Wilson Bull., 98(1), 1986, pp. 15–37

MATING SYSTEM AND REPRODUCTIVE SUCCESS OF A SMALL POPULATION OF POLYGAMOUS SNOWY PLOVERS

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ABSTRACT.—This six-year study describes the breeding of a partly resident, partly migrant population of Snowy Plovers (*Charadrius alexandrinus*) in California. Migrants arrived between 6 January and 27 April, with females preceding males. Migrant males did not pair as early as resident males, whereas resident and migrant females paired at about the same time. Early pairbonds often were with the same mate in two consecutive years. Egg laying occurred from 23 March to 13 July. Replacement clutches were initiated between 11 April and 11 July, typically seven days after loss of the preceding one, and usually with the same mate. Over the season, the time required for a pair to complete the three-egg clutch decreased from five days to four days. During egg laying, males spent more time in the nesting territory and on the incomplete clutch than did females. Incubation averaged 28.4 days early in the season, but only 26.9 days late in the season. During daytime, males averaged only 10.7% of the incubation time, but they appeared to be the main incubators at night. Over six years, 58.2% of 189 clutches hatched at least one chick. Females normally deserted hatched young within six days; males attended the young for 29 to 47 days. Fledging typically occurred at about 31 days of age. Over six years, 39% to 42% of 296 chicks fledged. After deserting broods, at least 22 of 60 females renested with new mates. At least 10 of 18 males fledging chicks before 1 July renested with new mates, and in at least 13 of 27 cases, males losing broods before 1 July renested, usually with new mates. Males appeared to outnumber females by 1.4:1. Sexual differences in survival rates are nearly sufficient to account for the difference in sex ratio. We suggest that the female's serial polyandry may be a facultative response to a skewed sex ratio. *Received 12 Mar. 1985, accepted 19 Sept. 1985.*

Despite the proliferation of shorebird literature during the past 20 years, information on breeding success and mating systems of several shorebird species is lacking (Johnsgard 1981). This deficiency encumbers attempts to understand the evolution of shorebird mating systems, a topic of considerable recent interest (Pitelka et al. 1974, Graul et al. 1977, Oring 1982, Erckmann 1983, Lenington 1984). This paper addresses that lack of information for the Snowy Plover (*Charadrius alexandrinus*). We trace events during the breeding cycle from the acquisition of mates and nesting territories to the fledging of the last chick of a partly migratory, partly resident Snowy Plover population. We quantify nesting success and describe a polygamous breeding system in a species previously reported as monogamous (Rittinghaus 1956, 1975; Palmer 1967; Boyd 1972; Johnsgard 1981; Cramp and Simmons 1983; for an exception see Lessells 1984).

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C. alexandrinus, a cosmopolitan species of temperate and tropical regions, comprises up to 13 subspecies, depending on the authority (Johnsgard 1981). Two subspecies are recognized for North America: *C. a. nivosus* west of the Rocky Mountains, and *C. a. tenuirostris* along the Gulf of Mexico, in the West Indies, and on islands off Venezuela (AOU 1957, Johnsgard 1981). Although breeding birds in Kansas, Oklahoma, and Colorado are reported to be *nivosus* (AOU 1957), some workers suspect they may be *tenuirostris* (J. Strauch, pers. comm.; R. Boyd, in litt.; Johnsgard 1981). In general, the species breeds along sandy coastal shores and on inland flats of high salinity or alkalinity (Cramp and Simmons 1983).

Knowledge of the breeding biology of *C. alexandrinus* is based chiefly on Rittinghaus's (1956, 1961, 1975) studies of the Kentish Plover (*C. a. alexandrinus*) and, for the North American subspecies, on Boyd's (1972) study of Snowy Plovers at Cheyenne Bottoms, Kansas. Both authors describe *C. alexandrinus* as monogamous, leading to a similar characterization in more general works (Palmer 1967, Johnsgard 1981, Cramp and Simmons 1983). Recently, Lessells (1984) documented polygamy in Kentish Plovers in southern France. We describe another polygamous breeding population of *C. alexandrinus* in California and provide details of its biology for comparison with Rittinghaus's and Boyd's studies.

STUDY AREA AND METHODS

We studied Snowy Plovers from 1977 to 1982 on the central California coast at the Pajaro River Mouth on Monterey Bay, and from 1978 to 1982 in the California interior at Mono Lake.

Pajaro River.—At the mouth of the Pajaro River, plovers nested on sand spits and on a salt pan (0.8 km from the spits). The pan, which was situated between a beach front development and the edge of a tidal slough, consisted of three flat, barren patches of saline mud surrounded by salt marsh (primarily *Salicornia virginica* and *Distichlis spicata*). The plovers used an area 300 × 125 m, which was little disturbed by people. After 1977, the potential breeding habitat at the south end of the salt pan expanded when some of the salt marsh was bulldozed and denuded of vegetation as part of a slough enhancement project. By 1982, enough vegetation had invaded the bulldozed area to deter nesting plovers. Suitable nesting habitat on the spits included barren to sparsely vegetated areas above the high tide line. Dimensions of the spits on both sides of the river varied yearly between 100 m and 200 m in width and 400 m and 900 m in length due to winter storm erosion and shifting of the river mouth position. Human use of the spits was high relative to that of the salt pan.

At the salt pan during the breeding seasons of 1977 to 1979, we observed birds daily from a parked car, found most nests before first eggs, and checked nests several times a day at egg-laying and hatching times. From 1977 to 1982 we searched daily for nests, broods, and banded adults on the north and, after 1977, the south spits of the Pajaro River. During the six years there were only six broods for which no nest was found.

We color banded chicks and, after 1977, adults. Chicks were distinctively color banded at the nest, by brood in 1977 and 1978, and by individual thereafter. We trapped adults with noose-covered wire mats placed in lines near plover flocks or around nests. The nooses snared the birds' legs as they ran over the mats.

The parental roles of the sexes were examined through the surveillance of birds at the salt pan in 1978 and 1979. One or two observers followed one to four pairs of plovers and recorded the time each bird spent in the territory and on eggs. There were 142.7 h of territory observation during the egg-laying period, 412.0 h during the incubation period, and 32.9 h during the hatching period. The average times each sex spent in the territory and on the nest were calculated by giving equal weight to observation time during each 3-h interval from 05:00 to 20:00 PST for the egg-laying period, to each h during the hatching period, and to each 3-h by 3-day period during the incubation period. Birds were easily sexed throughout the study through a combination of distinctive plumage (see Prater et al. 1977), observed copulations for many pairs, and, after 1977, individually color-banded birds.

During the breeding season we searched other Monterey Bay breeding sites for marked birds that had nested previously at Pajaro. Moss Landing salt evaporation ponds are 6 km south of the Pajaro River in Monterey County. Depending on water levels, up to 100 ha of dike margins and salt flats were available for nesting and feeding. One or more observers visited the Moss Landing evaporation ponds during each breeding season from 6 to 36 times between 1978 and 1982. Wilder Ranch State Beach, Santa Cruz County, is a 0.5-km long pocket beach between cliffs at the mouth of Wilder Creek, 27 km northwest of the Pajaro River. It was surveyed 6–17 times during the 1978 and 1979 breeding seasons, and from 1980 onwards, 3–5 times every week.

