontal threat charges at close range may occur between bouts of running.

Low intensity parallel run displays are expressed by parallel walking or simply by a form of upright display in which the two opponents face each other and engage in bouts of head-bobbing alternated with neck preening or pecking the ground.

The normal parallel run routine of alternate running and head-bobbing in erect posture may cover distances of up to 100 m before the birds reverse directions and repeat the display along the same line. Encounters may continue a half hour or more. Parallel run displays usually conclude with the gradual divergence of both birds, each moving away pecking the ground. There is not normally an obvious winner and the same (approximately) boundary line may be the site of further displays during the season.

Vocalizations used during parallel run displays are similar to those which characterize horizontal threat displays.

Comparison with other species. -- Among a number of plover species a head-up posture is indicative of defensive threat and a head-down posture of aggressive threat (Maclean 1972). This appears also to be true of Piping Plovers, which use head-down postures (as in horizontal threat) in chasing away conspecifics and head-up postures (as in parallel run) in the maintenance of territorial boundaries.

Various forms of the horizontal threat display have been reported for a number of other plover species including Ringed Plover (Edwards, Hosking and Smith 1947, Mason 1947 and Simmons 1953b), Semipalmated Plover Charadrius semipalmatus (Sutton and Parmelee 1955), Little Ringed Plover (Simmons 1953b), Wilson's Plover (Tomkins 1944), Killdeer (Phillips 1972), Mountain Plover (Graul 1973a and b) and Blacksmith Plover (Hall 1964). In general there are two basic versions of the display. Little Ringed Plover and Mountain Plover normally adopt a dorso-ventrally compressed stance with obscured neck markings (Little Ringed Plover) and flank feathers puffed laterally to cover the wrists, giving an appearance face on of a horizontally compressed oval presenting much white. Killdeer, Ringed Plover and Piping Plover swell the neck markings and breast feathers and present a more rounded frontal appearance.

Upright threat displays have been reported in Ringed, Little Ringed and Kentish Plovers (Simmons 1953b), Killdeer (Phillips 1972), Wilson's

Plover (Tomkins 1944) and Mountain Plover (Graul 1973b), but only Killdeer and Mountain Plover are known to use the displays in conjunction with parallel runs. Interestingly, Ringed and Little Ringed Plovers when in upright threat display rapidly mark time with the feet, in a manner identical to the pre-mounting display of courtship.

TERRITORIAL ESTABLISHMENT AND MAINTENANCE

Male territoriality. -- Soon after arrival males begin to establish themselves on prospective territories. A portion of raised spit is claimed for nesting and a stretch of waterfront beach for feeding. The two areas are usually but not always contiguous. Eight or ten feeding/nesting areas had been so claimed when I commenced field work at Cadden Beach on April 22, 1976.

Territorial establishment is fairly similar to that described for Killdeer (Phillips 1972). A lone male spends much time on his prospective nesting territory prior to the start of incubation, thoroughly traversing the area in short flights and brief runs. He may stop on slightly elevated parts of the terrain, in general on sand substrates rather than on logs, stumps, stones or clods of peat. Here the bird may remain watchful and motionless except when scanning the sky or preening. Scanning occurs at intervals and involves slowly rolling the tilted head from one side to the other, evidently in search of females or prospective intruders. Preening may be sustained for several hours

at a time, interrupted only by brief skyward glances. Most preening is concentrated on the neck ring, making it wider and darker than usual. Long periods on the ground are interrupted by advertisement calls and display flights (see section on Courtship). These may arise spontaneously or can be elicited by another male flying over or by a female in the vicinity, and apparently function to advertise possession of the territory to rival males and prospective females.

Unwanted intruders are met with horizontal threat charges and ground or aerial chases. Such encounters aid in establishing rough territorial boundaries. Boundaries, however, remain loosely defined and flexible, and often undergo considerable modification from one interaction to the next.

Occurrence of agonistic interactions. -- Although hostile interactions among Piping Plovers occur during encounters on neutral feeding areas, their primary function appears to be in the establishment and maintenance of territory. Advertising display flights, aerial and ground chases, and longer horizontal display charges are associated with territorial establishment, while parallel run displays and shorter horizontal display charges are more related to territorial maintenance. Agonistic activity is shown by both sexes although the male plays the greater role, at least during territorial establishment. Occasionally horizontal display charge is directed toward a mate on its return to the territory or when both partners meet in an assemblage of charging, swerving birds along a territorial boundary.

SPACING AND TERRITORY SIZE

Spacing. -- Piping Plovers generally locate their nests in highly localized habitats of restricted size, and it is not uncommon to find no more than 1 or 2 nests on a given beach. However, where sufficient continuous habitat is available, as at Cadden Beach, assemblages of up to 30 pairs may congregate in what may be described as loose colonies.

The tendency to nest in loose colonies is widespread among plovers, although the social relations within these vary somewhat with species. These may range from the division of the breeding colony into contiguous territories by the Yellow-wattled Lapwing Vanellus malabaricus (Jayakar and Spurway 1965) to the absence of territorial holdings around the nest by the Crowned Plover Stephanibix coronatus (Moore and Vernon 1973).

Lack (1968) has suggested that loosely colonial nesting in general may enable birds to combine to drive away predators. This may be true at Cadden Beach where birds often temporarily ignored territorial boundaries and gathered in small flocks to cope with an intruder (such as myself) or a predator. Presumably however nests are not placed sufficiently close together that risk of discovery by a predator would be increased. Thus the looseness of colonies may be a compromise between the advantages of predator defence and crypticity.

Territory Size. -- In the following, the term nesting territory will refer to the portion of the raised sandspit around a particular

nest which is habitually defended against intruders by the resident pair. Feeding territory is the section of tidal beach front regularly used and defended by a given pair.

Of the approximately 200,000 m^2 of raised sandspit that form Cadden Beach an estimated 120,000 m^2 can be considered prime Piping Plover nesting habitat. For the most part the spit was divided up into contiguous nesting territories (Figs. 4 and 5). In a few cases where distance between nests was especially great, small portions of suitable habitat were not part of any pair's territory. Given the presence of approximately 30 nesting territories in any particular year, they can be expected to average about 4000 m^2. The relative plasticity of boundaries made individual size of territories difficult to assess, but on Cadden Beach the largest nesting territory observed may have contained up to 8000 m^2 and the smallest about 500 m^2.

In addition to their nesting territories Piping Plovers also defended portions of waterfront beach as feeding territories. The great variability in amount of sand flats exposed at different times of the tidal cycle makes it impossible to evaluate the surface area of feeding territories. Indeed, some were not specifically located at all (Fig. 4). In general feeding territories occupied 50 to 100 m of waterfront.

In the less densely populated parts of the beach nesting and feeding territories were usually contiguous and often included waterfront on both sides of the spit. In the more densely populated areas families frequently had to traverse nesting territories held by neigh-

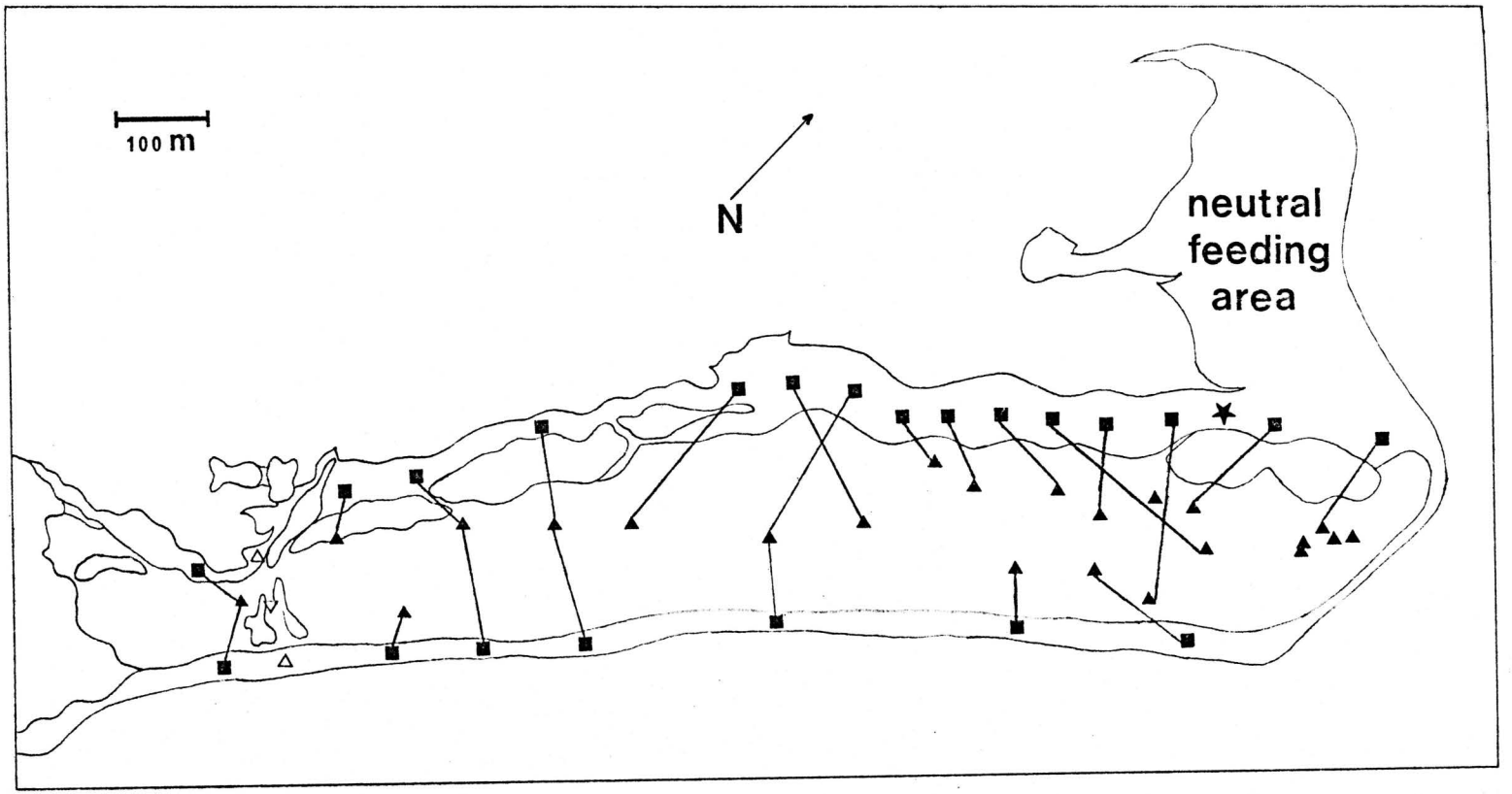

Fig. 4. Map of study area showing 1975 nest site locations (▲) on raised sandspit and general area of feeding territories (■) on tidal beach. Nest sites and corresponding feeding territories (where known) of individual pairs are joined.
( ) indicates the feeding territory of a pair which had no nest or brood.
( ) indicates territory held by an unmated male.

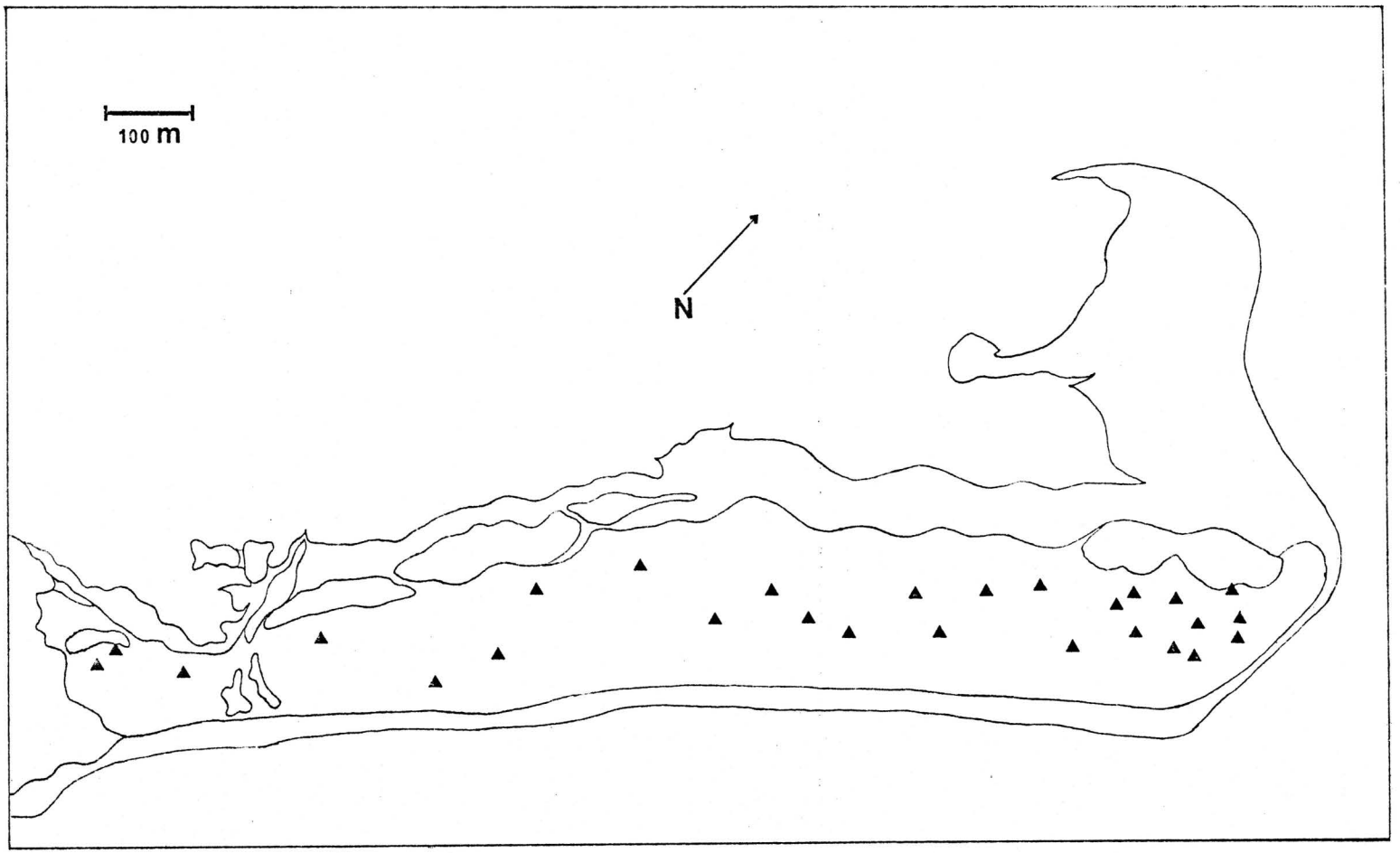

Fig. 5. Map of study area showing 1976 nest site locations on raised sandspit.

bours when travelling between nesting and feeding territories.

Both feeding and nesting territories were maintained until about mid July. In addition to those of breeding pairs, territories were held throughout the season by males which failed to attract mates, as well as by pairs which produced no clutch, or lost a clutch or brood too late in the season to renest.

Territory sizes among plovers vary greatly. Tomkins (1944) reports that territories of Wilson's Plover seldom have smaller radii than 100 ft ($\sim$ 190 m^2) but fails to mention average territory size for the species. Studies of some species have revealed territory sizes within the general range of those of Piping Plovers, for example 625-880 m^2 for Ringed Plover (Mason 1947), 5000 m^2 for Little Ringed Plover (Sluiters 1938) and 885 m^2 for Killdeer (Mace 1971). At least some species maintain considerably larger holdings: Yellow wattled Lapwing (Jayakar and Spurway 1965) defend territories of 25,000 m^2 while Mountain Plover territories have been recorded as about 160,000 m^2 (Graul 1973b). Size of territory probably reflects at least in part the relative amounts of feeding done within the territory and in neutral areas outside. The degree of feeding done within the territory varies considerably with species, and probably also with local conditions. The Red-capped Dotterel (= Kentish Plover) population described by Hobbs (1972) which did not feed near the breeding grounds but at a site 3 km away is probably an extreme case. Ringed Plovers (Mason 1947) and Little Ringed Plovers (Simmons 1956) have been reported to feed mainly on neutral feeding areas, while Mountain Plovers (Graul 1973b) and Piping Plovers do most of their feeding within their own territories.

