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BREEDING BIOLOGY OF WILSON'S PLOVERS

PETER W. BERGSTROM[1]

ABSTRACT.—The breeding biology of Wilson's Plovers (*Charadrius wilsonia*) was studied in Texas during 1979–81 and in Virginia in 1984. Nests were hundreds of meters apart on salt flats, roads, or unused runways. Ninety-eight percent of nests were within 30 cm of a clump of vegetation, but only 12% of the nests were near objects. Seven pairs renested after their first nest failed, and one pair laid a second clutch after its first brood was adopted. In Texas, egg laying occurred from mid-April to mid-June with two distinct peaks; in Virginia, egg laying was mainly in May. Clutches of 3 eggs were laid over 5–6 days, and about 8 days elapsed between the failure of a nest and a start of a renest. Mean egg size was 35.2 × 25.9 mm; length, breadth, and volume index (LB^2) varied significantly among females. Both sexes incubated; daylight attentiveness rose during the laying period; after clutch completion it averaged 77%. Parents were usually silent during nest relief. Eggs hatched over a span of 8–35 h after an incubation period of 25 days. Hatching success was low in Texas (12–54%), and it varied within and between years. Nest failure was associated with rain (usually flooding), mammalian predation, and cattle. The family moved to a wet area near the nest after hatching, and parents defended the chicks, but not a fixed territory. Chicks spent most of their time hidden in vegetation, attended by one parent at a time. *Received 8 March 1987, accepted 21 August 1987.*

Wilson's Plovers (*Charadrius wilsonia*) breed on American seacoasts from Virginia south to Brazil and from Baja California south to Peru, and on the shores of the West Indies (Johnsgard 1981). Except for anecdotal information (e.g., Bent 1929), there is only one previous published report on their breeding biology (Tomkins 1944).

This report includes the first quantitative data published on many aspects of the breeding biology of this species, including nest sites, laying and hatching dates and intervals, egg sizes, renesting, and nesting success. Details of incubation behavior have been reported elsewhere (Bergstrom 1981, 1982, 1986). This report supplements recent reports on the breeding biology of other plovers (e.g., Graul 1975, Cairns 1982, Warriner et al. 1986).

STUDY AREAS AND METHODS

I studied Wilson's Plovers in 1979 at Laguna Atascosa National Wildlife Refuge, Cameron County, Texas (26°15′N, 97°15′W). Wilson's Plovers nested on sparsely vegetated salt flats that are part of a former delta of the Rio Grande. These flats flooded during heavy rain. Bare soil with a salt crust was interspersed with clumps of halophytes, primarily saltwort (*Batis maritima*) and glasswort (*Salicornia* sp.). Fiddler crabs (including *Uca subcylindrica*) were abundant on the flats.

[1] Dept. Biology, Washington and Lee Univ., Lexington, Virginia 24450.

In 1980 my study area was on Matagorda Island, Aransas National Wildlife Refuge, Calhoun County, Texas (28°15'N, 96°30'W). On the bay side of this sandy barrier island, Wilson's Plovers nested on salt flats similar in appearance and vegetation to those at Laguna Atascosa. Fiddler crabs were also abundant there. Wilson's Plovers also nested on the sandy beach on Matagorda, but I did not study them there.

I revisited Laguna Atascosa and Matagorda Island for 10 days in June 1981. In June 1984 I spent 7 days observing plovers on the beach at the north end of Metompkin Island, Accomack County, Virginia (37°45'N, 75°30'W). Observations refer to the Texas study sites unless otherwise stated.

Texas sites were hot and humid during the breeding season. Average daily temperatures in Brownsville, 45 km S of Laguna Atascosa, ranged from 24.5°C in April to 29.7°C in July, with maxima in July of 35°C, and 50% relative humidity. Normal rainfall is 6–10 cm/month in May and June, but rainfall was 4.9 cm below normal during this period in 1979, 10.7 cm above normal in May 1980, and 8.4 cm below normal (no rain) in June 1980 (NOAA 1979, 1980).