We checked for color-banded Snowy Plovers at the Pajaro River during each nonbreeding season beginning in 1978. Each year this coverage ranged from 47% to 82% of the days between October and March. Six days was the longest period between counts; single days made up 56% to 82% of the days missed. During the censuses we recorded which birds associated with one another both in and apart from flocks in an effort to detect the formation of pair bonds.

We organized volunteers to survey other sites along the coast and in the southern deserts of California to ascertain the whereabouts of individually banded plovers during the nonbreeding season. Observers made 881 to 1057 surveys at 83 to 150 sites each September to March period between 1979–80 and 1981–82.

Mono Lake.—Mono Lake, an elliptical 20 × 15 km alkaline lake, lies at the eastern base of the Sierra Nevada in Mono County. Snowy Plovers nested on old sand and pebble shoreline ridges and on alkaline flats that were exposed recently when the lake's water level declined. Our study site at Mono Lake consisted of approximately 10 km^2 of gently sloped, barren to sparsely vegetated lakeshore as described in Page et al. (1983).

We studied breeding Snowy Plovers at Mono Lake to supplement our work at the Pajaro River. Because the plover population there is large (Page and Stenzel 1981), we selected it over Pajaro for measuring the sex ratio of the breeding population. We banded 129 adults at their nests using the trapping and marking methods described for the Pajaro adults.

In both 1981 and 1982, 10 censuses of Snowy Plovers were taken between 1 and 19 June along 4.5 km of seeps that bordered an old lakeshore ridge and along 4.5 km of corresponding current lakeshore. One person walked along the seeps, and another walked as close to the lakeshore as possible. Each counted all Snowy Plovers seen and recorded their age, sex, whether banded, color combination, and the time and specific locations of the sightings. To test field accuracy in sex determination, two primary observers viewed 30 museum specimens in breeding plumage from a distance of 15 m with 9 × 35 binoculars. One observer's determinations matched the museum labels 93% of the time, the other's matched the labels 100%.

Because of the 2-km width of the study area, we accounted for less than 100% of the plovers. Therefore, in the analysis of census data, we used a standard capture-recapture technique of estimating population size (Seber 1982) modified as described below to compensate for differences between recapturing and resighting as methods of detecting individuals. Because we observed a few marked plovers between censuses or found them in the study area on nests which we knew to be active during the census period, we were able to supplement our knowledge of which marked plovers were present in the study area during each census. Additionally, as marked individuals may be seen more than once on a census, we used multiple sightings of marked birds to estimate the overcounting of all birds due to movements of individuals. In the calculations for each year, we considered only birds marked in previous years, so that the nesting stages of marked birds represented those of all plovers. Population size estimates were made for each sex and year separately. The equality of corrected totals for each sex on each census was compared using Wilcoxon's matched-pairs signed-ranks test for each year.

RESULTS

Snowy Plovers occurred year-round at Pajaro, but not all birds were residents. From 1978 through 1982, 40.9% of 44 marked males and 23.7% of 59 marked females that nested also occurred regularly between October and March (residents). Another 43.2% of the males and 42.4% of the females bred at Pajaro but were absent from November to at least January (migrant breeders). During the same period at least 18 marked males and 16 marked females wintered at Pajaro (occurred regularly from at least November to February) and bred elsewhere (wintering birds). Other birds followed inconsistent patterns or disappeared too quickly to be categorized. Three males and six females changed patterns between years: one male, a resident the first year, appeared briefly in the second and third years, and became a migrant breeder in the fourth and fifth years; two males and three females that were migrant breeders and two resident females abandoned Pajaro as a breeding site, yet were known to be alive; and a sixth female was resident for four years, except for the third breeding season, when she was absent. The situation at Pajaro differs from the interior of western North America where most, if not all, breeders migrate to coastal wintering areas (unpubl. data).

Arrival of migrant breeders.—Female migrant breeders arrived at Pajaro as early as, if not earlier than, migrant male breeders (Fig. 1). Although the arrival dates of both sexes spanned about the same period, the overall mean arrival dates were 9 March for females and 24 March for males, a difference that was marginally significant (Mann-Whitney *U*-test, $P = 0.0586$).

Pairbonds.—We were unable to determine when and how pairbonds formed, but on numerous occasions we saw behavior that we believed led to pair formation. Such behavior was typified by a male repeatedly calling *turwheit* from a territory that he had defended against other male

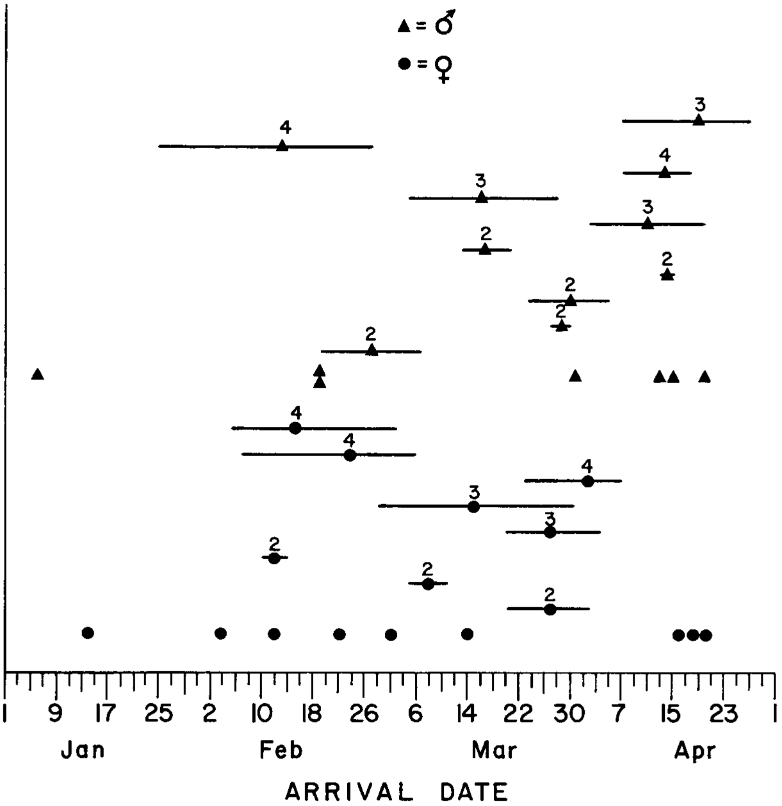

FIG. 1. Arrival dates of marked Pajaro Snowy Plovers. Horizontal lines give the ranges, circles or triangles the means, and numbers the sample sizes of years for individuals. Single dates for individuals are shown as circles or triangles without sample sizes.

plovers. When a female arrived, the male adopted a posture in which bill, body, and tail were parallel to the ground, the head was extended, and the throat feathers were puffed out as the bird moved about, almost gliding. The male approached and passed the female in this posture and then began scraping by lowering his breast to the ground and kicking backward alternately with his feet, gradually rotating his body. Usually, scraping occurred where the bird had scraped before so that there was a depression in the ground. Sometimes the female squatted in the depression and rotated slightly; although this occasionally led to copulation, the sequence usually was repeated at several scrapes before the first copulation occurred. Sometimes the female flew off or was driven off by the male, and no copulation occurred. Early in the season, however, birds that eventually