Distance between nests. -- In 1975 distances to nearest neighbouring nest averaged 51 m for the 23 nests and in 1976 53 m for the 27 known nests (3 of which were renests). If every nest on the spit had been discovered, average distance would be less. The shortest distance between two simultaneously active nests was 3 m.

Wilcox (1959) reported that Piping Plover nests were usually more than 200 ft. (60 m) apart and seldom closer than 100 ft (30 m). Distances between nests have been recorded for several other species (numbers in parenthesis indicate minimum distances recorded): Little Ringed Plover > 185 m (56 m) reported by Simmons (1956), Killdeer 244 m (14 m) by Mace (1971), Kittlitz's Sandplover 18 m (8 m) by Hall (1958), Snowy (= Kentish) Plover 85 m (15 m) by Boyd (1972), Mountain Plover 140 m (Graul 1975), and White-fronted Sandplover (Charadrius marginatus) > 46 m (> 18 m) by Shewell (1951). All these values are generally in the same range as those obtained for Piping Plover.

COURTSHIP

Aerial display. -- Male Piping Plovers embark from their territories (more frequently the nesting territory) on advertisement flights. Deep, slow wing beats and an alternate tilting of the body from side to side create the appearance of a fluttering white object (similar to the so-called Butterfly Flight of other species), and make the bird much

more conspicuous than in normal flight. In advertisement flight the male executes broad elipses and figures-of-eight above the general vicinity of his territory. Flights last up to about one-half hour and may reach heights of 35 m; in between the bird often sweeps to near ground level.

Flights are usually accompanied by one or both of the two advertisement calls. The more frequently used consists of a continuous rapid series of "bec-bec-bec" calls. Less frequently heard, and sometimes interspersed with the rapid call series is a series of long drawn out mournful sounding "queep-queep-queep"'s.

If a female enters the territory during such an advertisement display the flight will often terminate, frequently less than 30 m from where she stands. If the flight display fails to attract a female the male may extend his flight and accompanying calls over neutral feeding areas where unattached females tend to congregate, repeatedly approaching and departing from the area until he is successful in attracting a female to join him in flight back to his territory. Occasionally, mated pairs perform the advertisement flight together while simultaneously calling. More often when two birds are seen to execute the display concurrently, the two performers are rival males. Advertisement display flights and calls may be given during the night, particularly if the sky is not too dark.

Advertisement vocalizations and flights are associated with establishment of territories and acquisition of mates, and decline in frequency with the onset of egg-laying and incubation. Displays and

calls recorded later in the season can usually be attributed to renesting birds which have lost their first clutches or to lone males which have been unsuccessful in attracting mates.

Numerous observations of Butterfly Flight sequences suggest that their primary function lies in courtship. However, in densely populated breeding areas such as Cadden Beach it might equally alert neighbouring males to claim of territory.

Advertising display flight, or specifically Butterfly Flight, has been reported for several plover species. It has been described for Ringed, Little Ringed and Kentish Plovers by Witherby et al. (1965) and Killdeer by Phillips (1972). Tomkins (1944) remarks on the absence of any display flight in Wilson's Plover and Graul (1973b) reports the Butterfly Flight to be rare in the Mountain Plover, which more frequently has an aerial "Falling Leaf Display". While the Butterfly Display plays a greater role in courtship than in territorial aggression in Piping Plovers, Simmons (1953b) regards such flights in Ringed and Little Ringed Plovers to have an aggressive function.

The Butterfly Flight is the only aerial display I have observed in Piping Plovers. All other aerial activity consists of normal flying or the more rapid flight associated with chasing. The Piping Plover has no display similar to the Flight-Threat-Display described by Simmons (1953b) for the Little Ringed Plover.

Scraping. -- With a female present on the territory the male may begin to walk about with deliberate movements, often picking up small

bits of sea shell and tossing them over a shoulder with a deft flick of the head. Periodically he may stop, squat in the sand and, leaning far forward on his breast, pivot about in alternate directions while simultaneously kicking sand out behind. In such a manner a scrape some 10 cm in diameter is fashioned. The male may remain in the scrape for minutes occasionally uttering one or both of the advertisement calls. During pauses in kicking and rotating he will peck up any bits of seashell lying around the rim of the scrape and deflect them under his breast into the scrape. Alternatively the male may move about the territory in a crouched run, with head lowered and tail sometimes spread and elevated, as he quickly moves from scrape to scrape, nestling briefly in each. Sometimes the movement is a crouched walk with frequent pauses to look about. With a female in the vicinity the male may make up to twenty scrapes in series. The same scrapes may be returned to repeatedly. Occasionally a female following a courting male will also stop to scrape briefly. At the closer approach of the female, the scraping male erects and spreads his tail, and increases the tempo of rotations in the scrape.

Tilt display. -- With the female close by, the male may perform a Tilt Display, slowly rising to stand stiffly upright in the scrape, head, body, tail and the partly or completely spread wings all being held in one plane, with tail elevated at an angle of about 30°. The female crouches slightly behind the male and thrusts her beak one or more times among the feathers below the base of his tail. Alternatively

the female may approach from the side, and creeping under the male's now horizontally spread tail, nestle into the sand beneath it, her body perpendicular to his. The Tilt Display may be repeated several times in succession at different scrapes, or the female may move off immediately and await the approach of the male.

Mounting and copulation. -- Advancing toward the female, the male quickly slips into a low gliding crouch with head lowered below the horizontal and drawn well into the body (Fig. 6). As he nears the female the male gradually rises into a very erect posture with neck stretched tall, neck ring conspicuously broadened and the white breast expanded. Simultaneously he beats a high-stepping and increasingly rapid tatoo with his feet. In so doing the feet sometimes hit against the breast with sufficient force that the bird momentarily loses his balance backwards. When the male reaches the female (standing slightly crouched with her legs somewhat spread) he may stand by the base of her tail and continue the tatoo for several minutes longer before flapping his wings and jumping on her back. He remains there for as long as 1.5 min with his tail pumping down along one side of the female's. Following copulation, the female usually shakes herself, preens briefly and moves away from the area. The male usually stays in the vicinity, often preening, especially the neck area.

Frequently such courtship sequences on the ground do not result in copulation. At any point the female may run or fly from the territory, while equally often the male appears to lose interest and begins to preen. A frequent point of interruption occurs after the male has

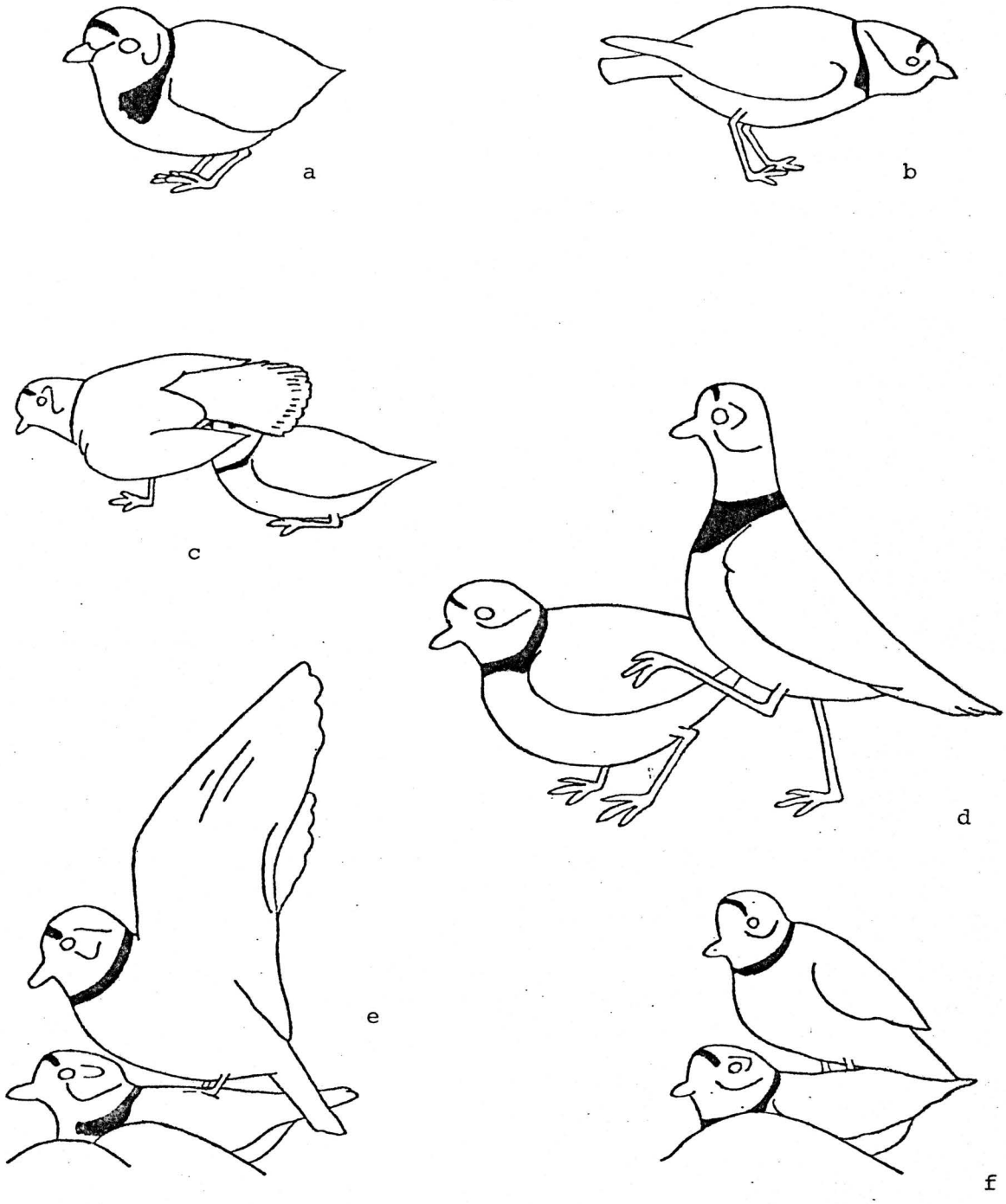

Fig. 6. Courtship postures: a - territorial male with exaggerated neck band, b - posture used during low gliding run, c - female thrusting beak among feathers beneath male's tail, d - male performing rapid high-stepping tatoo beside female, e - mounting, f - copulation.

begun his tatoo, when the quietly awaiting female may simply move away at his closer approach. If she is near enough the male will continue his advance in the high-stepping tatoo; otherwise he first reapproaches her by the low gliding run before commencing high-stepping again. If the female repeatedly moves away at the crucial moment, the male soon loses interest and often begins to preen.

Comparison with other species. -- Courtship behaviour in the Piping Plover is basically similar in pattern to that found in other Charadrius species, varying only in details. Sideways tossing and scrape displays are fairly standardized among plovers. Tilt Displays have been recorded in a number of other species of Charadrius plovers including Little Ringed (Sluiters 1938 and Simmons 1953a), Ringed (Laven 1940), Snowy (= Kentish; Boyd 1972), Mountain (Graul 1973b) and Killdeer (Phillips 1972). None of these accounts contains references to the female thrusting her bill among the feathers beneath the male's tail, as occurs in the Piping Plover. There is some variation among species in the position of the wings during the Tilt Display: both Little Ringed (Glutz et al. 1975) and Piping Plovers spread their wings on a uniform plane, while the Snowy (= Kentish) and Mountain Plover droop the wing that is toward the female. The Killdeer apparently does not spread its wings.

The details of mounting and copulation differ somewhat with species. In most, males approach females in a low gliding run which somewhat resembles the posture used during low intensity horizontal

threat (see p.13). Before actually mounting the female, male Snowy (= Kentish) Plover (Boyd 1972), Red-capped Dotterel (= Kentish Plover; Hobbs 1972), Killdeer (Phillips 1972), Mountain Plover (Graul 1973b) and Wilson's Plover (Tomkins 1944) as well as Piping Plover adopt an upright precopulatory posture with rapid high-stepping foot movements. The male of the Snowy (= Kentish) Plover, Red-capped Dotterel (= Kentish Plover), Killdeer, Wilson's Plover, Little Ringed Plover (Simmons 1953a) and Mountain Plover continue to tread while standing on the female's back; this has not been observed in the Piping Plover. The Snowy (= Kentish) Plover (Boyd 1972) and the Wilson's Plover (Tomkins 1944) are apparently the only species in which males grasp the female's neck feathers with their bills during copulation.

Piping Plover pairs copulate anywhere within their nesting and feeding territories but Snowy (= Kentish) Plover, Killdeer (Boyd 1972) and Mountain Plover (Graul 1973b) apparently only copulate on nest or scrape sites. Copulatory behaviour in Piping Plovers does not seem to persist after the clutch is complete. However in some species such as Killdeers (Davis 1943) it occurs frequently up until the time of hatching and apparently plays a role in maintenance of the pair bond.

DISTRACTION BEHAVIOUR

While an approaching intruder is still some distance off, the incubating bird usually steals away from the nest. I measured distances at which birds left their nests on 65 occasions when I approached them;

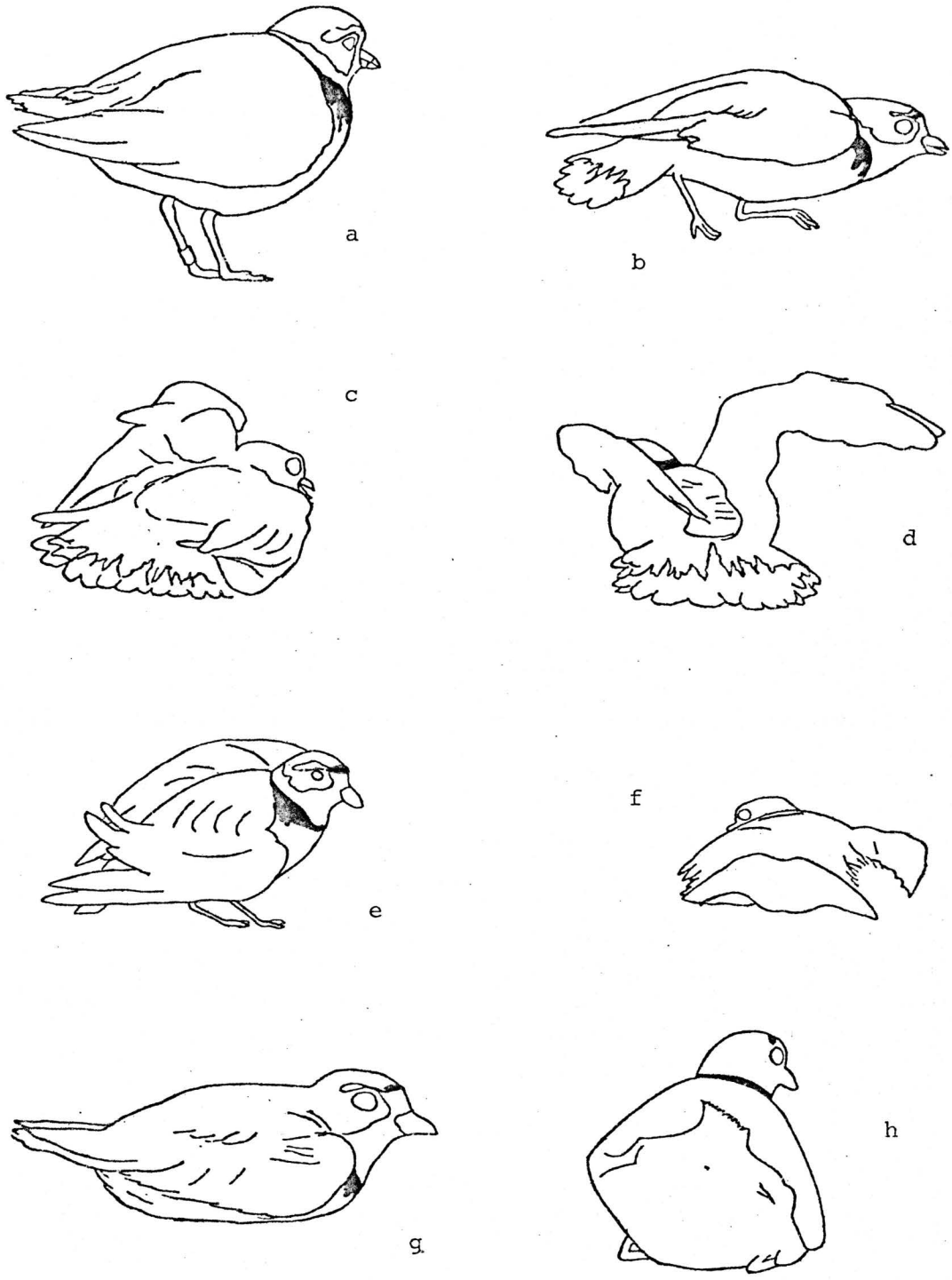

Fig. 7. Distraction behaviour: a to f - broken-wing displays, g and h - false brooding.

the average was 43 m. Some birds habitually left the nest when the approaching intruder was more than about 85 m away (the maximum distance at which I could see the bird's departure) while others regularly remained on the nest until approached to within 5 or 10 m. In general birds on heavily used recreational beaches were more tolerant of close approach than those on isolated beaches such as Cadden Beach. There was no indication of increasing reluctance to leave the nest as incubation progressed.