I found 29 nests each year in 1979 and 1980. I marked nest locations with wooden stakes (1979) or plastic flags on wire stakes (1980) 5–10 m from the nest. I observed behavior through 7 × 56 binoculars or a 55× spotting scope from a truck parked about 50–75 m from the nest in 1979 and from a portable canvas blind 15–25 m from the nest in other years. In 1980 I recorded incubation behavior with time-lapse movie cameras photographing at 1-min intervals. I trapped at least one member of each pair on the nest with a funnel trap and banded birds with a unique combination of aluminum and plastic (from A. C. Hughes) color bands. When both parents were banded at a nest, I usually allowed several days between trappings to minimize the risk of desertion. Measurements are given as mean ± SE. Eggs were measured with vernier calipers.

RESULTS

Nest site.—Nests were on bare soil or pavement, usually near a clump of vegetation, but rarely near objects. Fifty-seven of 58 nests had plant stems within 0.5 m of the nest cup, although 4 nests had only small plants nearby (about 1 cm tall). As there were large bare areas present near most nests, nest placement appeared to be deliberate. None of 29 nests was within 30 cm of objects in 1979, when few objects were present. In 1980, more objects were present, and 7 of 29 nests were within 30 cm of objects at least as large as an egg: 5 were near cow manure, 1 was near a black pipe, and 1 was near a stone. Mean distance to an object for those nests was 12 ± 3.6 cm (range = 2–30).

At Laguna Atascosa, 22 of 29 nests were either in sparse vegetation in the center strip or at the edge of a road. The roads were 1–2 m above the salt flat and surfaced with crushed rock, shells, or gravel. For the seven remaining nests, mean distance to the nearest road was 9.1 ± 4.1 m (range = 2–33). I looked for nests from roads, but repeated attempts to find other nests away from roads were unsuccessful. Salt flats were flooded by heavy rains in early June, and plovers were rarely seen far from roads or water. Of the 22 road nests, 9 were on gravel and 13 on other substrates, even though there were relatively few gravel roads. Eggs on gravel appeared to be better camouflaged than eggs on other substrates.

On Matagorda Island, only 1 of 29 nests was along a road: 13 were on unused concrete or asphalt pavement (parts of a former airfield), and 15 were on soil. The 13 soil nests which I measured were a mean of 36.3 ± 8.9 m (range = 6–108) from the nearest road. Distances to water ranged from 50 m to 1.1 km.

I recorded the presence of vegetation near the nest in eight sectors surrounding each Matagorda nest and found a significantly nonrandom distribution (Cochran $Q = 17.3$, $P < 0.02$), with more nests having vegetation on the south and southwest sides. Prevailing winds were from the southwest at Matagorda (pers. obs.).

Distances between nests.—In almost all cases, nests were far enough apart for incubating birds to be out of sight of each other. The closest pairs of simultaneous nests were 35.5 m apart on a salt flat, separated by a slight rise, and 39.3 m apart on opposite sides of a raised road. Other pairs of nests, within sight of each other, were 57 m apart on a runway and 64 m apart along a road. All other active nests were at least 250 m apart. The closest three pairs of Wilson's Plover nests in Virginia (out of 12 nests found) were 44, 45, and 52.5 m apart, and mean nearest neighbor distance for the 12 nests was 85 m (Bergstrom and Terwilliger 1987).

Wilson's Plover nests were sometimes near those of other species in Texas. Several nests on Matagorda were near nests of Least Terns (*Sterna antillarum*) and Common Nighthawks (*Chordeiles minor*), and two nests at Laguna Atascosa were near Common Nighthawk or Snowy Plover (*Charadrius alexandrinus*) nests. One nest on Matagorda was 11 m from an active American Avocet (*Recurvirostra americana*) nest, and there was a Black-necked Stilt (*Himantopus mexicanus*) nest nearby. In Virginia Wilson's Plover nests were always in the same area as Least Tern and Piping Plover (*C. melodus*) nests (Bergstrom and Terwilliger 1987).