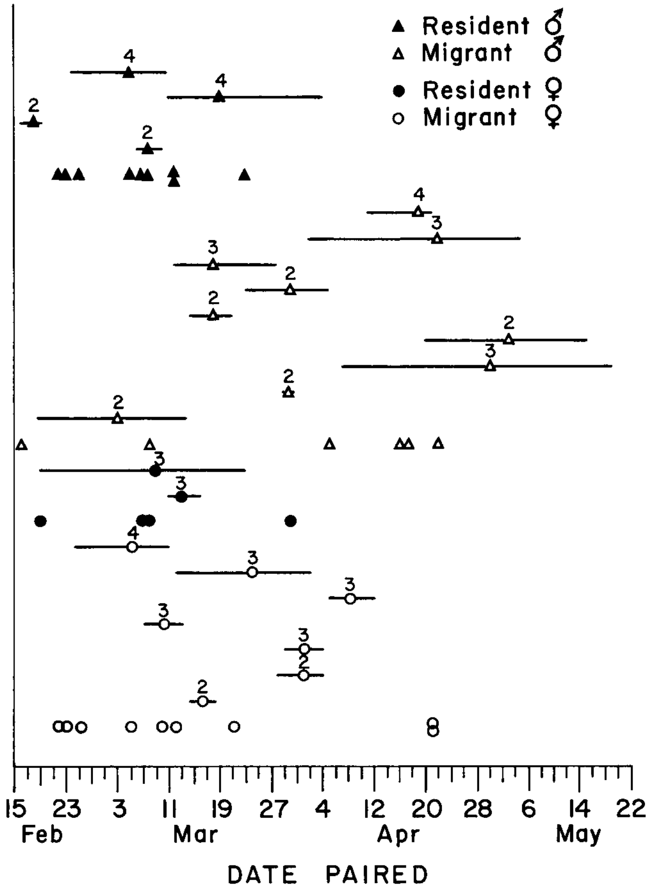

FIG. 2. Dates by which resident and migrant breeding Snowy Plovers were paired at Pajaro. For symbols see Fig. 1.

nested together were consistently beside each other within and apart from roosting flocks day after day, and we saw no scrapes or scraping activity. This suggests that pairbonds can be established before scraping occurs. We use the first date that eventual nesters were seen associating with each other to estimate the time of pair bond formation.

Early season pair bonds formed between residents (7 cases), migrant males and females (15 cases), migrant males and resident females (10 cases), and migrant females and resident males (11 cases). Mean estimated pairing dates were 10 March for resident females, 19 March for migrant females, 6 March for resident males, and 3 April for migrant males (Fig.

2). Residents were paired significantly earlier than migrant breeders for males (normal approximation for Mann-Whitney *U*-test, $P = 0.001$) but not for females ($P = 0.3$).

An individual's earliest nesting attempts were with the previous year's first partner on 13 of 29 possible occasions. In 5 of the 16 remaining cases, one adult appeared to be paired before the other arrived, but in 11 instances new mates were chosen, despite the apparent availability of the former mate. Kentish Plovers also pair with a previous year's mate, although a partner change from one year to the next is described as the rule (Rittinghaus 1956, 1961).

Territories.—Snowy Plovers posture, chase, and fight when defending territories. Territory sizes were always less than 0.5 ha at the salt pan, where boundaries on two to four sides were defined by the interface of barren flat with salt marsh vegetation. Beach territories may have been larger, but we lacked sufficient observations to determine their size.

A nesting territory was not a prerequisite for pair formation. Despite daily coverage at the salt pan, in only 14 of 47 cases did we find unpaired territorial males. The remaining males were paired when first seen on territories. Neither is a territory necessary for pairbond formation in Kentish Plovers (Rittinghaus 1961, 1975). When advertising, unpaired, standing Pajaro males called *turwheit* repeatedly from their territory. We did not see aerial advertisement such as the bat-like song flight Rittinghaus (1975) describes as rare, or the unsteady, tern-like flight Dement'ev and Gladkov (1969) mention for the Kentish Plover.

It was not always possible for Pajaro birds to occupy the same territory in consecutive years because of beach erosion during the winter. In the 21 possible cases where males and females could occupy the same territory and remate with each other two years in a row, males used the same territory in 15, and females in 9, instances. When pairing was with a previous year's mate, the pair used the previous year's territory in 7 instances and a different territory in 3 instances. When birds changed mates between years, males changed territories in only 3 of 11 cases and females in 9 of 11 cases. These results were consistent with those of Rittinghaus (1956, 1961) who reports that when Kentish Plovers change partners from one year to the next, it is usually the male that goes to the previous year's territory.

Snowy Plovers did not always retain a territory for renesting attempts after failure. After clutch failure induced by human or natural causes other than predation, pairs with at least one banded bird renested in the same territory in 12 of 23 instances. Pairs retained a territory in only 1 of 11 instances when a predator destroyed the clutch. Eight departing pairs moved 200–800 m to new Pajaro territories, one moved 4 km to a new

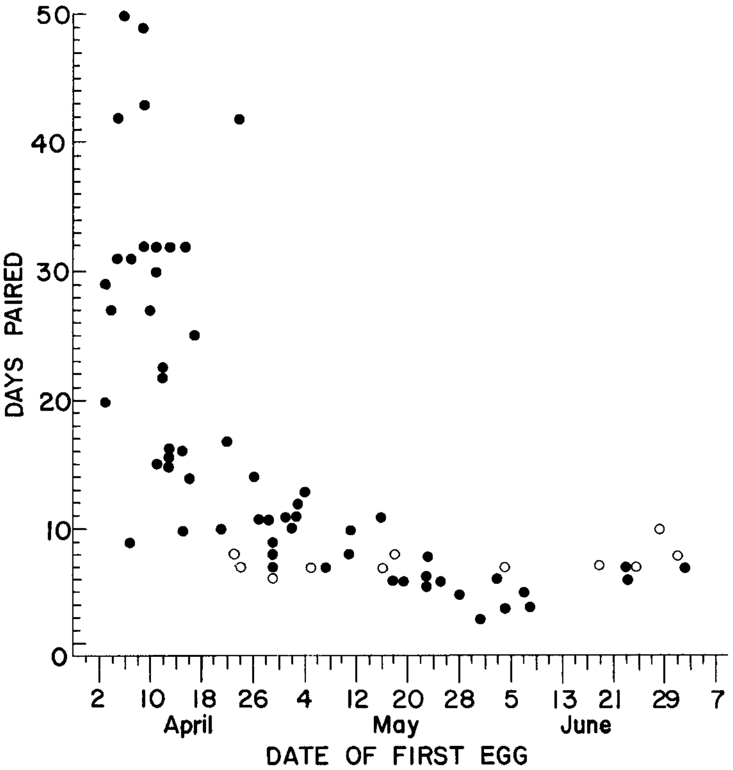

FIG. 3. Closed circles show the number of days paired before the first egg was laid. Open circles show the time between clutch failure and the first egg of renesting attempts of established pairs.

beach territory, 11 moved 6 km to the Moss Landing evaporation ponds, and one pair disappeared.

Egg laying.—Egg laying spanned 16 weeks at Pajaro with the earliest egg on 23 March and the latest egg about 13 July. Every year except 1982, egg laying began by late March and lasted to at least 29 June. Overall, at least 6 clutches were begun in March, 84 in April, 62 in May, 32 in June, and 6 in July. At least 10 of the April clutches, 8 from May, 9 from June, and 2 from July were renests after failure. At least 5 from May, 10 from June, and 1 from July were renests of females after the successful hatching of a previous clutch.