After a bird has initially left the nest it returns along a zigzag course toward the intruder, its advance punctuated by frequent pauses, head-bobs and single peep notes. If the mate was not previously in the area it usually soon appears, probably in response to the call notes of its partner. Typically, one member of the pair displays at close range while the other moves about at a greater distance, running, head-bobbing, flying and piping as it circles the intruder. In the lowest intensity form of distraction the bird scuttles away from the observer in a low crouch with the closed tail slightly raised to show the white underparts (Fig. 7). It frequently stops to squat on the sand with tail up, or to nestle flat as if settling onto a nest or brood. If the bird moves away at an angle from the intruder it bends its near leg and lowers that side of its body so that it becomes more visible. With increasing intensity the tail is partly spread and the closed wings, cupped and beating, are held out slightly from the body as the bird scurries off. At still higher intensity the tail is partly fanned and depressed so that it drags. The wings are fully spread, trailing in a

flutter of rapid beats as the bird scampers along. The nearer side of the body (including wing and tail) are again slanted toward the intruder. The far wing beats higher and touches the ground less frequently while the nearer wing beats a lower arc and often touches or rests on the ground. The display is generally given as the performing bird is actively moving away from the intruder; during pauses the bird may flap its wings dramatically, slowly wave one wing in the air, or simply hold the static posture of spread wings and tail. It frequently looks over its shoulder to observe the intruder.

During high intensity distraction, constant whirring sounds may be emitted. These vocalizations plus the flashy brown, white and black pattern presented by the moving bird help to attract attention to it. Some displaying birds have come to within 2 m of me while others have been observed (with binoculars) performing at distances of up to 100 m. Distraction display may occur at any time from prior to egg-laying until after fledging, although it is usually most frequent and intense around the time of hatching. Both birds of a pair may simultaneously engage in distraction displays, especially in areas of high density of nests or broods, where up to a dozen adults engaged in flying, piping, running, head-bobbing and distraction displays will converge on an intruder. I have not been able to establish any difference between the sexes in the partitioning of distraction behaviour. After hatching, one bird may take charge of leading the young to safety while the other displays toward the intruder.

The various forms of the distraction display (squatting, false brooding, high-tailed running, crouch run and injury feigning) have been reported widely among the plovers. In addition, Killdeer (Allen 1932) and Mountain Plover (Graul 1975) have a distinctive Wings-out Rush Posture which is apparently used for cattle and other large mammals. I have not observed such a display in the Piping Plover.

NESTING

Choice of nest site. -- Piping Plovers typically select nesting sites in relatively level, unvegetated terrain. Of 61 nests, 55 were located on raised areas of sandspits where little or no slope was evident to the eye. The remaining 8 were on the inclined bases of dunes. Fine gravel and stones (diameter 1 to 12 cm) were scattered across the sand around 31 of 38 nests examined.

Wisps of windblown seaweed were the nearest objects to 13 nests but since seaweed was constantly being redistributed across the beach by wind it has not been included in the following discussion. Nearest object to nest was located within 0-0.5 m in 10 cases, 0.5-1 m (5 cases), 1-3 m (6 cases), 3-6 m (4 cases), > 6 m (13 cases). Nearest objects to nests (within a 6 m radius) were clods of peat (5 cases), sprigs of Ammophila brevigulata (16 cases), Arenaria peploides (2) and Cakile edentula (2). In only 3 of the 15 cases in which nearest

objects were within 1 m of the nest were these objects (i.e. peat) other than vegetation. Considering that vegetation in the vicinity of nests was usually very sparse and that frequently spring growth did not begin prior to nest establishment, it thus seems that in almost all cases the object which was ultimately the closest to the nest was not present during initial scrape construction. These observations do not appear to indicate any tendency among Piping Plovers to nest close to conspicuous objects.

In general, on those beaches where a broad expanse of suitable nesting habitat was available most nests were on the bare sand (and scattered gravel, if present), away from all but very sparse vegetation. However, on beaches where suitable nest site was confined to a narrow (as little as 2 m wide) strip of sand between the wrack line and the grass of the seaward facing dunes nests were sometimes placed under sprigs of A. brevigulata. Where nest habitat is sufficiently expansive the birds seem to prefer nest sites which give them a clear view in all directions, and permit them to steal from their nests at great distances from intruders or predators. Where nesting habitat is restricted to a narrow belt which might be easily worked systematically by a predator, there may be benefits in nesting among the thinly growing A. brevigulata. By so doing the birds probably also reduce the chances that their nests will be innundated by high storm tides.

Several plover species show a strong preference for selecting nest sites on flat areas as opposed to ground with even a gentle slope.

Mountain Plovers locate nests on ground with less than 5° slope (Graul 1975). A similar tendency has been noted for the Three-banded Plover (Charadrius tricollaris) by Brown (1948) and for the Double-banded Courser (Rhinoptilus africanus) by Maclean (1967). It has not yet been established whether the proclivity toward level nesting sites is as strongly developed in the Piping Plover.

Among the Charadriidae there is a widespread tendency to locate nests close to conspicuous objects. The practice has been reported for Kittlitz's Sandplover (Hall 1958), Snowy Plover (= Kentish) (Boyd 1972), White-fronted Sandplover (Maclean and Moran 1965), Mountain Plover (Graul 1975), Spur-winged Plover (Hoplopterus spinosus) (Hall 1965), Lapwing (Cott 1966), Killdeer (Bunni 1959), St. Helena Sandplover (Charadrius sanctaehelenae) (Pitman 1965) and the Black-breasted Plover (Vanellus tricolor) (Favaloro 1944). Maclean and Moran (1965) suggest that the main selective advantage to nesting next to a prominent object comes from the disruptive effect of extraneous objects in rendering the eggs and the incubating bird less conspicuous rather than from facilitation of relocation of the nest by returning adults.

Nest structure. -- Some Piping Plovers line their nests with fragments of broken sea shell. Shells are accumulated in the nest as a result of the stone-tossing activities of courtship and incubation (see section on Courtship). Nests located on beaches of pure sand or sand mixed with fine gravel and stones tend to be unlined while those in areas where broken sea shells are present in the sand usually contain

some lining. Six of 38 nests examined contained no shell lining, 15 were sparsely lined, 14 were noted as moderately lined, and 3 were sufficiently well lined that little sand was visible beneath the shell fragments.

Nest sites on mixed gravel and sand tend to be less conspicuous than those on pure sand. However a lining of bleached sea shells makes a nest more easily noticed from above. This probably does not aid adults in relocating the nest, since they normally approach the nest site on foot from a long distance or after a low and direct flight to at least 15 m from the nest. On the other hand, a well-lined nest is likely more obvious to aerial predators such as gulls and crows. Well-lined nests become particularly conspicuous in wet weather when the sand colour darkens and the sea shell fragments by contrast appear whiter. It may be significant that the 3 clutches which disappeared in 1976 came from lined nests (2 moderately, 1 sparsely) and were lost during days of heavy rains. At the time, 2 of the clutches were incomplete and full-time incubation had probably not begun. It appears then, that these nests were predated during the portion of the nesting cycle when they were exposed to aerial observation for the longest periods of time, and when their visibility was greatly increased by the damp conditions.

Other plover species are reported to line their nests with a variety of materials including cow manure, roots, leaves, mud, sticks, pebbles, shell fragments, dried seaweed, and quartz chips (Jeffery and

Liversidge 1951, Graul 1975 and Boyd 1972). Hall (1958) states that in Kittlitz's Sandplover the lining of the nest consists almost exclusively of the material upon which the scrape is located. Thus in most species lining material is a reflection of either scrape substrate or easily transportable materials available in the general area or both.

A possible advantage conferred on eggs in lined nests may be improved drainage during wet conditions. In Red-capped Dotterels (= Kentish Plover) the amount of nesting material has actually been found to depend on the dampness of the nest site (Hobbs 1972). In 1975 3 clutches of Piping Plover eggs at various stages of incubation were subjected to sufficiently heavy rainfall to cause marked discolouration and staining from watermarks. The successful hatching of all eggs in these clutches suggests a tolerance of at least temporary conditions of excess moisture. Perhaps any advantages of improved drainage in a well-lined nest only become obvious during prolonged damp conditions.

Among other plover species nest-lining may indeed increase egg survival by providing material for egg-covering in some species, or by improving drainage. However the adaptive value of this practice to Piping Plovers appears to be at best slight.

EGG LAYING

Onset. -- I observed courtship activity and copulation to occur repeatedly within an established pair during the early part of the repro-

ductive season, although it did not always ensure egg-laying . For first nests, scrapes appeared in the territory up to two weeks before the female selected a scrape and began egg-laying, but I was unable to determine how long before the first egg is laid that copulation is usually initiated.

Piping Plovers continue to copulate throughout the egg-laying period. The possibility that repeated copulation may indeed be necessary during this period to assure fertilization of each egg is suggested generally by the presence of infertile eggs in some nests, and more particularly by one instance in which the first and third eggs of a clutch were infertile while the second and fourth produced viable young. Copulation and associated displays fall off rapidly after the clutch is complete and apparently do not contribute to the continued maintenance of the pair bond.

The onset of egg laying is probably to some extent associated with weather conditions. Laying began in 1976 about one week earlier than in 1975 (Table I), probably a reflection of the earlier spring in 1976.

Reports on when copulation is initiated in other plover species are few, but Boyd (1972) notes that in Snowy (= Kentish) Plovers copulation may occur up to 5 days before the first egg is laid. Sluiters (1938) further notes that in Little Ringed Plovers not all copulations are successful and Parsons (1971) and Pierotti (pers. comm.) have found a correlation in Herring Gulls (Larus argentatus) between the decline in copulation frequency which occurs after egg-laying has commenced, and the higher incidence of infertility in later eggs of a clutch. The

Table I. Seasonal distribution of clutch initiation and hatching in 1975 and 1976.

	1975		1976	
	# of clutches initiated[1]	# of nests hatching[2]	# of clutches initiated[1]	# of nests hatching[2]
April 18-24			2	
April 25-May 1	1		7	
May 2-8	8		9	
May 9-15	8		4	
May 16-22	3		5	
May 23-29	2		3	2
May 30-June 5		1	2	6
June 6-12	2	10	3	8
June 13-19		6	1	4
June 20-26		1		4
June 27-July 3		3		4
July 4-10		0		1
July 11-17		2		3
July 18-24				1

1 Calculated from known incubation and laying periods or by subtracting 34 days (means of incubation [28 days] plus egglaying [6 days] from known or calculated hatching dates.

2 Calculated from known hatching dates or by comparison of growth curves of unknown chicks with growth curves of known age chicks.

observations of these workers tend to support the suggestion that it may indeed be necessary for a successful copulation to occur prior to the laying of each egg to ensure fertilization of the entire clutch.

The role played by weather in clutch initiation has been mentioned by several workers. Graul (1975) reports that rainy weather inhibits egg-laying in Mountain Plover, and Rittinghaus (1956 and 1961) related onset of laying in Kentish Plovers to temperatures above 10°C.

Duration of laying period. -- At three nests it was possible to determine laying dates for both first and last eggs laid. In two nests the fourth egg was laid on the sixth day after the first egg was laid, and in one nest on the seventh day. Wilcox (1959) reports that Piping Plovers lay eggs on alternate days, completing the clutch in six days.

Intervals between the laying of successive eggs are shown in Table II and were usually in the vicinity of two days.

The three eggs for which precise times of laying are known were laid between 1000 and 1400 hours. However it is not known if all eggs are laid during the day as has been reported to be the case for the White-fronted Sandplover (Blaker 1966).

Egg-laying behaviour. -- One female was observed laying an egg. The egg, the second in the clutch, was laid immediately after the male and female had participated in a tilt display on the nest. Following

Table II. Intervals between the laying of subsequent eggs.

Nest	Position in clutch	Duration of interval (hr)
A	2-3	$\sim$ 44 ($<$ 46)
	3-4	$\sim$ 54 ($>$ 51)
B	3-4	$\sim$ 53 ($>$ 48)
D	1-2	$\sim$ 72
	2-3	$>$ 52
	3-4	$<$ 47
F	1-2	$\sim$ 48
	2-3	$\sim$ 48
5	3-4	$>$ 77

copulation nearby the female settled onto the scrape and remained there 45 minutes. Part of the time she actually sat down on the nest but most often maintained a semi-crouched position, frequently changing directions, shuffling about, looking around, pecking at the edge of the scrape, poking under her breast, in almost continuous restless activity. While the female was crouched so, her tail was sometimes spread slightly and depressed. The egg was not actually observed emerging. The restless shuffling activity might have been associated with release of the egg or with rolling and rotating it in an effort to dry it. Some freshly laid eggs were distinguished from others in the clutch for up to about eight hours. They were usually darker in colour and often had sand or remnants of membraneous material stuck to them. On one newly laid egg it was still possible to smear the spotting.

Accounts of egg-laying in other plovers are few. Graul (1975) describes Mountain Plovers pumping the tail and then rocking sideways as the egg drops out. Boyd (1972) observed two female Snowy (= Kentish) Plovers limping prior to egg-laying and then walking normally afterward.

Relaying. -- If a clutch or brood is lost, courtship activity (including butterfly flights and scrape displays) begins very soon afterward. If the loss occurs after mid June a second clutch normally does not ensue. Two pairs of Piping Plovers that had lost their first nests were later observed with four tiny chicks not more than one or

two days old. Allowing six days for egg-laying and 28 for incubation (see section on Incubation), the first eggs of the second clutches were probably laid about five days after the loss of the first nests.

Although I have observed no second attempts to renest by Piping Plovers, successive renestings have been recorded for other plover species. Boyd (1972) reports a Snowy (= Kentish) Plover female producing three clutches, and Ringed Plovers in southeastern Britain apparently regularly produce up to five clutches per year (Prater 1974).

EGGS

Appearance. -- The pale buff eggs are marked with fine splotches of black, brownish-black or purplish-black. The markings are usually distributed quite evenly over the shell but in some eggs there is a tendency towards more, larger and darker spotting at the broad end. Within clutches intensity and size of markings are usually quite similar.