Renesting.—The mean distance between first and second nests of 7 pairs whose first nest failed was 58.2 ± 17.6 m (range = 24–157). All of the second nests were on the same substrate as the first nest. Eggs in 2 of the 7 first nests had been eaten by coyotes, 4 were deserted, and in 1 nest the eggs disappeared for unknown reasons. One pair that hatched a second brood after its first nest hatched and its young were adopted (see below) moved 29 m for its second nest. Both parents were banded on the first nest in 5 of these 8 cases, and in all 5 cases the pairs remained together to renest. Birds sometimes changed nest substrates between years. Two pairs banded on Matagorda in 1980 were found nesting there in 1981; one was nesting 40.6 m from its previous nest on the same substrate, while the other had moved 303 m to nest on a different substrate.

Nest starting dates.—The first peak in nest starts came a week earlier in 1980 than in 1979 (Fig. 1). The earliest known nest each year was started on 15 April; however, as I found young chicks at Laguna Atascosa

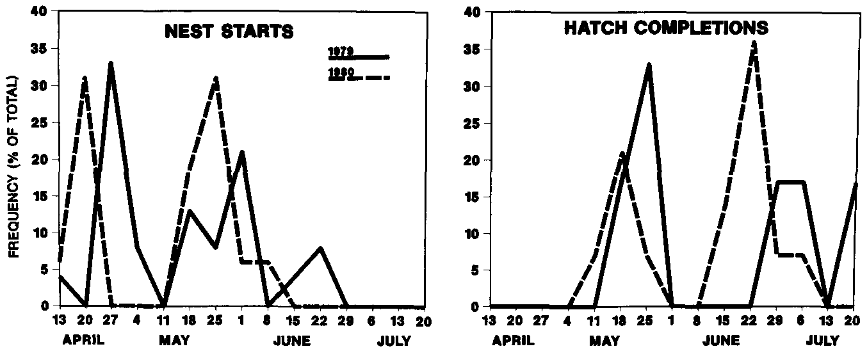

FIG. 1. Phenology of nest starts and hatch completions for Wilson's Plovers in Texas. Nest start = date when first egg was laid; Hatch completion = date when last egg hatched.

on 1 May 1979, egg laying there began by 1 April. There was a second peak of nest starts in both years during late May and early June (Fig. 1), which probably represents renesting. Egg laying ended in 1979 on 20 June and in 1980 on 7 June. The lack of rain in June 1980 (NOAA 1980) may have been a factor in the earlier ending that year.

Egg dates for Wilson's Plovers in Texas were similar to those in Georgia (Tomkins 1944) and in Surinam (Renssen 1974). In Virginia, egg laying started later (early May, first chicks seen 8 June) and ended sooner (end of May, latest eggs 20 June; K. Terwilliger, pers. comm.), suggesting that renesting is less common there than in Texas.

Laying intervals.—Time required to lay a complete clutch was estimated for 6 nests. In one nest where I saw the laying of the first egg (at 11:36), the second egg was laid 54–68 h later, and the third egg 104–125 h after the first (about 5 days later). At another nest it took a minimum of 144–149 h to lay 3 eggs (about 6 days). Estimates at four other nests were 119, 120, 142, and 145 h to lay three eggs. At one nest where a minimum of 52.5 h elapsed between the laying of the second and third eggs, the time of laying of the third egg was determined from a film (16:26).

Mean time from nest failure to the start of a new clutch for 7 renests (after the first nest failed) was 7.6 ± 1.6 days (range = 5–13). One pair started a new nest 13 days after the hatching of its first nest, after its first brood was adopted (see below).