The clutch sizes in completed Snowy Plover nests at Pajaro were 1 with four eggs, 160 with three eggs and 10 with two eggs. Three of the two-egg clutches were discovered after incubation had begun and might have held a third egg at one time. Larger clutches are possible. Page, Peaslee,

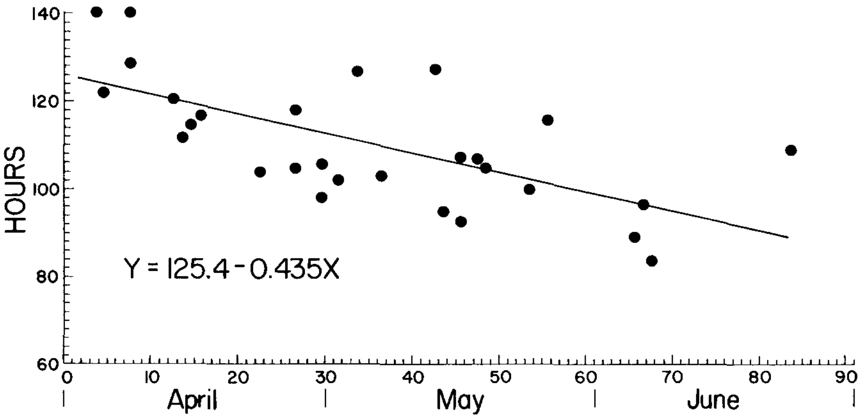

FIG. 4. Seasonal variation in the hours elapsing between the laying of the first and last of the three eggs in Snowy Plover clutches at Pajaro. The slope of the regression line is significantly different from 0 ($P = .00016$).

and Widrig (unpubl. data) found one clutch with five eggs and two with six in 1977 at Big Lagoon, Humboldt County, California. One female-plumaged bird sat on one of these nests readily when the observers were near, but she was aggressively displaced by another female on two occasions when the observers retreated. This suggested that two females laid the eggs. Cramp and Simmons (1983) mention a similar situation in the Kentish Plover, where a male and two females attended a single nest with five eggs.

At Pajaro, the interval from pairbond formation to the first egg ranged from 50 to 3 days and decreased during the breeding season (Fig. 3). Copulations, which are well-described in Rittinghaus (1956) and Boyd (1972), occurred from 25 days before to 3 days after the first egg was laid. At the salt pan, 89% of 172 observed copulations were prior to the first egg and none was after the second. By contrast, Piping Plovers (*C. melodus*) copulate throughout the egg-laying period (Cairns 1982), and Killdeers (*C. vociferus*) copulate throughout the incubation period (Bunni 1959).

During the egg-laying period, Snowy Plovers were often absent from their salt-pan territories. In the 10 territories, males were absent 37.7% (SE = 7.6%) and females 52.6% (SE = 5.6%) of the time during the day; in 9 of the 10 territories males were absent during less time than females (randomization test for matched pairs, $P = 0.0078$). The 10 males averaged 16.6% (SE = 3.0%) and the 10 females 10.3% (SE = 2.7%) of the time during the day on the eggs. In 7 of the 10 cases, males spent more time on the eggs than females ($P = 0.0186$).

We know the time at which 58 eggs were laid. Two to seven were within each hour interval between 06:01 and 19:00, indicating laying occurs at any time during daylight. The daytime (06:01–18:00) to nighttime ratios for eggs were 20:3 for egg one, 22:17 for egg two, and 23:6 for egg three. The difference is significant ($\chi^2 = 7.91$, $P < 0.02$), indicating that egg two was more likely to be laid after dark than eggs one or three. The usual time between consecutive eggs ranged from 46.5 to 77.5 h and averaged 61.6 h (SE = 4.2, N = 8) between eggs one and two, and 55.4 h (SE = 2.2, N = 17) between eggs two and three, a difference that was not significant (*t*-test, $P > 0.05$). Rittinghaus (1956) reports 18–72 h between Kentish Plover eggs, but that 48 h is normal. The time required to complete Pajaro clutches decreased from an average of about five days for early nests, to about four days for late ones (Fig. 4).

Incubation.—Snowy Plovers typically began sustained incubation when the last egg of the clutch was laid. Incubating plovers were found as early as 29 March and as late as 9 August at Pajaro, and during the six years were always present at least from 2 April to 4 July. Incubation from the last egg laid to the last young hatched ranged from 26 days to 32 days ($\bar{x} = 27.4 \pm 0.2$ [SE]) with the earlier nests averaging longer periods than later ones ($\bar{x} = 28.4 \pm 0.3$ for 19 nests started before 8 May; $\bar{x} = 26.9 \pm 0.1$ for 38 nests begun later; *t*-test, $P < 0.01$). The same trend was observed at Mono Lake where incubation periods ranged from 25 days to 32 days, but averaged 28.8 days in four nests started before 1 June and only 25.4 days for five later ones. Even the late season Pajaro incubation periods were longer than Boyd (1972) gives for Cheyenne Bottoms, Kansas, where eight clutches hatched within 24 to 26 days ($\bar{x} = 25.5$ days). Rittinghaus (1975) gives a range of 23–29 days and a mean of 26.3 days (N = 43) for incubation in the Kentish Plover.

During daytime, male Snowy Plovers spent less time incubating than females until hatching began. In eight salt-pan territories, males were absent 84.1% (SE = 3.1%) and females 11.2% (SE = 1.7%) of the time during the day. Males incubated an average of 9.5% (SE = 3.3%) and females 79.7% (SE = 3.4%) of the time during the day. In all territories, males spent less time incubating than females. Our results concur with those of others who reported that in *C. alexandrinus* females take the bulk of the daytime incubation duty (Boyd 1972, Rittinghaus 1975, Nakazawa 1979, Cramp and Simmons 1983).

We know less about nighttime incubation, but we suspect that males incubate at night. We found males incubating in 90.4% of 73 dusk nest checks. This differed from the daytime, when males averaged 10.7% (SE = 2.0%) of the incubation time on the eight salt-pan territories. At Mono Lake, Page and Stroup (unpubl. data) found only the male incubating a clutch when they photographed a nest one night using a flash every 45 min from 23:00 to dawn. Boyd (1972) reported that the female Snowy Plovers incubate at night, and Rittinghaus (1975) reported that male Kentish Plovers incubate from late afternoon or early evening to the early morning hours.

Clutch Failures.—During the study, we found 187 nests and 6 broods at Pajaro. Our banding caused failure at four nests, which are excluded from all calculations of productivity. The six broods are included for a total of 189 nests.

Desertion caused failure at four nests; three additional desertions that occurred after the study supplement our information. In seven cases where one sex (two males and five females) deserted during the first 16 days of incubation, the other sex eventually also abandoned the clutch, whereas in two cases (one male and one female) where abandonment occurred between the eighteenth and twenty-second day of incubation, the remaining parent hatched the clutch. Lessells (1983) reports that single-parent Kentish Plovers also hatched clutches deserted by the other parent during the later period of incubation. In addition, Lessells (1983) found female Kentish Plovers were more likely to desert than males.