Dimensions and weight. -- For 215 eggs from 56 clutches, mean length was 32.5 mm (range 29.6-35.4, S.D. 0.955 mm) and mean breadth was

24.8 mm (range 23.4-26.1, S.D. 0.500 mm). The mean index of egg volume (length x breadth^2) was 19,927 mm^3 (range 16,486-22,387, S.D. 1,054.3 mm^3). (Further data appears in Appendix A.) Table III presents data for the 16 eggs whose order of laying in the clutch was known. A one-way analysis of variance showed no significant difference at the 0.05 level among the four clutch positions for length, breadth or volume (Table IV). One-way analyses of variance indicated highly significant differences in length, breadth and volume of eggs among the clutches of individual females (Table V). Egg weight decreases with the approach of hatching, according to the relationship shown in Fig. 8.

Wilcox (1959) records mean length of 31.7 mm and mean breadth of 25.1 mm for 26 Piping Plover eggs on Long Island, values close to those in Nova Scotia. He also reports that the last egg of the clutch tends to be the longest and often the widest and heaviest. However, one-way analyses of variance on the data shown in Table III combined with Wilcox' data showed no significant difference (0.05 level) in length, breadth or volume among the four clutch positions (Table VI). Interestingly, Wilcox' average weight of 9.6 grams for 35 fresh eggs is somewhat lower than that expected from Fig. 8.

Clutch size. -- Of 68 complete clutches examined 65 (or 95.6%) contained four eggs and three contained three for a mean of 3.96 eggs per clutch. Wilcox (1959) found 85.2% of 526 nests checked on Long Island to contain four eggs, and obtained a mean clutch size of 3.84 eggs. Means for Nova Scotia and Long Island are significantly different at

Table III. Measurements of Piping Plover eggs of known order of laying.

Egg order	Number	Length (mm)		Breadth (mm)		Index of volume (mm^3)	
		Mean	Range	Mean	Range	Mean	Range
1	4	32.9	31.9-34.5	24.5	23.9-24.9	19783.3	18221.5-21390.3
2	4	32.6	32.1-33.3	24.7	24.3-25.0	19791.4	19328.0-20111.8
3	4	32.6	30.9-33.2	25.1	24.8-25.8	20549.8	19158.3-22099.2
4	4	32.9	32.4-33.7	25.3	24.8-26.1	21037.8	20234.8-22071.2

Table IV. Results of one-way analyses of variance for differences in length, breadth and volume of eggs with position in the clutch (based on Nova Scotia data).

	Source of Variation	df	Sum Squares	Mean Squares	F
Length (mm)	Among Groups	3	0.457	0.152333	0.1948203
	Within Groups	12	9.383	0.7819166	n.s.[1]
	Total	15	9.84		
Breadth (mm)	Among Groups	3	1.6069	0.535633	2.365261
	Within Groups	12	2.7175	0.2264583	n.s.[1]
	Total	15	4.3244		
Index of Volume (mm) (lb^2)	Among Groups	3	4,300,000	1,433,333.3	1.3333
	Within Groups	12	12,900,000	1,075,000	n.s.[1]
	Total	15	17,200,000		

[1] not significant

Table V. Results of one-way analyses of variance for differences in length, breadth and volume of eggs among the clutches of individual females (based on Nova Scotia data).

	Source of Variation	df	Sum Squares	Mean Squares	F
Length (mm)	Among Groups	49	107.51	2.19	5.311
	Within Groups	150	61.97	0.41	sig.[1]
	Total	199	169.48		
Breadth (mm)	Among Groups	49	33.06	0.67	7.061
	Within Groups	150	14.33	0.10	sig.[1]
	Total	199	47.39		
Index of Volume (mm) (lb^2)	Among Groups	49	148,433.4	3,029.3	7.633
	Within Groups	150	59,526.9	396.8	sig.[1]
	Total	199	207,960.3		

[1] significant

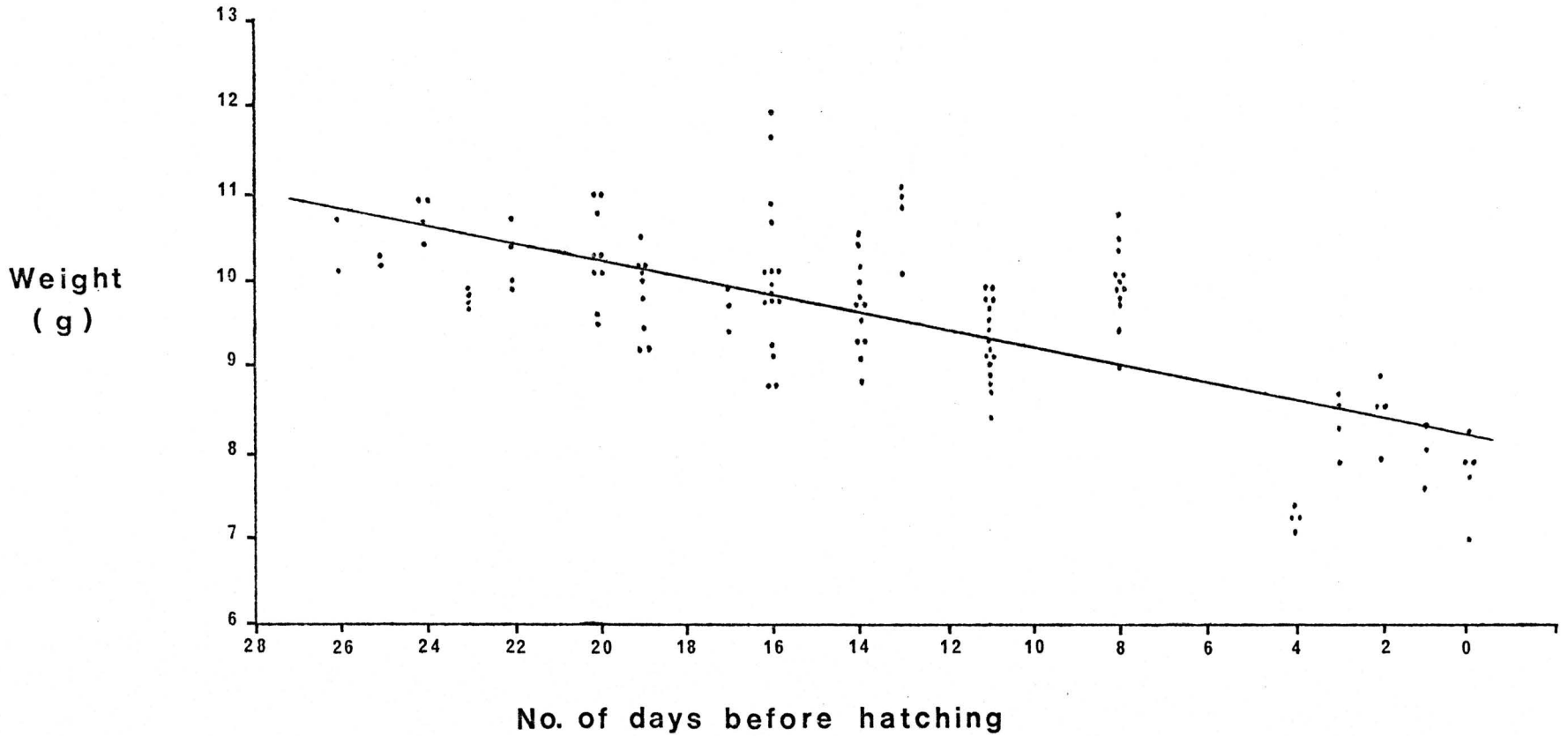

Fig. 8. Decline in egg weight with nearness to hatching.

Table VI. Results of one-way analyses of variance for differences in length, breadth and volume of eggs with position in the clutch (based on Nova Scotia data combined with that reported in Wilcox (1959).

	Source of Variation	df	Sum Squares	Mean Squares	F
Length (mm)	Among Groups	3	3.064	1.02	1.166
	Within Groups	35	30.61	0.8746	n.s.[1]
	Total	38	33.674		
Breadth (mm)	Among Groups	3	0.987	0.329	1.4205
	Within Groups	35	8.105	0.23157	n.s.[1]
	Total	38	9.092		
Index of Volume (mm) (lb^2)	Among Groups	3	3,978,000	1,326,000	1.1961649
	Within Groups	35	38,799,000	1,108,542.8	n.s.[1]
	Total	38	42,776,000		

[1] not significant

the 0.05 level (t-test for unequal variances; Steele and Torrie 1960). However in Wilcox' study some nests containing fewer than 4 eggs may not have held complete clutches at the time of examination so the mean clutch size for Long Island Piping Plovers may actually be larger than that calculated from his data.

Clutch size decreases in a number of bird species as the season progresses. Prater (1974) reports such to be the case for Ringed Plovers in Britain while Tufts (1973) suggests that Piping Plovers in Nova Scotia tend to lay fewer eggs in second clutches. My data do not support this contention. The three three-egg clutches observed were all first clutches and no second clutches containing fewer than four eggs were discovered.

INCUBATION

Onset. -- Full-time incubation usually begins with the completion of the clutch, but in some four-egg clutches at least partial incubation may commence following the laying of the third egg. Females spend up to 45 minutes on the nest while laying an egg, warming any previous eggs at the same time. I have observed males briefly sitting on or standing over clutches containing one or two eggs but this always appeared to be associated with courtship display. Male Snowy (= Kentish) Plovers (Boyd 1972) and Black-bellied Plovers (Hussell and Page 1976) have also been noted standing over or sitting on incomplete clutches.

Role of the sexes. -- During the daytime both sexes incubate, probably about equally. This is suggested by observations of partner exchange at the nest and from results of trapping adults. Of 9 birds of known sex trapped on their nests, 5 were females and 4 were males. Wilcox (1959) presents further evidence: in 206 nests in which both sexes were trapped on the same day, 104 first captures were females and 102 were males.

In other monogamous plover species the sexes also share incubation, although considerable variation may exist in the proportion undertaken by each partner. The male Killdeer is thought to incubate more than the female, particularly as hatching approaches (Davis 1943). In several species female plovers assume most daytime duty: Chestnut-banded Sandplover (Jeffery and Liversidge 1951), Snowy (= Kentish) Plover (Boyd 1972) Red-capped Dotterel (= Kentish Plover) (Hobbs 1972), and Wilson's Plover (Tomkins 1944). I have no data on the partitioning of nighttime incubation by Piping Plovers, although Boyd (1972) reports that female Snowy (= Kentish) Plovers are on their nests during the night and much of the day, while males incubate for a few hours each morning and evening.

Behaviour on the nest. -- At intervals the incubating Piping Plover may engage in various activities: poking beneath its breast, pecking at objects along the rim of the scrape, changing direction in the nest, fluffing itself and resettling, and kicking sand out from beneath the

eggs. Sometimes it steps off the nest and preens or stone-tosses briefly. The bird also leaves the nest when intruders enter the territory. During extreme conditions of wind or sun there seems to be some tendency to face into the wind and away from the sun. When the weather is damp, windy or cold the incubating bird sits flattened into the scrape with head drawn well into the shoulders. Under more favourable conditions a higher more alert position is adopted. During very hot weather the incubating bird stands or crouches over the nest, shading the eggs. The closed wings are drooped and held slightly out from the body and the beak is open.

The behaviour of Piping Plover on the nest has much in common with that reported for other plover species. Pecking and side-throwing movements are frequently observed displacement activities used in various contexts by a number of plover species including Killdeer (Davis 1943), Snowy (= Kentish) Plover (Boyd 1972) and Blacksmith Plover (Hall 1964).

A number of Charadrii species nest in sparsely vegetated habitats. The extremely high ground temperatures which may occur in such locations have probably led to some specialized incubation behaviour. The tendency to face away from the sun during hot periods has been reported for Mountain Plover by Graul (1975) and Double-banded Courser (Rhinoptilus africanus) by Maclean (1967), and is clearly of advantage in giving a better view of the surrounding area. The habit of shading rather than incubating the eggs during extreme heat has been noted by

Graul (1975) in Mountain Plover, Boyd (1972) in Snowy (= Kentish) Plover, and Davis (1943) and Pickwell (1930) in Killdeer. Standing over the nest presumably allows the eggs to remain at air temperature while permitting heat dissipation from the adult. A third method used by certain Charadriiformes for the cooling of eggs is to wet the belly feathers to bring water to the eggs. The air temperature in the environment of the Piping Plover probably rarely exceeds incubation temperature and belly-soaking has not been observed in this species.

Incubation relief. -- Relief from incubation is normally initiated by the relieving bird, which announces its arrival on the territory with one or two single peeps. The sitting bird usually responds in the same manner and sometimes also makes sideways-throwing movements with shell fragments along the edge of the nest. Whether entering the territory in flight or on foot the relieving bird always goes to the nest for the last 20 m or so on the ground, occasionally making stone-tossing movements as it advances. Individuals have preferred directions and routes for approaching and leaving the nest, indicated by sets of tracks radiating from the scrape. At the approach of the mate the incubating bird walks away from the nest; it too may stone-toss. Male birds when being relieved sometimes move away in a low crouched walk similar to the low gliding run of courtship. The relieving bird settles immediately onto the eggs uttering soft throaty peeps. Often the departing bird preens briefly. If it leaves the territory one or two single peep notes or peep-lo calls may be given. If it remains it

usually squats on the sand at some distance from the nest and closely resembles an incubating bird. These resting spots may be reused regularly.

During the day partner exchange takes place at intervals of about 0.5 to 2.5 hr, occurring on average about every 80 minutes. Results from observations of incubation relief are presented in Table VII. These few data suggest the birds may prefer to leave the nest for periods of either less than 1 hr or greater than 2 hr, but not for intermediate periods.

The use of sideways-throwing and stone-tossing movements during incubation relief has been reported for a number of other plover species including Snowy (= Kentish) Plover (Boyd 1972), Red-capped Dotterel (= Kentish Plover) (Hobbs 1972), Killdeer (Davis 1943), Kittlitz's Sandplover (Hall 1958) and Blacksmith Plover (Hall 1964). Boyd (1972) also reports that in Snowy (= Kentish) Plover the pecking and tossing movements become reduced to mere nods and bobs as incubation progresses. These movements may be considered to derive from nest building behaviours; decline subsequent to nest construction therefore seems logical.

Length of interval between partner changeover on the nest may average longer in Piping Plovers than in some other species. Times of 15 to 90 minutes for Killdeer (Davis 1943) and 20 to 80 minutes for Blacksmith Plover (Hall 1964) have been reported.

Table VII. Intervals of incubation relief.

Interval between partner exchange (min)	0-30	31-60	61-90	91-120	121-150
No. of observations	3	5	1	2	5

Finding covered eggs. -- Although birds go unerringly to nests, some observations suggest that they may at times have to search for eggs covered with windblown sand. Occasionally when a trap was set up over a nest the displaced adult returned to the area and moved about with slow, deliberate steps, in turn rapidly shuffling each foot beneath the surface of the loose sand. The movement appeared to be identical to the foot-trembling motion sometimes used by feeding plovers (see section on Feeding). Evidently the birds were trying to find their eggs.

Drifting sand is regular on Cadden Beach and untended nests fill in rapidly. On occasion I have seen eggs with as little as one- quarter of their surface area visible. Before resuming incubation adults remove the sand by leaning forward on the breast in various positions in the scrape and kicking sand out behind. Although I have never observed it in Piping Plover a number of tropical and subtropical Charadrii including four Charadrius species deliberately cover their eggs with nest material or sand. Kittlitz's Sandplover (Blaker 1966; Conway and Bell 1968; Hall 1958, 1959, and 1965; Pitman 1965), White-fronted Sandplover (Hall 1960, Liversidge 1965 and Shewell 1951) and Kentish Plover in Arabia (Meinertzhagen 1954) are all reported to use a rapid kicking motion of the feet to cover the eggs. Milon (1951) has suggested there may be an evolutionary relationship between foot-vibrating during feeding and courtship, and the movements used for

egg-covering. Jehl (1975), however, sees a clear distinction between foot-paddling behaviours used in foraging and the various movements associated with nest-making.

Accounts of eggs becoming uncovered are scarcer. Several species not known to cover their eggs have the ability to locate and uncover buried eggs. Nickell (1943) describes Killdeer using the bill to find and dig out eggs buried beneath about 18 cm of snow. Little Ringed and Kentish Plovers in Germany can locate and uncover experimentally buried eggs with their bills (Walters 1956). It is interesting to note that in Kittlitz's Sandplover, in which egg-covering is highly developed, the bill is used only to begin uncovering the eggs, while the bulk of the material in the nest is removed by kicking movements similar to those used in scrape construction (Conway and Bell 1968). This presumably is more efficient than the use of the bill alone shown by those species whose eggs are only accidentally or experimentally buried.

The lack of bill probing and the use of feet to clear sand out of nests in Piping Plover suggest that this species, like Kittlitz's Sandplover, is well adapted to contend with routinely buried eggs. However I have found no accounts in the literature of foot-trembling being used to find eggs. This may be uniquely adapted to the highly unstable windblown beaches where the Piping Plover makes its summer home.

Loss of mate. -- One lone female incubated a clutch of four eggs for a minimum of 39 days before deserting. Death of the embryos probably resulted from chilling during the periods the nest was untended. Boyd (1972) and Rittinghaus (1956) report that widowed female Snowy (= Kentish) and Kentish Plovers desert within four to six days after the disappearance of a mate. It therefore seems surprising that the widowed Piping Plover tended its nest alone for such a long period.

HATCHING

Incubation period. -- Based on 7 nests the average incubation period (time from laying of last egg until hatching of last egg to hatch) was 28 days. Five clutches hatched in 28 days, one in 27 days, and one in 29 days. In addition two clutches in nests located 3 m apart took minimums of 31 and 38 days to hatch, the delay presumably caused by the greater than normal amounts of time devoted to territorial interactions observed between these adjacent pairs.

Out of 14 nests checked, Wilcox (1959) obtained incubation periods for Piping Plovers ranging from 27 to 31 days, with an average incubation time of 28.1 days. Abnormally protracted incubation periods have also

been described for individual clutches of Oystercatchers (Haematopus ostralegus) and are attributed to time the adults were kept off the nest by human disturbance (Keighley and Buxton 1948). Hayes (1972) cites a case of prolonged incubation in the Spotted Sandpiper (Actitis macularia), which she attributes to a delay in initiation of steady incubation due to the too close proximity of another nest.

Hatching of Eggs. -- Tiny star-shaped cracks first appear around the broad end of eggs up to 5 days prior to hatching. Peeping calls can be heard up to 2 days in advance. Eggs usually are not pipped until within 6 hr of hatching. There was no indication of a relationship between sequence of hatching and order of laying.

Several other workers have reported cracking and peeping in eggs before hatching. Mountain Plover eggs first show cracking 3 to 4 days and pipping as early as 12 hr before the emergence of the chick (Graul 1975). Peeping in the egg can be heard up to 3 days before hatching. Snowy (= Kentish) Plover eggs are cracked 2 to 4 days and pipped 4 to 5 hr before hatching (Boyd 1972). Peeping was not reported but tapping has been heard inside the shell, as early as 84 hr prior to hatching. Davis (1943) reports pipping as early as 36 hr and peeping by 48 hr before Killdeer eggs hatch. She also notes that adults peep in response.

Synchrony of hatching. -- In most clutches eggs hatch witin 4 to 8 hours of each other. However in several clutches the hatching period lasted up to 45 hr. In such cases the delay normally involved

only one egg. Eggs failing to hatch were abandoned within 1 to 2 days of the hatching of the rest of the clutch. Presumably peeping noises and movements of the chick within the shell enable adults to distinguish between dead embryos and ones which would imminently hatch. The usual hatching period in Piping Plovers lies in the range reported for several other plover species: 6 to 24 hr for Snowy (= Kentish) Plover (Boyd 1972), 6 to 16 hr for Killdeer (Davis 1943) and 3 to 41 hr for Mountain Plover (Graul 1975).

Egg shell removal. -- Egg shells apparently are not removed immediately upon hatching but only as they become visible to the incubating bird. This occurs if a shell fragment gets worked out from under the breast onto the rim of the scrape or when partner exchange takes place. The incubating bird removes the shell by picking it up in its bill and walking up to 40 m away before dropping it. One bird flew with the shell after it had walked about 10 m from the nest.

Seasonal distribution of hatching. -- Numbers of nests hatching per week are shown in Table I. In 1975 the peak period of hatching occurred during the second and third weeks of June while the 1976 peak came during the first two weeks of June. How many of these were renests is unknown, but probably a number of the late June and July hatchings fit in this category. Harris (1969) raises the possibility that in Oystercatchers individuals breeding for the first time are usually late nesters. The one nest that I observed of a known first

year bird hatched July 6, 7 and 8, possible evidence that inexperienced birds are late nesters.

Hatching success. -- Out of 25 nests checked on Cadden Beach in 1975, 77 young hatched from 97 eggs, a 79.4% hatching success. Average number of young hatching per nest was 3.08. In 1976 104 eggs were found in 26 nests of which 75 hatched for a success rate of 72.1% or an average of 2.88 chicks hatched per nest.

Wilcox (1959) found somewhat higher hatching success among Long Island Piping Plover over a twenty year period. He obtained 91% hatching success with an average of 3.52 young hatched per nest.

Reasons for failure. -- Forty-nine of 201 eggs observed on Cadden Beach failed to hatch. Of these, 9 were damaged during handling or trapping; 17 were destroyed by mammals or birds (cattle, and probably gulls or crows); and 23 were abandoned in the nest. The eggs in the last category were presumably infertile or contained inviable embryos.

YOUNG

Departure from nest. -- Newly hatched chicks dry within several hours and leave the nest on short forays soon after. At first they do not stray far from the scrape site (usually < 10 m) and return repeatedly to be brooded. In their early wanderings they stop often to peck at the ground or to rest on their heels. Contact with the

parents is maintained by high pitched cheeping calls. Adults respond with soft single peeps. The nest is usually abandoned within several hours of the hatching of the last chick. However, during cold or wet weather, or in the case of a prolonged hatching period, some chicks may remain on or in close vicinity of the nest for up to 2 or 3 days. Chicks probably do not receive much nourishment for the first few days of life: pecking on the dry sand of the nesting territory probably proves quite unrewarding.

Brooding. -- Both sexes brood and care for the young. Bouts of brooding generally last about 5 to 10 min. Parents must crouch or stand to brood chicks of more than about 12 days, particularly if all chicks are to be brooded at once. Chicks desiring to be brooded usually approach or follow an adult until it chooses a place to settle and accept them. The total amount of time per day spent in brooding varies considerably with weather conditions but in general declines with age. Chicks older than 21 days are brooded only infrequently.

Daily behaviour patterns. -- Both feeding and nesting territories are maintained at least until the young fledge. When the weather is not adverse and at least a portion of the feeding flat is exposed, adults and chicks spend much of the daytime on the feeding territory. When the chicks are tiny both adults usually stay close by, often feeding among them and brooding as necessary. During non-feeding periods the young are conducted back to the nesting area, one adult at each end of the

procession. Uncooperative chicks are chased and herded in the desired direction. On occasion I have seen adults knock down and several times viciously peck the upper back region of chicks which appeared to be particularly recalcitrant. By the time the brood is about one week old the chicks are frequently tended by only one parent. The other usually remains in the vicinity, feeding, resting, at intervals flying overhead with piping calls, or engaging in encounters along boundaries elsewhere in the territory. The off-duty bird returns immediately to the area of the brood if danger threatens. The birds maintain contact with peep calls and at intervals of several hours relieve each other. As fledging time nears the young become more independent, straying further from the family group and becoming increasingly resistant to the herding efforts of their parents. However a limited family association may be maintained for 1 or 2 weeks after fledging.

Body care activities. -- During periods of warm weather chicks when not feeding often spend their time sunning and preening. Young of less than about 12 days tend to rest sitting well back on the heels while older chicks nestle fully down on their breasts as adults do. Preening is concentrated in the region of neck, breast and upper back. While running freely chicks may stop to stretch and flap their wings. Sometimes they hold one wing out and scratch the foot along the underside. I have not observed the young to bathe but adults do so by entering the water to almost belly depth and repeatedly bobbing the head and tail to splash water over the rest of the body.

Accounts of grooming, bathing and resting activities for other plovers are few but the brief descriptions available for Killdeer (Davis 1943) and Blacksmith Plover (Hall 1964) indicate behaviours quite similar to those found in Piping Plovers.

Recognition of young. -- Adults and their chicks appear to be able to recognize each other. On occasion I have observed adults chasing neighbouring chicks away from their territories. This most often occurs when chicks are being led across foreign territories by their parents. Once while the resident brood and a neighbouring chick of approximately the same age were feeding along a common boundary, the resident adults approached and one chased the foreign chick into its own territory. The adult then turned toward the neighbouring adult in a horizontal threat charge. At the time it was chased the foreign chick seemed to be feeding normally and did not appear to exhibit any unusual behaviours which might allow the resident adults to distinguish it from their own brood. On two other occasions I observed chicks which I had upset running desperately across neighbouring territories. In each case the resident adults chased the fleeing chicks as they passed through.

Sometimes chicks appeared to be absent from their territories for up to four hours. When these chicks reappeared they were immediately accepted into the family group. However, in certain cases the intolerance for neighbouring chicks appeared to decline well before fledging and it was possible to see groups of up to 7 young moving about the

beach conducted by a single adult. Such chicks are usually greater than 2 weeks old and normally assemble only during times of resting, preening or sunning and not during active feeding. Generally the groups dispersed within several hours and chicks returned to their rightful parents. A possible example of this type of chick creching behaviour in Killdeers appears in Deane (1944).

Reaction to danger. -- Very tiny chicks react to danger by crouching and remaining still. As they grow chicks increasingly rely on running to escape. However I once saw a fledged juvenile lie down and freeze before flying away on my nearer approach.

Growth. -- Measurements of culmen, tarsus, forewing (radius-ulna), wing and tail of Piping Plover chicks at various ages varied widely (Table VIII and Appendix B). (For comparative purposes weights and measurements of adults are presented in Appendix C.) It appears that chicks which fail to achieve about 60% of normal weight by day 12 are unlikely to survive (Fig. 9). Wilcox (1959) reports chick weights which are somewhat lower than those obtained on Cadden Beach: 1 day - 6.8 g, 7 days - 8.5 g, 10 days - 12.4 g, 14 days - 17.0 g, 21 days - 25.7 g, 29 days - 29.4 g. Cadden Beach chicks having growth increments during their first 10 days as low as those reported by Wilcox without exception failed to survive.

Rate of growth may be slow during the first day or two after hatching, particularly in unfavourable weather. Graul (1975) reports that chick mortality is highest in Mountain Plovers in the first three

Table VIII. Lengths of culmen, tarsus, forewing (radius-ulna), wing and tail of Piping Plover chicks.

Age (days)	n	culmen (mm) & range	tarsus (mm) & range	forewing (mm) & range	wing (mm) & range	tail (mm) & range
0	50	7.1 (6.5- 7.8)	18.3 (16.8-20.1)	11.5 (10.2-13.6)		
1	10	6.9 (6.3- 7.5)	18.5 (17.1-19.8)	12.2 (11.6-13.0)		
2	1	7.8	18.3	11.8		
3	3	7.7 (7.7- 7.8)	18.8 (18.7-18.9)	11.7 (11.4-12.0)		
4	8	8.1 (8.1- 8.8)	18.3 (17.3-20.9)	13.2 (11.4-14.2)		
5	5	8.7 (8.3- 9.4)	20.0 (19.3-20.8)	14.0 (12.1-15.7)		
6	7	8.5 (8.1- 9.0)	19.5 (17.4-20.9)	15.3 (12.1-20.1)		
7	2	8.9 (8.4- 9.4)	19.8 (19.6-20.0)	14.3 (12.2-16.4)		
8	8	9.5 (8.7- 9.8)	20.6 (19.9-21.0)	18.7 (13.7-22.0)		
9	8	9.7 (8.8-10.3)	20.8 (19.6-21.9)	18.8 (13.9-22.2)	18.9 (1)	
10	2	9.4 (9.2- 9.6)	20.5 (19.7-21.2)	16.9 (13.7-20.0)		
11	4	9.9 (9.2-10.9)	21.0 (19.5-22.0)	18.8 (14.5-21.9)	26.8 (24.8-28.8) (2)	
12	6	10.2 (9.3-11.0)	21.8 (20.6-22.9)	22.9 (14.9-27.7)	32.3 (29.2-34.9) (3)	
13	3	11.3 (10.9-11.7)	22.1 (21.8-22.7)	25.2 (22.9-27.6)	35.7 (29.9-39.4) (3)	
14						
15						
16	5	11.1 (10.5-11.4)	21.6 (20.7-22.0)	28.5 (26.3-31.9)	44.0 (37.2-52.5) (5)	
17	1	11.6	22.6	32.3		
18	1	11.4	20.9	31.7		
19						
20	1	12.3	22.4	36.0	87.4 (1)	28.4
21	2	12.1 (11.9-12.2)	23.0 (22.6-23.4)	36.6 (33.5-39.7)	67.8 (63.2-72.3) (2)	21.0 (19.6-22.5)
22	3	11.6 (11.2-12.1)	22.9 (20.4-24.8)	36.8 (33.4-38.8)	71.2 (67.2-75.2) (2)	
23						
24	3	12.3 (11.7-12.8)	22.8 (22.1-23.4)	35.7 (35.1-36.2)	79.2 (73.3-87.6) (3)	27.0 (25.0-30.9)
25	1	12.6	22.4	35.7	73.7 (1)	26.9

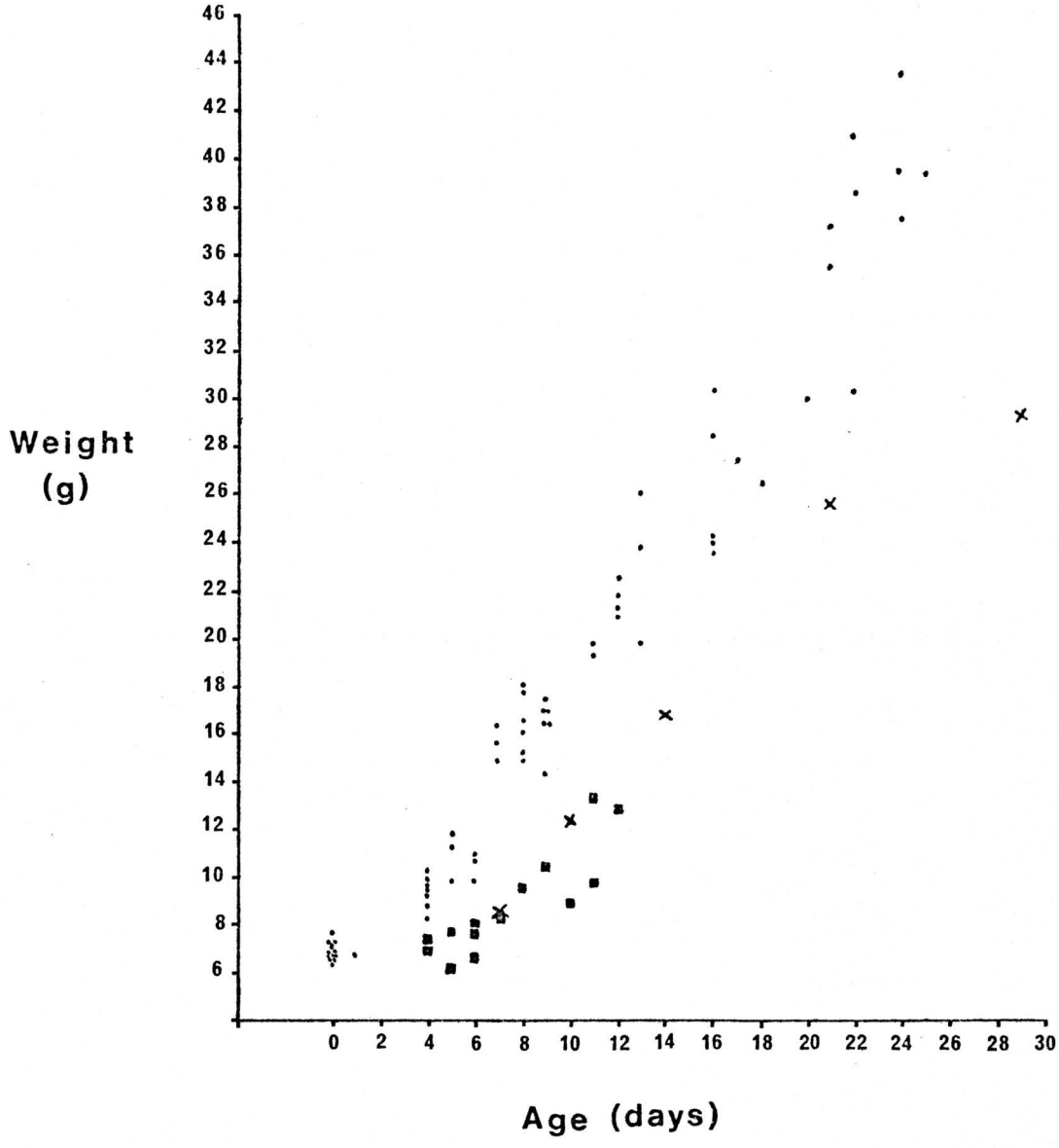

Fig. 9. Weight development of chicks. Dots denote chicks believed to have fledged, squares denote chicks dying before 14 days, and x's indicate values given by Wilcox (1959).

days of life. Little Ringed Plovers (Holzinger and Schilhansl 1971 and Walters 1961), Kentish Plovers (Walters 1960) and Snowy (= Kentish) Plovers (Boyd 1972) grow most slowly during the first few days of life. Walters (1961) suggests that Little Ringed Plover chicks hatched early in the season grow more rapidly than those hatching later but my data do not suggest a similar trend among Piping Plovers.