Both parents sometimes deserted Pajaro clutches that were reduced to one egg, and these desertions also appeared related to length of incubation. Parents abandoned four clutches reduced to single eggs at between 3 and 13 days of incubation, but not two clutches reduced to one egg on the twenty-sixth and thirtieth days. After this study, two other clutches reduced to single eggs, one between the twelfth and eighteenth day, and the other between the eighteenth and twenty-fourth day, were not deserted, and both hatched. We classified clutches reduced to one egg and then deserted as "destroyed."

Seventy-five of 189 nests at Pajaro were destroyed by causes other than desertion. People destroyed 26 nests, all but one of them on the beach, by driving over them, stepping on them, or by taking the eggs. All wind losses ($N = 12$) and losses of unknown cause ($N = 4$) were on the beach. Seventy-five percent of the clutches lost to wind, and all lost to unknown causes, disappeared on weekends and holidays, although these days made up only 30% of the time nests were in existence. As most human use of beaches occurred on holidays and weekends, we believe people indirectly or directly caused many losses we attributed to wind or unknown factors. People may have kept incubating birds off nests during strong winds, allowing eggs to be scattered or buried.

Predators destroyed 19 Pajaro nests; at least one was taken by an American Crow (*Corvus brachyrhynchos*), 6 by unidentified gulls (*Larus* spp.), and the remainder by various mammals. Gulls did not actively seek clutches, but destroyed them when individuals in roosting flocks trampled on or accidentally discovered the eggs and ate them. At Mono Lake, gull predation is deliberate, and many clutches are taken (Page et al. 1983).

High tides caused destruction in nine instances, rain caused destruction in three, and the embryos inexplicably died in two. We identified no other causes of clutch loss at Pajaro.

Renesting after clutch failure.—Snowy Plovers typically renested after clutch loss until July. Renesting occurred between 11 April and 11 July. In 12 of 13 accurately determined instances, six to eight ($\bar{x} = 7.1$, SE = 0.2) days elapsed between clutch destruction and subsequent clutch starts; in the thirteenth instance, 14 days elapsed. In five additional cases a new clutch was begun in two to four days after the destruction of a partially completed one, resulting in a second clutch of three eggs. Pairs renested up to five times. Rittinghaus (1975) reports that Kentish Plovers renest readily after clutch destruction, in as few as four to five days after loss of the first. Renesting from 5 to 14 days after clutch failure in other *Charadrius* plovers is not uncommon (Bunni 1959, Graul 1975, Cairns 1977, Bergstrom 1982).

Snowy Plovers remained paired in 26 of 30 cases involving renesting of banded pairs at Pajaro. One female chased off the female of a pair attempting to renest, and the aggressive female nested with the male whose mate she had driven off; otherwise we could not account for the reasons that pair bonds dissolved. Lessells (1984) reported that Kentish Plover pairs remained together in 11 out of 13 instances after clutch failure, and Rittinghaus (1975) reported that Kentish Plover partner changes after clutch loss are rare.

Hatching.—Eggs hatched during any time of the day and at night. From 1 to 33 h elapsed from the emergence of the first to the third young in 28 three-egg clutches; 43% hatched in less than 6 h. During hatching, males were present in nine territories an average of 72.3% (SE = 7.6%); females were present 87.5% (SE = 4.7%) of the time. Males spent 39.0% (SE = 5.3%) and females 54.0% (SE = 5.0%) of the time on the nest.

Fledging.—At Pajaro, we found unfledged chicks between 27 April and 9 September. We determined the fledging period for 22 chicks (from hatching to a first flight of at least 3 m) at no more than 29 to 33 days ($\bar{x} = 30.9$); at least 15 appeared unable to fly at 29 days. Subsequent to this study 3 chicks fledged at 28 days. Two captive chicks studied by Boyd (1972) took 28 and 32 days to fledge. Thus, it appears the Snowy Plover requires four to four and one-half weeks to fledge. Rittinghaus (1956, 1975) gives an average of 41 days for Kentish Plovers on Oldeoog and 27 and 32 days for two young at Amsterdam. Cramp and Simmons (1983), aware of these differences, feel 27 to 31 days is the more likely fledging period.

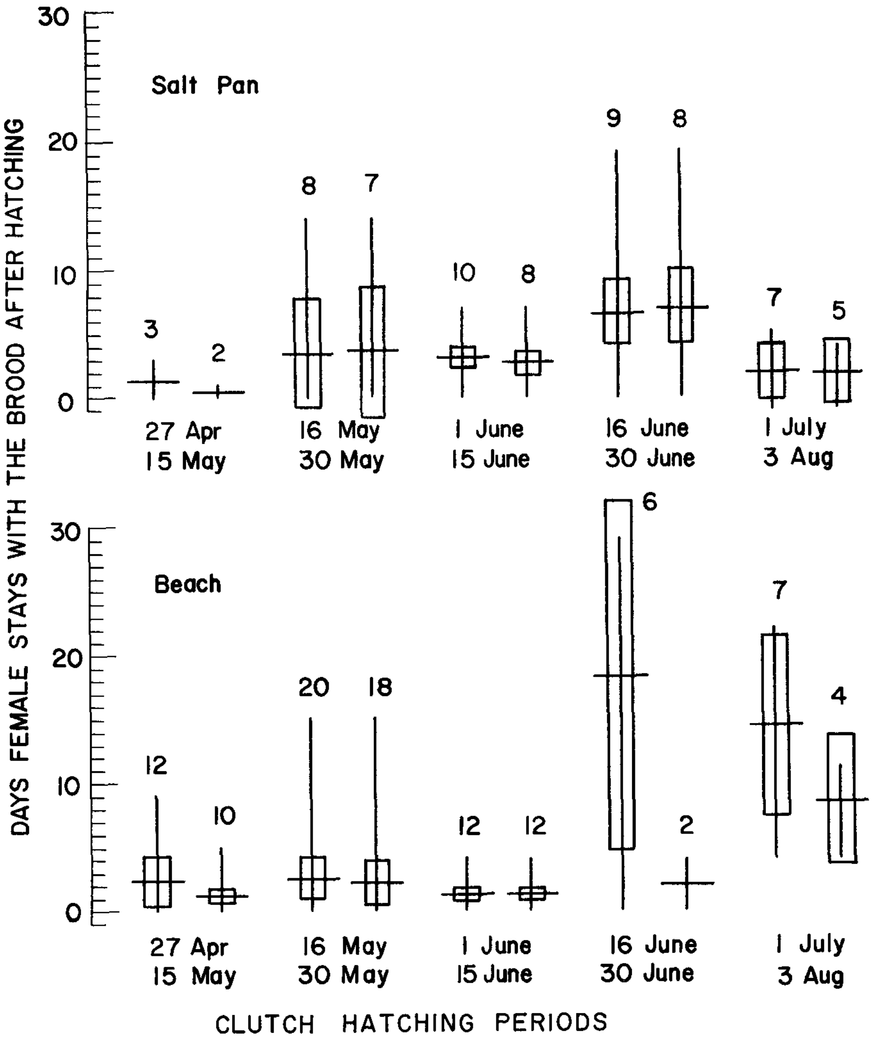

FIG. 5. Number of days the female remains with the brood after the chicks hatch at the Pajaro beach and salt pan. Data are broken into five clutch-hatching periods. For each period the left component of a data set includes all 6 years and the right component includes all years except 1977. The vertical line is the range, the horizontal line the mean, and the rectangle the 95% confidence interval of the mean; sample sizes are above.