Fledging time. -- Fledging period is difficult to ascertain since many chicks apparently choose not to fly until at least several days after they are capable of flight. At this stage they often can outrun a human pursuer and prefer to do so rather than resort to flight, so it is difficult to determine when flight capability is actually achieved. The oldest chick captured was 25 days, when it was able to sustain flight for distances up to 2 m by flapping erratically. I therefore judge that fledging probably takes place at a minimum of about 27 days. This is somewhat shorter than the 30-35 day fledging period reported by Wilcox (1959), but his delayed fledging times are probably a reflection of the slower growth rate of the Long Island population.

Fledging Success. -- Assessment of fledging success poses some difficulty. With increasing age chicks become more elusive and as fledging nears are rarely recaptured. I have therefore made decisions regarding fate of chicks somewhat arbitrarily, bearing in mind the following guidelines. If a chick when last caught was at least about 10 days old and was exhibiting a normal growth pattern at the time, it was considered to have survived to fledging. For certain broods of

greater than 12 days estimates of survival were based on numbers of chicks observed regularly associating with known pairs. Chicks were considered not to have survived if between days 3 and 12 their weights were consistently less than 60% of the approximate normal for similarly aged healthy chicks, and if they were not subsequently resighted on the beach. In certain cases chick mortality was also assumed if a known territory and its environs were thoroughly searched without discovering chicks or evidence of parental activity indicative of the presence of chicks.

The fate of the 75 chicks hatching from known nests has been assessed as follows: 29(38.9%) presumed dead, 28(37.3%) presumed fledged and 18(24%) unknown. In the unlikely event that all 18 chicks of unknown fate actually fledged, it is possible that as many as 46 chicks fledged from the 26 known nests. In addition at least 11 chicks from unknown nests are believed to have fledged. Thus, between 39 and 57 chicks may have fledged from Cadden Beach in 1976. This represents approximately 1.3 to 2.1 chicks fledged per pair.

Data on fledging success in other plover species are scarce. In Ringed Plover fledging rates of 1 chick per pair (Laven 1940) and 1.28 chicks per pair (Prater, 1974) have been reported. Boyd (1962) gives 1.55-2.22 young fledged per pair per year in Little Ringed Plovers.

INTERACTIONS WITH OTHER SPECIES

Terns. -- About 70 pairs of Arctic and Common Terns (Sterna paradisaea and S. hirundo) nested on Cadden Beach each year, the densest part of their colony occurring in the area of highest concentration of plover nests. Generally the terns and plovers co-existed in close proximity with few interactions. Occasionally terns swooped low over plovers or hovered directly above them at heights of 1 to 2 metres. The plovers responded by flapping or jumping aside or by ignoring the harassment. Piping Plovers sometimes chased terns in flight, and rarely charged them with horizontal threat displays. Normally plovers tolerate terns roosting on their territories and even allow their own young to move freely nearby. Once an Arctic Tern chick was approached by two adult plovers in horizontal threat display; one adult continued with the display while the other deployed various aspects of distraction display until the adult terns appeared and led the chick away.

Whenever I chased Piping Plover chicks I was accompanied by a group of plovers, circling, displaying and piping. Numbers of swooping screaming terns usually were also present. On one such occasion I had gotten within 6 metres of a 20-day old Piping Plover chick which was standing at the water's edge, when an adult Arctic Tern swooped low, picked the chick up by the neck with its bill and lifted it up about 2.5 metres, before dropping it over the water. The chick was

slightly stunned by the fall but soon recovered. The tern was evidently in a highly excited state when it carried out the action, but why this particular behaviour resulted is unclear.

On another occasion I arrived at a Piping Plover nest containing three freshly hatched chicks and one pipped egg. It was cold and raining heavily at the time, and during the half hour that I remained at the nest the female ran about nearby, piping steadily. The male was sitting about 10 m away, squatted as if on a nest. At intervals a freshly hatched Arctic Tern chick popped out from beneath him. The male plover each time assisted the tern chick in working its way back under his breast by leaning forward and shoving it in with his bill. On checking, I discovered the male plover was also incubating a pipped tern egg. As I left the area the female plover returned to the plover nest and the male returned to the tern scrape. An hour later the situation remained the same but the following day an Arctic Tern was on the tern nest and both plovers were tending their brood.

It appears that when I disturbed the plover pair I also put an Arctic Tern off its nest. As the male plover moved about the area it discovered an untended egg and chick which he immediately took charge of while the female continued to protest my presence. Each time the tern chick emerged from under its surrogate parent the plover had ample opportunity to look it over. This suggests that adult Piping Plovers are not immediately able to distinguish their newly hatched offspring even from those of other species. Yet by the time the chicks leave the nest the parents apparently know them from neighbouring chicks.

How recognition is established is not known but the vocal contact maintained between adults and chicks may be a factor.

Rittinghaus (1953) reports adoption in Ringed and Kentish Plovers of each others chicks. He also describes adoption of Kentish Plover chicks by a Least Tern (Sterna albifrons) and suggests that chick recognition of adults may result from early imprinting.

Gulls. -- A flock of several hundred Herring and Great Black-backed Gulls (Larus marinus) often rested on the nesting or feeding territories of the plovers. Adult plovers generally kept a distance of 10 m or more from these birds but otherwise ignored their presence most of the time. Piping Plover chicks were sometimes observed feeding as close as 30 m from roosting gulls, but I have never seen any direct evidence of gulls preying on plover chicks. However, on occasion adult Piping Plovers have been seen to pursue and attack Herring Gulls in flight and I once observed eight Piping Plovers mob a single Herring Gull with horizontal threat charges, distraction displays and dive-bombing.

Other shorebird species. -- During the breeding season Piping Plovers normally do not tolerate other species of shorebirds on their feeding and nesting territories. The first few southward migrants arriving in late June were vigourously chased but the reaction subsequently declined either due to diminished territorial activity or habituation to the newcomers or both. Spotted, White-rumped (Calidris fuscicollis), Least (C. minutilla) and Semipalmated (C. pusilla)

Sandpipers, Semipalmated Plovers and Red Phalaropes (Phalaropus fulicarius) were all observed being chased by the plovers.

Other avian predators. -- Incubating adults react to the presence of Common Crows (Corvus brachyrhnchus) by leaving their nests and running to stand piping near the intruder. Chicks immediately freeze at the approach of a Marsh Hawk (Circus cyaneus) and adults commence piping as they form a tight flock and mob the Marsh Hawk by flying above, beside or behind it while keeping a minimum distance of 3 to 5 m.

Hobbs (1972) reports incubating Red-capped Dotterels (= Kentish Plovers) running from the nest to stand motionless some distance away when Ravens (Corvus coronoides)or Little Crows (C. bennetti) flew over. However the sitting birds flattened themselves onto their scrapes when a Nankeen Kestrel (Falco cenchoides) flew by. Hall (1964) reports small flocks of Blacksmith Plovers keeping their distance while air-harrying Lanner Falcons (Falco biarmicus) and Marsh Harriers (Circus ranivorus). Simmons (1955) interprets the close packing of a flying wader flock as a defensive escape-reaction against large falcons, probably a wise precaution since falcons have been known to take adult plovers (Simmons 1961b).

Mammals. -- The cattle which pasture on Cadden Beach seem to be largely ignored by the Piping Plovers unless they closely approach a nest. Plovers then react by circling them with repeated head-bobbing and peeping calls. Most dogs are unaware of the presence of Piping Plovers on a beach and are ignored by the birds. However some

dogs do notice the plovers and may harass the birds by chasing them. Since the plovers react by running or flying very low in broad circles the pursuit may continue for some time, with resulting danger that the nest will be trampled as the dog runs across the bird's territory.

Graul (1975) and Deane (1944) report Mountain Plover and Killdeer (respectively) rushing or flying with spread wings towards mammals which approach the nest closely. I have not observed this reaction in Piping Plovers.

Humans. -- Piping Plovers usually react to humans by performing distraction displays or by circling and head-bobbing. In densely populated parts of the colony territorial boundaries are ignored as a number of neighbouring birds converge to combine their distraction efforts. However, considerable variation in reaction exists among pairs and among beaches. Some birds nesting on isolated beaches will regularly leave the nest if approached within 85 m and remain away from the area while the intruder is present. By contrast I have observed on heavily used recreational beaches that certain individuals may remain on the nest unless approached to within three m. In such cases the sitting birds flatten themselves into the scrape.

FEEDING

Use of neutral areas. -- Subsequent to arrival in early spring many birds feed in loose flocks on certain parts of the tidal flats. Hostility is rampant in these so-called neutral areas, with constant bouts of chasing, charging and horizontal threat display. Graul (1973b) also found aggressiveness early in the season in Mountain Plover flocks, apparently associated with efforts by the birds to maintain individual distances of from 6 to 15 m.

From mid-April onward the number of Piping Plovers using neutral feeding grounds decreases as does the frequency of hostile interactions there. By mid-May these neutral areas have become confined to the more distant flats from shore as feeding sites closest to suitable nesting terrain are increasingly claimed by territorial pairs. From then until early July such neutral areas are used by few birds, mostly unpaired individuals. Pairs do most feeding within their own territories, but particularly during the incubation period may also use the neutral flats to varying extents. After the second week of July the numbers of birds using the neutral feeding flats are bolstered by migrants, plus local juveniles and post-breeding adults.

Use of feeding territories. -- After pairs have claimed feeding territories they do much of their feeding there. While one bird incubates the other often feeds and defends the feeding territory. After hatching, the adults feed with the small chicks on the feeding territory.

Time of feeding. -- Most feeding occurs in the period of low or falling tide. When the tide is too high, the weather too inclement, or darkness falls, chicks are escorted to the nesting territory.

Feeding behaviour. -- When feeding on the sand flats of the inner bay where wave action is minimal, plovers feed largely by means of short rapid runs interspersed with series of rapid pecks. Pecks and runs occur in succession with such rapidity that it appears the bird is simply probing randomly, rather than directing pecks at specific food items.

On the sea side of the spit, where each wave rolling up the beach retreats to leave a glassy wet sand surface, the plovers sometimes feed very differently. Moving about this wet area, a bird stops, and holding one foot slightly forward, rapidly vibrates it against the water-saturated sand. A number of such foot-trembling movements may occur on successive steps before an actual peck is made. The deliberate manner employed suggests that these movements enable a bird to detect a food morsel before probing for it. Possibly the vibrations help to locate irregularities beneath the sand or cause a sand-dwelling organism to react in some way which makes it more readily detected by plovers.

Feeding techniques involving various forms of foot movements (paddling, trampling, puddling) are well known from other groups of birds, including sandpipers, gulls, ducks, geese, swans, flamingos

and herons (Simmons 1961a), but true foot-trembling seems to be distinctive to plovers. The foot-trembling technique as described above has been reported for various other plover species including Three-banded Plover (Freeman 1976), Blacksmith Plover (Hall 1964), Lapwing (Spencer 1953), Little Ringed Plover (Simmons 1953 and Sluiters 1938), Ringed Plover (Simmons 1961) and Kentish Plover (Glutz, Bauer and Bezzel 1975). Hall's (1964) evidence suggests there is some relation between foot-trembling and feeding on wet surfaces, which is supported by my observations. However Heinroth and Heinroth (1928) report captive Little Ringed Plovers performing on hard surfaces.

Adult Piping Plovers when feeding intensively by the foot-trembling technique make about 30 pecks per minute. Piping Plover chicks feed in the usual manner of adults, by alternate runs and pecks. When feeding intensively by this method chicks average about 35 to 40 pecks and 20 to 25 running spurts per minute. Pecking occurs at about one-quarter of the stops. I have not observed foot-trembling in unfledged birds; very young chicks in particular tend to feed on the firm sand at some distance above the water line, where foot-trembling probably cannot be applied to advantage. I have not found any references to foot-trembling by plover chicks. The soil-patting reported in Killdeer chicks of greater than four weeks probably does not involve the same movement (Davis 1943).

Food organisms. -- Bent (1929) cites marine worms, insects (including fly larvae and beetles), crustaceans, molluscs and other small marine animals and their eggs as food taken by Piping Plovers, but the actual food items which form the diet of the species in southern Nova Scotia are not known. On Cadden Beach I once observed numbers of insects moving on the surface of the sand underfoot of Piping Plover chicks. At the time the chicks were active, running and probing in the sand for food, evidently showing no interest in catching the insects. On another occasion when swarms of insects were hovering low over the feeding flats, adults present continued pecking into the sand for food. The only food items I have observed being taken are marine worms (up to 15 cm in length), the larger of which after being pulled from the sand, were shaken several times while dangling from the bill before being swallowed whole. Once a bird picked up a worm from the sand, carried it to the water's edge and dunked it several times before eating it. During 60 minutes of feeding in late April, I observed an adult take 58 worms from the sand. Forty-two of these were estimated to be 2.5 to 7.5 cm long, the remainder less than 2.5 cm. Except on the few occasions when the plovers were feeding on worms, I have not been able to observe actual organisms being eaten. However, given the nature of the preferred feeding substrates, it appears the bulk of the diet is probably minute molluscs and crustaceans. Defecations consist largely of sand with no recognizable organic material present.

During 1976 efforts were made to obtain regurgitated food samples from four feeding chicks. Orally administered antimony potassium tartrate and saline solutions failed to induce vomiting although chicks appeared to be under considerable physical stress for up to several hours afterward.

FLOCKING AND DEPARTURE

By early July some adults and the oldest of the fledged juveniles increasingly flock on neutral feeding areas and associate with other migrants, particularly Least Sandpipers. Earliest departures probably occur during the second week of July, since this is when the first migrating Piping Plovers arrive from other beaches. I once observed 16 Piping Plovers in a flock with 50 Least Sandpipers heading away from Cadden Beach southward, but most Piping Plovers probably leave in smaller groups. Migrating birds often give peep-lo calls while in flight. The birds leaving Cadden Beach apparently move leisurely southward along the coast of Nova Scotia, probably following the shoreline fairly closely. This is suggested by sightings during August of banded plovers from Cadden Beach at two locations, 12 km (Little Port LeHebert) and 25 km (Hemeon's Head) southward along the shore. With the exception of adults and chicks of late nests, most of the plovers have left the breeding ground by mid August. One bird hatched on June 12 departed about July 29 (47 days later) while one which hatched about August 1 departed about September 2 (approximately 32 days after hatching).

Several other workers have reported sociality and flocking tendencies in plovers prior to departure, but in at least Kentish and Little Ringed Plovers (Sluiters 1954) sociality does not extend to other species. Boyd (1972) suggests that family groups of Snowy (= Kentish) Plovers may remain together during migration. Limited 1976

observations of migrants further south along the coast of Nova Scotia apparently do not indicate a similar tendency in Piping Plovers. On August 1 an unidentified adult and 6 juveniles from 5 different broods were observed at Hemeon's Head. An unidentified adult and 2 juveniles from 2 broods were observed at the same location on August 12. On August 17, 1 adult and 3 juveniles, all unidentified, were seen at Little Port LeHebert and a lone juvenile was present at the same place on August 21.

Among Black-bellied Plovers (Hussell and Page 1976), Ringed Plovers (Laven 1940) and Little Ringed Plovers (Gatter 1971) there is a tendency for females to depart before males. Gatter reports female Little Ringed Plovers departing on average 23 days and males 40 days after their eggs hatch. I observed one lone male defending his territory for at least one week after the female and chicks had left. Gatter also cites average departure times for chicks: 49 days after hatching for May-hatched chicks, 39 days for June hatchings and 34 days for those in July.

SUCCESS RATE ON OTHER BEACHES

Table IX presents a summary of nesting effort on eight beach areas other than Cadden Beach. The 15 breeding pairs laid a minimum of 64 to 72 eggs of which a maximum of 11 to 17 young fledged. This represents an estimated .73 to 1.1 chicks fledged per pair, somewhat lower than the fledging rate of 1.3 to 2.1 chicks per pair on Cadden Beach.

Table IX. 1976 nesting effort on eight beaches in Nova Scotia.

	Estimated no. of pairs	No. of eggs laid	Hatching date	No. eggs hatched	No. chicks fledged
Halifax County					
Conrad's Beach	3	4		0	0
		4		0	0
		4		0	0
		4	~Jul. 1	4(?)	2(?)
		4	~Jun. 19	4	4
Lunenburg County					
Cherry Hill	2	4	~Jun. 4	≥1	1
		4?		?	
Queens County					
Summerville	1	4		0	0
		4		0	0
Sandy Cove	1	4	Jul. 12	≥2	0
Shelburne County					
Little Port LeHebert	1	4		0	0
Louis Head	1	4		0	0
Baccaro	3	4	~Jun. 12-25	≥1	1
		4		?	?
		4?		?	0
Cape Sable Island	3	4	Jul. 16	≥3	2
		4	Jun. 30	≥3	3
		4	~Jul. 17	4	0
Total	15	64-72		18-44	11-17

The high proportion of late hatching dates suggests that some of these nests may have been renests whose corresponding first nests were not discovered. However it is possible that later nest initiation is usual on beaches with single pairs, where pre-season social interactions that might stimulate early territorial establishment and courtship activity are considerably fewer than on more densely populated beaches. Early nesting is probably advantageous for two reasons. If the first clutch or brood is lost more time is available for renesting. Early nesting also permits a large portion of the breeding cycle to be completed before the onset of heavy recreational pressure and its associated dangers.

The reasons for the evidently lower success rates obtained on beaches other than Cadden Beach cannot be precisely established. However these beaches do have in common a much greater degree of recreational use than does Cadden Beach. Riding horses, dogs, foot traffic and motorized vehicles of several sorts all occur regularly on one or more of the eight beaches. It seems reasonable to assume that risk to eggs and chicks increases in relation to increase of movement by humans, animals and vehicles on a given beach. Eggs, being immobile, may be particularly vulnerable, especially if they are located in areas which receive heavy traffic. Since chicks are able to run and hide they may be safer from foot traffic, but it is doubtful if they could always successfully evade rapidly moving vehicles. Their ability to move may in fact make them more visible and therefore more vulnerable to dogs and cats. Quinn and Ryan (1966) consider feral dogs and cats to be among the major enemies of the species today.

Disturbance may prolong incubation and fledging periods by reducing the proportion of time spent in incubation and feeding, thereby increasing the risk of failure. Disturbance may also prevent a pair from successfully carrying out the courtship activities necessary for renesting. Other possible contributing factors to chick mortality may be natural predators (foxes, gulls and crows), inclement weather at crucial times or the inexperience of first-time parents.

The disruption of breeding behaviour and renesting in Little Ringed Plovers has been attributed to human disturbance on the breeding grounds (Holzinger 1975).

NUMERICAL STATUS

A brief account of historical changes in the status of the Piping Plover is contained in Bent (1929). Piping Plovers were common summer residents of eastern North America during the time of Audubon. However, by the late nineteenth century the species had been brought close to extinction by many seasons of spring and autumn hunting. Legislation protecting the smaller shorebirds was subsequently introduced, and by the 1920's Bent (1929) reported that the Piping Plover was fast regaining its status as a common summer resident. Wilcox (1939) estimated more than 500 pairs nesting on Long Island, up from the few scattered pairs of 1900. Between 1937 and 1958 a maximum of 64 pairs (in 1941) was reported on a particular seventeen mile stretch of Long

Island Beach (Wilcox 1939). The subsequent decline from the maximum was attributed to habitat change brought about by the revegetation of the locally building dune system. Wilcox does not speculate on long term population trends over a broader geographical area, mentioning simply that departing birds left his study locale for more suitable habitat without elaborating on the possible availability of such habitat. At about the same time Piping Plovers were regarded as common on certain of the sandy beaches of Maine (Palmer 1949).

However, Arbib(1972) accorded the species a place on a so-called Blue List for 1973 made up of those species which, in all or in a significant part of their range, are in potentially dangerous, apparently non-cyclical population declines. Piping Plovers have maintained their place on subsequent Blue Lists. Arbib (1974) in the 1975 Blue List concluded that the species was becoming endangered in the mid-western prairie region, chiefly as a result of habitat disturbance.

In western Canada Wayne Renaud (pers. comm.) estimates at least 150 breeding pairs in Saskatchewan, and preliminary correspondence suggests that figures for Alberta and Manitoba may be of the same order.

Within central Canada there is evidence of a decline. In 1927 and 1928 at Long Point Bird Observatory in Ontario, Snyder (1931) estimated 100 or more pairs annually. Cartar (1976) estimates 3 to 4 pairs nest there now, and feels that Long Point is probably the only part of the Lower Great Lakes region which regularly supports breeding populations of this species. By contrast Barrows (1912) stated: 'This little plover is found everywhere along the shores of the Great

Lakes during the summer, and probably breeds wherever conditions are suitable'.

In Atlantic Canada the species seems to be faring poorly. Breeding apparently no longer occurs along the south shore of the Gaspé Peninsula (David, pers. comm. in Arbib 1976). Strauch (1971) estimated that in 1969 no fewer than 50 pairs were present on the Magdalen Islands, an area containing extensive suitable habitat. Old records (Bishop 1889 and Gross 1937), while containing no population estimates, indicate that Piping Plovers are a fairly abundant nesting species on the Magdalens. McNeil et al. (1973) record maximums there of more than 250 birds during fall migration, which suggests a relatively high fledging rate among local birds or a considerable influx of fall migrants or both. The most probable breeding area for southward bound migrants passing through the Magdalen Islands is the north shore of the Gulf of St. Lawrence, but I have been unable to obtain population estimates for this region. Robert Lamberton and Stuart Tingley (pers. comm.) estimate that on average 10-15 pairs breed annually in western Newfoundland.

Suitable nesting habitat exists along parts of the north shore of New Brunswick. David Christie (pers. comm.) estimates there may be up to 50 nesting pairs in that province. Roger Burrows (pers. comm.) considers that 6 to 8 pairs may nest in Prince Edward Island National Park. The species may also breed in small numbers on certain other beaches along Prince Edward Island's north shore.

In Nova Scotia the Piping Plover once nested on Sable Island, Macoun and Macoun (1909) reporting its status there as quite common. No breeding has occurred on Sable in recent years, even though the island has miles of seemingly suitable habitat. Table X summarizes data on the more recent breeding of Piping Plovers within the province. The numbers reported are considered to give a fairly accurate representation of actual numbers of breeding pairs along the southern and eastern shores. It is possible there may be a few additional beaches harbouring small numbers of birds along Northumberland Strait. Thus it appears that in 1976 60 pairs may be a reasonable minimum estimate for Piping Plovers breeding in Nova Scotia. That the number exceeds 75 seems improbable.

Summarizing the above estimates for number of breeding pairs in central and eastern Canada (with the exception of the north shore of the Gulf of St. Lawrence) gives a minimum of the order of 200 to 250 pairs. In Canada there may well be fewer than 1000 pairs.

While destruction of habitat probably figures prominently in the decline of this species, many beaches in the Maritimes which appear to offer suitable nesting habitat do not host breeding pairs. There is also some evidence to suggest that nesting birds may be fairly old (Wilcox 1939 and Miller 1976). It appears then that recruitment rate of first year birds to the breeding population may be crucial.

Table X. The status of the Piping Plover in Nova Scotia in 1975 & 1976.

	Total number of adults seen			Estimated no. of breeding pairs in 1976
	1975[1,2]	1976[1]	1976[3]	
Halifax County				
Clam Harbour	4	4	-	2
Seapool Beach	1		-	
Lawrencetown Head	2	2	-	1
Conrad's Beach	9	5	4	3
Lunenburg County				
Conrad Beach (Cherry Hill)	2	5	5	2
Kingsburg	3		0	
Conrad Island Causeway	6	5	-	2-3
Crescent Beach			1	
Queens County				
Summerville			3	1
Carter's Beach			1	1
Cadden Beach			60-70	27-29
Sandy Cove			2	1
Shelburne County				
Little Port LeHebert	1	2	2	1
Louis Head Beach	2	1	3	1
Lockeport Second Cove	1		1	
Crane's Point Cove	3		0	
Baccaro Beach	2	6	6	3
Roseway Beach	3+		0	
Roseway Head	2	1	-	
Red Head Beach	+	3	-	
Cape Sable Island		2	6	3
Cape Sable light			-	6
				54-57

[1] based on breeding shorebird surveys of the N.S. Dept. of Lands & Forests

[2] these figures may include migrants

[3] results of surveys carried out by the author; a dash indicates a beach not visited

CONCLUSIONS

The eastern population of the Piping Plover breeds only in the highly restricted habitat offered by unstable coastal dune systems. In its nesting habits it has shown itself to be sensitive to the pressures imposed by multiple beach use. The birds nesting on Cadden Beach may comprise up to one-half the breeding population in Nova Scotia in any given year, and apparently achieve a fledging success considerably higher than that found on other beaches. Indeed it is possible that the Cadden Beach colony may be the source for restocking smaller colonies elsewhere in the province, where reproductive success may be too low to maintain the population. Considering the low overall numbers and the current decline throughout its range, it would be highly desirable to afford the species more protection in Nova Scotia. In view of the relative importance of the Cadden Beach population to the province, it would be helpful if access to Cadden Beach by humans and their animals and vehicles were limited during the breeding season. On other more accessible and traditionally used beaches access should be restricted on the portions where nests are located.

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Appendix A. Sizes of Piping Plover eggs.

Clutch designation	Position in clutch	Length (mm)	Breadth (mm)	Length x Breadth^2 (mm^3)
1		32.1	24.4	19,111
1		31.6	24.1	18,354
1		31.4	24.2	18,389
1		31.8	25.0	19,875
2		32.4	25.1	20,412
2		32.1	25.1	20,223
2		31.7	24.5	19,028
2		32.8	24.6	19,849
4		32.5	23.8	18,409
4		32.8	23.8	18,579
4		31.8	24.4	18,932
4		32.8	24.5	19,688
5		31.4	25.3	20,099
5		32.1	24.6	19,426
5		31.3	25.1	19,719
5		31.5	25.1	19,845
6		31.9	24.8	19,620
6		31.6	25.0	19,750
6		32.3	24.6	19,547
6		31.4	25.1	19,782
7		32.8	25.0	20,500
7		32.3	25.1	20,349
7		33.4	24.7	20,377
7		34.1	24.8	20,973
8		32.8	24.8	20,173
8		32.8	24.8	20,173
8		33.6	24.7	20,499
9		35.0	25.0	21,875
9		33.0	25.1	20,790
9		34.0	25.7	22,457
9		32.8	25.8	21,833

Clutch designation	Position in clutch	Length (mm)	Breadth (mm)	Length x Breadth^2 (mm^3)
10		32.9	25.0	20,563
10		33.6	25.3	21,507
10		33.5	25.2	21,274
10		32.7	25.1	20,601
11		31.8	25.7	21,004
11		32.7	25.7	21,598
11		32.8	25.3	20,995
11		33.0	25.3	21,123
12		33.7	24.0	19,411
12		33.5	24.6	20,273
12		34.6	24.6	20,939
12		33.0	24.8	20,296
13		31.3	26.0	21,159
13		31.3	25.0	19,562
13		30.5	25.1	19,215
14		33.8	24.4	20,123
14		34.5	24.3	20,372
14		33.5	24.8	20,604
14		33.7	24.3	19,900
15		31.8	24.6	19,244
15		32.4	25.0	20,250
15		33.4	24.3	19,722
15		32.7	24.4	19,468
16		32.4	24.6	19,607
16		33.8	24.7	20,621
16		32.0	24.2	18,740
16		32.8	24.8	20,173
17		31.9	24.0	18,374
17		32.0	23.8	18,126
17		32.7	24.5	19,628
17		31.8	24.5	19,088
18		33.3	24.3	19,663
18		33.0	24.7	20,133

Clutch designation	Position in clutch	Length (mm)	Breadth (mm)	Length x Breadth^2 (mm^3)
18		32.2	25.0	20,125
18		33.0	24.3	19,486
19		31.9	24.5	19,148
19		31.8	24.6	19,244
19		31.0	24.5	18,608
20		33.9	24.5	20,348
20		33.7	24.6	20,394
20		32.5	24.6	19,668
20		32.8	25.0	20,500
21		31.8	24.7	19,401
21		31.9	24.5	19,148
21		32.6	24.7	19,889
21		33.4	24.6	20,212
A	1	31.9	23.9	18,222
A	2	33.3	24.3	19,663
A	3	33.1	24.9	20,522
A	4	33.7	25.3	21,571
B		31.1	24.1	18,063
B		31.3	24.8	19,251
B		31.1	24.8	19,128
B	4	32.7	24.9	20,274
C		32.3	25.9	21,667
C		33.6	25.3	21,507
C	3	33.2	25.8	22,099
D	1	32.6	24.9	20,212
D	2	32.1	25.0	20,063
D	3	30.9	24.9	19,158
D	4	32.4	26.1	22,071
E	1	34.5	24.9	21,390
E	2	32.7	24.8	20,112
F	1	32.7	24.3	19,309
F	2	32.2	24.5	19,328
F	3	33.2	24.8	20,419