Although both sexes attended Snowy Plover broods, the female usually deserted before the young could fly (Fig. 5). Females had deserted by the sixth day in 17 of 21 early salt-pan broods, 13 of 16 late salt-pan broods, and 40 of 44 early beach broods, using a 15 June hatching date to divide the periods. In contrast, only three had left by the sixth day in 13 late-

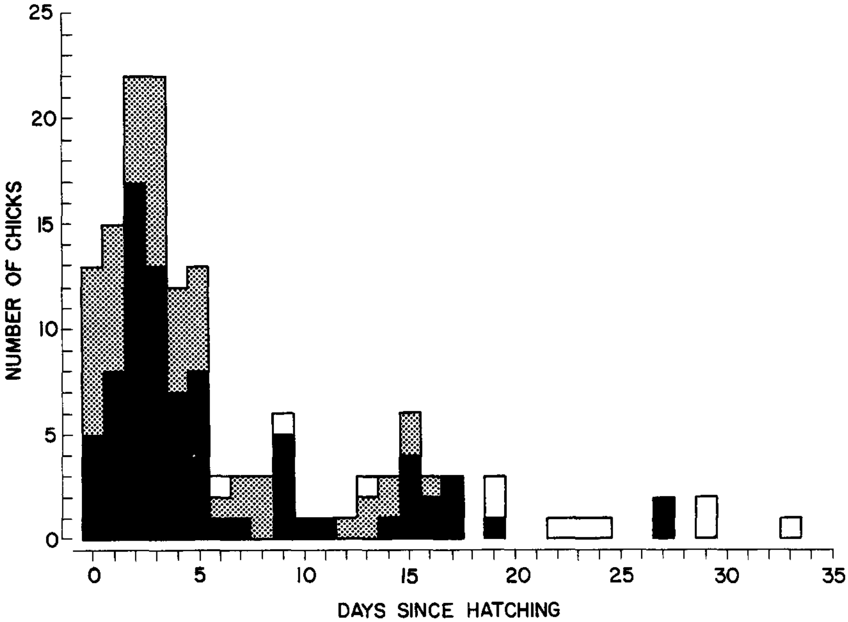

FIG. 6. Age of chicks lost during fledging at Pajaro. Solid areas represent the beach and stippled areas the salt pan. Blank areas represent periods (from either location) of chicks last seen when fledging was not certain.

season beach broods. Seven of 10 females that remained for more than six days with the late beach broods did so in 1977; all stayed for more than 20 days, longer than any other female with a brood that had not been deserted by the male. In 1977, a year with high reproductive success, the north spit nesting area was small, and nests hatched in rapid succession with as many as eight broods sharing a 6.8-ha area. Parents from neighboring broods clashed with each other frequently, leading us to suspect that both parents may have been needed to keep track of their chicks or to prevent them from being attacked by neighboring adults. Such long-term sharing of fledging duties was unusual, as at Pajaro in other years. And at other locations we found that only the male usually cared for the young after they were a few days old. Males usually accompanied chicks until they were 29 to 47 days old. In three additional cases, females that were deserted by mates from seven days before to six days after the eggs hatched, cared for the broods alone: two fledged young from these broods.

Broods rarely remained in the nesting territory until fledging, although they sometimes remained in the general area. Broods crossed other birds' territories, sometimes causing neighbors to attack the young, and at least once causing abandonment and death of a chick. Despite this, there were two cases of chick adoption, with chicks incorporated into the broods of foster parents by the time the adopted chicks were nine days old. Adoption of young by the Killdeer (Lenington 1980) and by the Wilson's Plover (*Charadrius wilsonia*) (Bergstrom 1982) are also reported to occur on rare occasions.

Most chick mortality occurred before chicks were six days old (Fig. 6). In at least 15 of 29 cases in which all three young in a brood were lost, all chicks disappeared on the same day. At least 92.7% of the 124 chicks reaching 16 days of age fledged. Predators and encounters with other birds were the only causes of chick mortality we witnessed. Loggerhead Shrikes (*Lanius ludovicianus*) took at least 14 chicks at the salt pan in 1979. Another chick at the salt pan failed to leave with the rest of the brood after its parents had a 14-min confrontation with a pair of American Avocets (*Recurvirostra americana*) and their brood.

Second broods and polygamy.—Some Snowy Plovers attempted second broods at Pajaro. Females initiated second nesting attempts with different males after deserting their first broods and mates. Males, and rarely females, attempted second broods after successfully fledging young from a previous brood. Sixty Pajaro females abandoned broods before 1 July and had time for further breeding. Seventeen renested with new mates at Pajaro, four at the evaporation ponds, and one at Wilder State Beach. Five formed pair bonds with new mates and disappeared, and 32 left unmated, but stayed away at least 38 days (long enough for a successful nesting attempt). The remaining female, which had laid three clutches previously, was absent only 13 days and may not have attempted a new nest.

Twelve of 16 marked males at Pajaro that had fledged chicks early enough for a subsequent successful nesting attempt either renested or were thought to have done so; the status of the other 4 males was unknown. Five of the 12 renested at Pajaro (only one in its original territory) and three at the evaporation ponds; the other four were found paired at the evaporation ponds, but their nests were never found. Ten of the 12 had acquired new mates by the time their chicks were 29 to 38 days old, and two paired on unknown dates. In seven instances the male deserted his brood first, but in at least four others, he continued to tend his chicks during the early part of courtship. All second mates were acquired by 2 July.

Two additional males paired and renested with new females before their chicks from the first nest had fledged. One male's second nest had its first egg when his first brood was only 29 days old. Another male was helping with the incubation of a new three-egg clutch by the time his two chicks, which he still brooded, were 25 days old. The male struggled to brood and incubate nightly, with the chicks elevating him well above the eggs. They fledged when 32 days old, and at 34 days flew away, but returned each evening and were brooded on the nest until they were 38 days of age. The only female that both tended a brood alone and acquired a new mate did so when her two chicks were 26 days old.

On 27 occasions, banded males losing broods still had time for a second attempt at nesting. We are certain that renesting occurred at Pajaro or the evaporation ponds on 13 occasions, and it probably took place five additional times at the evaporation ponds as well. In eight instances, males left the area with time left for an attempt elsewhere. One male that lost a brood in late June definitely failed to renest.

The above examples describe a serially polygamous breeding system that differs little from a monogamous double-brooded one, except that the second broods of both sexes were with new mates. Polygyny occurred rarely, although the previously discussed clutches of five and six eggs at Big Lagoon may have represented polygyny as did the following: a banded male, nesting with a banded female, was observed courting a different female in a different part of the salt pan. Nine days later, we found him on a one-egg clutch, 110 m from his other nest, and seven days later we captured him on the new nest. When his first clutch hatched, he and his first mate attended the chicks. His second nest was destroyed by a predator two days later. In addition, we saw or captured males on others' nests at least three times. Because male Snowy and Kentish Plovers (Rittinghaus 1956) sometimes sit on another's eggs, caution is necessary when documenting polygyny.

Breeding success.—Yearly variation in Snowy Plover breeding success at Pajaro is summarized in Table 1. Combining areas over the six years, we calculated a clutch-hatching rate of 58.2% (N = 189), an egg-hatching rate of 55.2% (N = 534), a chick-fledging rate (percent of hatched chicks fledged) of 39% to 42% (N = 296), and a production rate of 0.8 to 0.9 fledged young per female (N = 151). Over all years, 94.5% of the 293 eggs from successful nests hatched. Six eggs were deserted with a large living embryo, one with a large dead embryo, eight were rotten without evidence of an embryo, and one was not checked.

Return rate, survival rate, and sex ratio.—Mortality and degree of site fidelity are the two factors that affect return rates of migratory birds to specific breeding areas in consecutive years. We determined that at least 78.6% of 56 male and 72.6% of 73 female breeding Snowy Plovers were alive at least one year after being banded on the nest (or after laying the first egg for those banded prior to nesting). Of the surviving males, 34 nested in the banding location in the second year, eight were seen but

TABLE 1

REPRODUCTIVE SUCCESS OF SNOWY PLOVERS DURING SIX YEARS

Year	Est. no.[a] of females	Est. no.[a] of males	Total no. of clutches[a]	% successful clutches/ % eggs hatched	Eggs hatched per female	Eggs hatched per male	Percent young fledged[b]	Young fledged per female	Young fledged per male[b]
1977	25	23	27	85/74	2.4	2.6	75–83	1.8–2.0	2.0–2.2
1978	24	24	36	50/47	1.9	1.9	20–27	0.4–0.5	0.4–0.5
1979	26	22	43	53/53	2.5	3.0	26–29	0.7	0.8–0.9
1980	13	14	21	38/40	1.7	1.6	18–19	0.3	0.3
1981	23	24	31	58/51	2.0	1.9	63–67	1.3	1.2–1.3
1982	23	24	31	65/63	2.4	2.3	20	0.5	0.5

[a] Includes 6 clutches inferred from broods and excludes 4 clutches we accidentally destroyed.

[b] Minimum and maximum possible because of the uncertain fate of some chicks.

were not known to nest in the banding area the second season, one returned after the breeding season, and one, not known to return to Pajaro, was located at another area. Comparable figures for females were 30, 15, 3, and 5. Thus 65.8% of 73 females and 76.8% of 56 males were in the breeding area one or more years after banding, and 6.8% of the females and 1.8% of the males were outside the breeding area.

Females may be less site-faithful and have lower survival rates than males, but this cannot be demonstrated with our small samples. We can estimate the sex ratio of the population if we assume that (1) our survival estimates are accurate, (2) the population size is stable, and (3) the proportion of males and females hatching and reaching breeding age is the same, from the following equation:

$$\frac{1 + S_m + S_m^2 + S_m^3 + \ldots + S_m^n}{1 + S_f + S_f^2 + S_f^3 + \ldots + S_f^n}$$

Where S_m (0.786) is the annual adult male and S_f (0.726) is the annual adult female survivorship applied each year (1, 2, . . . , n), and S_m^n and S_f^n approach zero. The predicted ratio is 1.28 males per female.

At Pajaro, males typically outnumbered females during the breeding season. For example, on 15 May 1980, 1981, and 1982, the number of males to females was 8:7, 24:22, and 19:16, respectively. On 15 June 1980, 1981, and 1982, it was 8:5, 14:7, and 12:6, respectively; however, a larger population is needed to measure sex ratio. This was available at Mono Lake, where one of the state's largest breeding populations occurs (Page and Stenzel 1981).

Our results from two seasons of adjusted censuses at Mono Lake were similar. In each year males outnumbered females on all 10 censuses, a result which differed significantly from equality (Wilcoxon matched-pairs signed-ranks test, $P = 0.0010$). Adjustment factors calculated from the color-marked bird sightings revealed fewer males were overlooked at Mono Lake because their behavior made them easier to see. For 1981, we calculated an average of 1.901 marked males and 2.951 marked females were present for each one found on a census. As some marked birds were seen more than once on a census, we assumed overcounts of unmarked birds were also probable. We calculated that only 0.844 of the males and 0.949 of the females on censuses were different birds. Combining factors, we concluded there were (1.901 × 0.844 =) 1.604 males, and (2.951 × 0.949 =) 2.800 females for each one counted (whether duplicate or not) in 1981. Our results in 1982 were similar, with (1.859 × 0.905 =) 1.682 males and (3.333 × 0.966 =) 3.220 females for each one counted. This difference in detection rates was undoubtedly due to the difficulty of finding the females, which incubated most of the day on widely scattered nests from which they attempted to depart undetected when approached. By contrast, males concentrated around feeding areas where they were easily observed. The average number (from adjusted totals) of males was 115.3 (SE = 5.3) and females 82.3 (SE = 2.7) in 1981, and in 1982, 119.1 (SE = 7.0) males to 85.3 (SE = 7.4) females for a M:F ratio of 1.40:1 in each year.

DISCUSSION

The polygamous, double-brooded breeding system described for Snowy Plovers at Pajaro is probably commonplace in *C. alexandrinus* west of the Rocky Mountains. Our findings at Pajaro were corroborated by observations of banded breeding birds at Wilder Beach, Mono Lake, and, subsequent to this study, at two other sites on Monterey Bay (unpubl. data).

Comparison with other C. alexandrinus.—Snowy Plovers at Cheyenne Bottoms, Kansas, differ from those west of the Rockies mainly by being monogamous single-brooders, with both sexes caring for the young (Boyd 1972, in litt.). All individuals in this population are migrants; the earliest arrivals reaching the breeding grounds in the beginning of April. Most clutches are laid between late May and late June. An exceptionally early clutch was started on 22 April and the last on 26 June, giving a maximum interval for clutch initiation of 65 days. As about 58 days elapse between laying the first egg and fledging of the young at Cheyenne Bottoms, the length of the breeding season is scarcely long enough for males to participate in double broods. Because egg laying is concentrated in June at Cheyenne Bottoms, there is not time for most females to initiate second clutches, even if they were to desert the first one at hatching. Boyd (1972) believes that high water levels do not allow for earlier nesting.

We noted a few other differences between Snowy Plovers at Cheyenne Bottoms and Pajaro. Although Boyd (1972) states that the female incubates during most of the day, we differ on the sex of the nocturnal incubators. On three occasions he determined that only the female incubated at night, drawing his conclusion from an electronic device that indicated when birds got on and off the nest. This differs from patterns at Pajaro and Mono Lake, and from the Kentish Plover, which Rittinghaus (1956) and Nakazawa (1979) characterize as being mainly female by day and male by night.

The behavior of the off-duty parent also differed between Cheyenne Bottoms and our study locations. At Cheyenne Bottoms, Boyd (1972) reports that "throughout the period that the female was on the nest the male could be seen standing 20 m to 30 m away." Males preened, slept, or at other times fed near the water's edge. At Pajaro and Mono Lake, males were not within sight of their nests during much of the day. The difference might be related to the distance between nesting and feeding areas at the two locations.