Clutch designation	Position in clutch	Length (mm)	Breadth (mm)	Length x Breadth^2 (mm^3)
F	4	32.9	24.8	20,235
G		32.6	24.3	19,250
G		33.0	25.0	20,625
G		33.8	24.9	20,956
G		32.6	24.9	20,212
H		33.4	24.8	20,542
H		33.0	24.6	19,970
H		32.8	24.8	20,173
H		32.5	24.7	19,828
I		32.2	25.2	20,448
I		33.3	25.7	21,994
I		34.8	25.0	21,750
I		32.4	25.7	21,400
J		32.0	24.9	19,840
J		31.8	25.0	19,875
J		32.6	24.9	20,212
J		32.6	25.2	20,702
K		32.1	24.1	18,644
K		32.4	23.7	18,199
K		32.9	24.3	19,427
K		32.7	24.4	19,468
L		32.7	25.0	20,438
L		33.1	24.6	20,031
L		33.7	24.2	19,736
L		33.2	24.7	20,255
M		32.6	24.0	18,778
M		33.6	23.6	18,714
M		31.4	24.2	18,389
M		32.2	23.8	18,239
N		30.6	25.0	19,125
N		31.7	24.9	19,654
N		31.2	26.2	21,417

Clutch designation	Position in clutch	Length (mm)	Breadth (mm)	Length x Breadth^2 (mm^3)
N		32.0	25.9	21,466
O		32.7	24.4	19,468
O		31.8	24.8	19,558
O		33.0	24.8	20,296
O		32.1	25.6	21,037
P		33.8	24.8	20,788
P		32.9	24.6	19,910
P		33.9	24.4	20,183
P		33.0	24.7	20,133
Q		32.4	24.5	19,448
Q		33.2	24.7	20,255
Q		32.3	25.1	20,349
Q		33.7	24.9	20,894
R		33.8	24.5	20,288
R		33.4	24.7	20,377
R		33.2	24.7	20,255
R		33.0	24.7	20,133
S		33.3	25.4	21,484
S		34.2	25.2	21,718
S		33.7	25.4	21,742
S		33.7	25.0	21,063
T		32.7	25.3	20,931
T		33.1	25.2	21,020
T		33.6	24.9	20,832
T		33.2	25.1	20,916
U		33.0	25.4	21,290
U		33.6	25.7	22,192
U		34.7	25.4	22,387
U		32.5	24.4	19,349
V		31.4	24.0	18,086
V		33.8	24.4	20,123
V		32.8	24.6	19,849
V		32.3	24.0	18,605

Clutch designation	Position in clutch	Length (mm)	Breadth (mm)	Length x Breadth^2 (mm^3)
W		33.2	25.1	20,916
W		35.4	24.6	21,423
W		32.5	25.1	20,475
W		32.5	25.1	20,475
X		32.8	24.2	19,209
X		31.8	24.6	19,244
X		33.9	24.8	20,850
X		32.8	24.9	20,336
Y		29.6	23.6	16,486
Z		30.7	24.6	18,578
Z		31.9	24.6	19,305
Z		31.9	24.9	19,778
Z		32.1	24.7	19,584
AA		31.4	25.1	19,782
AA		32.5	24.4	19,349
AA		31.5	25.0	19,687
AA		32.6	25.4	21,032
S-2		31.4	24.7	19,157
S-2		30.8	24.5	18,488
S-2		31.2	24.5	18,728
S-2		31.9	24.7	19,462
C-1		30.9	24.6	18,699
C-1		32.4	24.5	19,448
C-1		31.6	24.3	18,659
C-1		31.8	24.7	19,401
C-2		33.0	24.8	20,296
C-2		32.1	24.8	19,743
C-2		32.7	24.8	20,112
C-2		31.7	24.9	19,654
C-3		32.5	24.8	19,989
C-3		31.4	24.9	19,468
C-3		31.5	24.5	18,908
C-3		32.3	24.5	19,388

Clutch designation	Position in clutch	Length (mm)	Breadth (mm)	Length x Breadth^2 (mm^3)
JP-1		31.0	23.8	17,560
JP-1		30.5	24.1	17,715
JP-1		30.4	23.8	17,220
JP-1		31.7	24.0	18,259
LH-1		32.2	25.3	20,611
LH-1		31.8	25.2	20,194
LH-1		32.2	25.6	21,103
LH-1		32.9	25.6	21,561
B-1		32.6	24.9	20,212
B-1		32.4	24.6	19,607
B-1		31.9	24.6	19,305
B-1		31.4	24.5	18,848
B-2		31.5	25.0	19,688
B-2		30.7	24.9	19,034
B-2		31.1	25.1	19,593
B-2		31.3	25.0	19,563
SI-1		31.5	23.6	17,544
SI-1		32.2	23.4	17,631
SI-1		31.7	24.0	18,259
SI-1		31.1	23.7	17,469

Appendix B. Weights and measurements of Piping Plover chicks.

Date	Age (days)	Brood	Chick	Culmen (mm)	Tarsus (mm)	Radius-ulna (mm)	Wing (mm)	Tail (mm)	Weight (g)
June 4	0	D	151383	6.9	19.1				5.7
June 4	0	D	151384	6.9	18.4				5.3
June 4	0	D	151385	6.7	18.9				5.6
June 7	0	F	151391	6.9	18.1	12.0			6.7
June 7	0	F	151396	7.8	18.5	12.4			5.9
June 2	0	G	151377	6.8	17.6	11.7			5.7
June 2	0	G	151378	7.9	18.7	12.3			5.9
June 2	0	G	151379	7.1	17.6	12.3			5.8
June 2	0	G	151380	7.2	18.0	12.0			6.4
June 7	0	K	151702	6.8	17.6	11.8			6.1
June 7	0	K	151703	6.9	17.2	12.0			6.2
June 12	0	L	151716	7.1	18.3	10.2			6.8
June 12	0	L	151717	6.5	19.0	11.3			6.7
June 12	0	L	151718	7.3	18.2	11.5			7.1
June 11	0	M	151713	6.9	17.3	11.6			6.2
June 11	0	M	151714	7.2	17.9	11.8			6.1
June 11	0	M	151715	7.0	17.7	11.1			6.6
June 7	0	N	151397	6.8	19.2	13.6			7.1
June 7	0	N	151701	7.0	18.3	11.8			6.7
June 8	0	N	151704	7.1	18.8	11.8			5.9

Date	Age (days)	Brood	Chick	Culmen (mm)	Tarsus (mm)	Radius-ulna (mm)	Wing (mm)	Tail (mm)	Weight (g)
June 10	0	P	151709	6.9	18.6	12.3			6.7
June 10	0	P	151710	7.2	16.8	11.2			6.6
June 10	0	P	151711	7.3	18.9	12.0			7.7
June 7	0	Q	151395	7.1	18.2	11.6			7.0
June 8	0	Q	151705	6.0	17.8	12.3			6.6
June 8	0	Q	151706	6.3	16.8	12.0			7.0
June 8	0	Q	151707	7.5	17.3	11.7			7.5
June 15	0	R	151721	7.5	19.2	12.0			6.5
June 15	0	R	151722	7.6	19.7	11.8			6.6
June 16	0	R	151723	7.4	18.6	12.3			7.3
June 27	0	T	151738	7.5	18.2	12.0			7.2
June 27	0	T	151739	7.2	18.5	11.0			7.5
June 27	0	T	151740	7.0	18.0	11.7			7.2
June 28	0	T	151741	7.2	18.0	11.7			7.4
July 2	0	V	151750	7.1	18.4	11.2			6.8
July 2	0	V	151751	7.3	18.3	11.1			7.0
July 2	0	V	151752	7.3	18.6	11.3			7.6
June 20	0	X	151724	6.7	17.7	11.7			6.8
June 20	0	X	151725	6.7	17.7	12.0			7.0
June 20	0	X	151726	7.2	17.9	11.3			6.4
June 21	0	X	151727	6.8	18.2	11.5			7.1

Date	Age (days)	Brood	Chick	Culmen (mm)	Tarsus (mm)	Radius-ulna (mm)	Wing (mm)	Tail (mm)	Weight (g)
June 25	0	Z	151734	7.6	19.2	12.1			6.1
June 25	0	Z	151735	7.3	17.3	11.8			6.6
June 25	0	Z	151736	7.1	17.3	11.4			6.9
July 8	0	AA	151759	7.3	18.7	11.3			8.0
July 8	0	AA	151760	7.6	20.1	12.4			7.2
July 13	0	SC	151762	7.1	19.1	10.9			6.9
July 13	0	SC	151763	7.4	19.4	10.5			6.9
July 16	0	DH-1	151766	7.8	19.5	11.1			7.0
July 16	0	DH-1	151768	7.4	19.6	11.4			6.8
July 16	0	DH-1	151769	7.2	19.1	11.5			7.3
May 28	1	I	151369	6.3	17.3				6.3
May 28	1	I	151370	7.0	18.5				6.7
May 28	1	I	151371	6.6	17.1				7.2
May 28	1	I	151372	6.5	18.0				7.1
June 8	1	N	151397	6.8	19.8				7.1
June 8	1	N	151701	6.9	18.7				6.7
June 8	1	Q	151395	7.2	18.2	12.1			7.0
June 16	1	R	151721	7.5	19.6	11.6			7.0
June 16	1	R	151722	7.0	18.9	13.0			6.4
June 16	1	R	151723	7.4	18.6	12.3			7.3
June 30	2	T	151741	7.8	18.3	11.8			6.9

Date	Age (days)	Brood	Chick	Culmen (mm)	Tarsus (mm)	Radius-ulna (mm)	Wing (mm)	Tail (mm)	Weight (g)
June 30	3	T	151738	7.7	18.9	11.4			7.2
June 30	3	T	151739	7.8	18.8	11.8			7.5
June 30	3	T	151740	7.8	18.7	12.0			7.4
June 28	4	U	151742	8.4	19.5	12.8			8.4
June 28	4	U	151743	8.6	20.9	14.2			9.6
June 28	4	U	151744	8.5	20.6	14.0			10.0
June 28	4	U	151745	8.5	20.2	13.2			8.9
July 6	4	V	161750	8.3	19.2	11.4			7.5
July 6	4	V	151751	8.6	19.0	12.0			7.6
June 29	4	Z	151734	8.8	19.8	14.2			10.3
June 29	4	Z	151735	8.1	17.3	13.7			9.2
July 3	5	T	151740	8.0	19.8	12.7			7.9
July 3	5	T	151741	8.3	19.3	12.1			6.2
June 29	5	U	151742	9.4	19.8	13.8			9.9
June 29	5	U	151743	8.9	20.8	15.5			11.5
June 29	5	U	151744	8.8	20.5	15.7			11.8
June 2	6	H	151373	8.1	20.0	20.1			10.7
June 2	6	H	151374	8.5	20.9	19.9			11.0
June 2	6	H	151376		19.8	16.0			9.9
June 8	6	Q	151707	9.0	19.0	13.3			7.3
July 3	6	T	151738	8.4	20.0	12.8			8.3

Date	Age (days)	Brood	Chick	Culmen (mm)	Tarsus (mm)	Radius-ulna (mm)	Wing (mm)	Tail (mm)	Weight (g)
July 11	7	V	151761	9.4	20.0	16.4			14.3
July 15	7	AA	151759	8.4	19.6	12.2			8.6
June 7	8	J	151392	9.2	21.0	19.1			15.0
June 7	8	J	151393	9.8	20.6	20.6			16.5
June 7	8	J	151394	9.8	20.8	22.0			15.6
June 28	8	X	151724	9.4	20.3	19.3			17.9
June 28	8	X	151725	9.8	20.7	19.2			16.5
July 3	8	Z	151734	9.6	21.1	18.5			15.0
July 3	8	Z	151736	9.6	19.9	17.0			15.1
July 15	8	AA	151765	8.7	20.4	13.7			9.8
June 8	9	J	151392	9.6	21.4	19.5			14.3
June 8	9	J	151393	9.8	21.2	22.2			18.1
June 8	9	J	151708	9.8	19.9	20.6			16.4
July 3	9	U	151743	9.5	21.9	18.6	18.9		17.0
July 3	9	U	151745	10.0	21.3	18.8			17.0
July 11	9	V	151752	9.9	20.4	17.8			16.6
June 29	9	X	151725	10.3	20.3	19.9			17.6
July 15	9	AA	151758	8.8	19.6	13.9			10.4
July 6	10	I	151369	9.6	21.2	20.0			16.9
July 18	10	AA	151759	9.2	19.7	13.7			8.8

Date	Age (days)	Brood	Chick	Culman (mm)	Tarsus (mm)	Radius-ulna (mm)	Wing (mm)	Tail (mm)	Weight (g)
June 22	11	M	151713	9.2	19.5	17.4			13.6
July 6	11	Z	151734	10.9	22.0	21.9	28.8		19.5
July 6	11	Z	151736	10.2	21.8	21.5	24.8		19.9
July 18	11	AA	151765	9.3	20.8	14.5			9.8
June 11	12	B	151712	10.3	21.0	27.7			23.4
June 19	12	N	151397	9.3	21.9	25.6			21.9
July 6	12	U	151742	10.8	21.7	21.8	29.2		21.2
July 6	12	U	151743	10.4	22.5	22.9	32.7		21.3
July 6	12	U	151744	11.0	22.9	24.5	34.9		22.6
July 18	12	AA	151758	9.4	20.6	14.9			10.9
June 28	13	R	151722	10.9	21.8	22.9	29.9		19.8
July 3	13	X	151724	11.3	22.7	27.6	39.4		26.1
July 3	13	X	151725	11.7	21.9	25.1	37.7		23.9
June 28	16	L	151716	11.3	20.7	26.3	39.2		24.1
June 28	16	L	151717	10.5	22.0	26.6	37.2		23.7
June 28	16	L	151718	11.3	21.4	27.5	40.7		24.0
July 6	16	X	151724	11.2	22.0	31.9	52.5		30.3
July 6	16	X	151725	11.4	21.9	30.3	50.4		28.6
June 14	17	H	151373	11.6	22.6	32.3			27.5
June 15	18	I	151372	11.4	20.9	31.7			26.4
July 15	20	Z	151764	12.3	22.4	36.0	87.4	28.4	30.0

Date	Age (days)	Brood	Chick	Culman (mm)	Tarsus (mm)	Radius-ulna (mm)	Wing (mm)	Tail (mm)	Weight (g)
July 15	21	U	151742	11.9	22.6	33.5	63.2	19.6	37.2
July 11	21	X	151725	12.2	23.4	39.7	72.3	22.5	35.6
June 19	22	I	151369	11.4	20.4	33.4			31.3
June 29	22	N	151397	11.2	24.8	38.8	75.2		40.9
June 29	22	N	151701	12.1	23.7	38.2	67.2		38.7
July 6	24	L	151718	12.5	23.4	35.1	73.3	25.1	37.7
July 18	24	U	151742	12.8	22.1	35.9	76.9	25.0	39.6
July 14	24	X	151724	11.7	22.8	36.2	87.6	30.9	43.7
June 22	25	I	151370	12.6	22.4	35.7	73.7	26.9	39.4

Appendix C. Weights and measurements of adult Piping Plovers.

	Culmen (mm)	Tarsus (mm)	Wing (mm)	Tail (mm)	Weight (g)
Females	11.8	23.0	115.7	52.5	56.4
	11.9	21.5	118.4	53.9	53.2
	12.5	21.8	111.7	52.1	59.3
	11.9	21.1	114.7	48.6	55.6
	12.4	22.4	114.6	44.8	52.2
Mean	12.1	22.0	115.0	50.4	55.3
Males	11.9	22.1	118.1	51.7	55.9
	12.5	22.6	121.2	52.3	59.1
	13.8	24.0	116.1	50.9	54.8
	13.5	21.7	119.5	54.8	55.1
Mean	12.9	22.6	118.7	52.4	56.2
Birds of unknown sex	12.5	22.4	114.9	51.4	56.5
	12.4	24.8	117.4	56.9	57.4
	11.2	22.4	114.8	50.9	61.1
	12.8	22.4	116.9	55.2	59.2
	12.0	21.4	116.7	51.0	55.1
Mean for all birds	12.4	22.4	116.5	51.9	56.5