Snowy Plovers at Pajaro differed from Kentish Plovers at Oldeoog in several major ways. Unlike Snowy Plovers, Kentish Plovers at Oldeoog typically attempt a single brood, although in rare instances two broods are known (Rittinghaus 1956). Rittinghaus reports that, for two years in a row, one female successfully incubated a clutch with one male and, after the young hatched, paired with another male and successfully reared a brood with him. This was a common pattern at Pajaro. Rittinghaus (1956, 1961, 1975) is not clear as to the duration of the egg-laying period at Oldeoog, so we do not know if the period extends long enough for double brooding to be probable. Some female Kentish Plovers desert first broods and renest with new mates at the Camargue in southern France, where the egg-laying period of the plover population spans three months (Lessells 1984).

Rittinghaus's 1956 and 1975 reports differ on parental roles in the rearing of broods. In the 1956 paper he states that the parents initially share responsibility equally, though at times only one parent takes on most of the chick-tending duties. The female's share generally increases toward the end of the fledging period, and in late broods the female usually tends the young while the male joins large flocks of successful pairs with their fledged young. This differs from the Snowy Plover, and from Rittinghaus's 1975 Kentish Plover report in which he states that the young, though cared for by both parents during the first two weeks, are cared for normally by the male when only one parent is with the brood. Cramp and Simmons (1983) add to the confusion by reporting that one parent leaves the chicks when they are half-grown, but that the sex of the departing parent varies with location: in Amsterdam more males than females stay with the young, but at Oldeoog more females than males stay with the young. At the Camargue, female Kentish Plovers normally desert the brood a week after hatching, although there are instances of male desertion (Lessells 1984). At Pajaro, female Snowy Plovers typically had left the brood by the time the young were 6 days old.

The prolonged period of biparental brood care at Oldeoog may be a consequence of the extremely high density of nesting birds—96 pairs on 0.7 ha in 1948 (Rittinghaus 1975). The only time females remained with broods for extended periods at Pajaro was on the beach in 1977 when we had our highest density of active nests and broods. High breeding density, which might reduce food availability and increase the rate of antagonistic interactions between broods, may cause the lengthy 41-day Kentish Plover fledging periods (Rittinghaus 1956, 1975), which are at least 10 days longer than for Snowy Plovers at Pajaro or Cheyenne Bottoms (Boyd 1972).

Factors underlying polygamy in Snowy Plovers.—New mates are apparently available to female Snowy Plovers because of a breeding population with surplus males. The skewed sex ratio could arise in several ways; we have no data that would eliminate any of the various possibilities. As demonstrated earlier (see Results), small differences in survival rates of breeding male and female Snowy Plovers by themselves could be sufficient to account for the asymmetry. The differences in survival rates could, in turn, be accounted for by differences in the sexes' exposure to risks or in effort expended due to the different parental roles.

Sequential polyandry could also occur in the absence of an absolute difference in the sex ratio if (1) females indirectly limit access of other females to males via territoriality; or (2) directly limit access by guarding more than one mate (Oring 1982); or (3) if males breed at an earlier age than females. We found no evidence that females or guarded males defended territories occupied by more than one male. Furthermore, females bred at as early an age as males. We found nests or broods for 10 of 15 first-year males (banded as chicks) and 9 of 14 first-year females on Monterey Bay. The first egg in nests of three males was laid when they were 308, 326, and 358 days old (measured from hatching date) and those of three females when they were 267, 308, and 354 days old.

With a surplus of males when females were physiologically ready for second broods, it could be advantageous for females to leave brood care solely to their mates, and then start another nesting attempt with a new partner. In contrast, a male would have little to gain from abandoning broods to a female's care; his chances for new mates would be limited by the unfavorable sex ratio. The advantage of brood desertion by females would be particularly clear when uniparental care was not a serious constraint in raising young, and when the chance for fledging two broods in one season was increased by minimizing the number of days spent with the first brood. Uniparental brood care is widespread in plovers (Bunni 1959, Hussell and Page 1976, Bergstrom 1982, this study) and other shorebirds (Jenni and Collier 1972, Oring and Knudson 1972, Pitelka et al. 1974). We believe the females' emancipation from brood-rearing duties increased their chances for double broods. Although the breeding season was long enough for double brooding with the same mate, the high rate of clutch destruction often necessitated one or more replacement clutches before a female hatched a brood. As the extra time needed for the replacement clutch greatly reduced the time available for second broods, any mechanism that allowed females to start second clutches sooner would increase the chances of two broods fledging.

This raises the question of why Snowy Plover females do not desert initial clutches sooner than they do. Female Spotted Sandpipers (*Actitis macularia*) desert clutches during the incubation period (Oring and Knudson 1972), and females of other polyandrous species such as the Red Phalarope (*Phalaropus fulicaria,* Schamel and Tracy 1977), Red-necked Phalarope (*P. lobatus,* Hildén and Vuolanto 1972), and Northern Jacana (*Jacana spinosa,* Jenni and Collier 1972), or of multi-clutch species such as the Mountain Plover (*Charadrius montanus,* Graul 1975) and Temminck's Stint (*Calidris temminckii,* Hildén 1975) desert clutches as soon as they are completed. The ability to implement a single-parent incubation scheme is an important factor promoting their breeding systems. In contrast, Snowy Plover adults remaining after mates had deserted or died typically deserted the clutch unless it was 10 or fewer days to hatching.

Other species that make more than one breeding attempt per season do so monogamously. For example, monogamously established pairs of Killdeers and Wilson's Plovers produce multiple clutches sequentially, and females are frequently emancipated from brood-rearing duties for second clutches (Bunni 1959, Bergstrom 1982), demonstrating that these males can rear broods alone. It would be valuable to know whether the sex ratios differ from equality in these species. The females may remain with the first broods only because surplus males with which they could start second broods are not available. This hypothesis implies that in the Snowy Plover serial polyandry may simply be a facultative response to the conditions of a skewed sex ratio. The key evolutionary step to this mode of reproduction would then be the female's ability and tendency to make more than one breeding attempt per season.

The only other shorebird known to employ this type of polyandrous strategy is the Dunlin (*Calidris alpina schinzii*) in Finland (Soikkeli 1967). Typically, Finnish female Dunlins desert first broods about six days after hatching and after a few more days leave the breeding area. In one of six years, however, when nesting commenced very early, three females undertook second broods with new mates. None of these males had yet bred that season (Soikkeli 1967). The Dunlin's polyandry also appears to be a facultative response to an elongated breeding season and to the availability of additional mates.

ACKNOWLEDGMENTS

We thank the many people who made this study possible. We name only a few, but everyone has our heartfelt thanks. B. Allen-Ramer, S. Allison, F. Bidstrup, S. Corbus, C. Frederiksen, S. Gellman, D. Houle, S. Mayer, P. Metropulos, R. Morgan, D. Parker, S. Peaslee, B. Ramer, D. Ramer, B. Sauppe, B. Swarth, C. Swarth, E. Vollmer, R. Widrig, and D. Winkler contributed countless hours of field observations. F. Bidstrup, C. Frederiksen, B. Ramer, and N. Spear managed the volunteer beach survey project; D. Hunt compiled color-marked bird sightings; C. Cutler drafted the figures; J. Stroup took night photographs; L. Gotschalk, F. Lanting, and H. Loring translated German papers; and R. Wilson-Jacobs shared German translations. E. Tuomi and O. B. Young typed and made useful suggestions on the manuscript. J. Church edited, and in addition to P. Bergstrom, M. Howe, and L. Oring, critically reviewed the manuscript. This is contribution 313 of Point Reyes Bird Observatory.

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