Egg size.—The 78 eggs measured were laid by 20 different females. All egg dimensions (Table 1) varied significantly among females (oneway ANOVA, $P < 0.001$ for length, breadth, and volume index [LB^2]). Eggs of the same female were not significantly smaller in second nests than in first nests (paired *t*-tests on clutch means, $P > 0.05$) (Table 1), as they often

TABLE 1
EGG MEASUREMENTS FOR WILSON'S PLOVERS IN TEXAS

	Length	Breadth	Volume Index (LB^2)
All eggs	35.23 ± 0.14 (78)[a]	25.85 ± 0.06 (78)	23,552 ± 128 (78)
First nests	35.48 ± 0.26 (15)	25.49 ± 0.12 (15)	23,046 ± 216 (15)
Second nests	35.71 ± 0.42 (14)	25.83 ± 0.09 (14)	23,818 ± 299 (14)

[a] All measurements are mean ± SE (N).

are in shorebirds (Miller 1979). There were no significant regressions of egg dimensions on female culmen length, although the two are often correlated positively in shorebirds (Miller 1979). Laying order within the clutch was recorded at 4 nests; there was no consistent trend in egg size with laying order in this small sample.

Clutch size.—Complete clutch size was four at 1 nest, three at 45 nests, and two at 5 nests (2.92 ± 0.047). Only one of the clutches of two eggs hatched, so some of the small clutches may have been deserted and incomplete. Modal clutch size in this species is also three in other areas (Bent 1929).

Incubation.—Regular incubation did not begin until the third egg was laid; however, the parents attended increasingly during clutch completion. Total daylight attentiveness (% of the daylight period that either parent was on the nest) was 16%, 13%, and 50% at one nest on days when there were 1, 1, and 2 eggs in it. At another nest, daylight attentiveness went from 53% to 80% and 84% after the third egg was laid. Most attentiveness during clutch completion was by the male, while after it, most was by the female (Bergstrom 1986). Mean daylight attentiveness (both sexes, 14 pairs) was 77% (range = 70–86%, Bergstrom 1986), but it was strongly affected by air temperature and nest substrate (Bergstrom 1982). Incubation behavior functioned both to warm and to cool the eggs (Bergstrom 1982).

Nest relief.—The noisy nest relief ceremony described for other plovers (Bunni 1959) was not observed in Wilson's Plover. Often one parent left the nest a few minutes before its mate arrived. When the parents saw each other at the nest there was normally no call, but the departing bird (especially the male) occasionally tossed small objects over its shoulder. Occasionally the female gave *Fweep* calls (Bergstrom 1988) when she arrived at the nest. Nest relief changed shortly before hatching began, when the relieving bird usually came to the nest before the sitting bird left. There was also a reduction in incubation shift length at this time (Bergstrom 1986).

Incubation period.—At one nest, 25 days 3 h elapsed from the laying to the hatching of the third egg. Estimates of the incubation period at five other nests were 23–27 days. Bent (1929) reported an incubation period of 24–25 days for this species.

Hatching.—Hatch completions had two peaks per season, about 30 days after the peaks of nest starts (Fig. 1). These peaks were more distinct than those of nest starts, with no known nests hatching between 28 May and 25 June 1979, or between 22 May and 14 June 1980.

Parents removed eggshells within 30 min of hatching, usually flying off with them but sometimes running away with them. At a nest where I observed hatching on Metompkin Island, the shell was carried away 16 min after I first saw the chick's head, during the parent's second absence after hatching.

Hatching intervals.—At some nests, hatching took less than 24 h: three chicks hatched in a total of 8 h at one nest, and within 19 h at another nest, and two chicks hatched 4.5 h apart in a third nest (only two of the eggs hatched in that nest; the parents continued incubating for 24 h, and then deserted the third egg). In three other nests the hatching intervals were longer: three eggs hatched over a total of 34.5 h and 25–40 h, and two eggs in a third nest hatched 24–37 h apart. At Metompkin Island the first and last eggs in a nest hatched 23 h 56 min apart, but one egg or chick disappeared in the interim. Hatching intervals were usually unequal within a clutch, with one interval of about 24 h and one shorter, about 5–10 h, but which occurred first was not consistent.

Hatching success estimates.—The three estimates of hatching success I used (Table 2) are all biased to some degree. The first two estimates are probably too high because some nests that failed were not found (Mayfield 1961), but exposure estimates are probably too low, because the probability of failure within years was not constant (Green 1977). In 1980 clutch hatching success rose from 36% to 75% for nests found after 16 May ($G = 4.14$, $P < 0.05$). This date corresponds to the start of the second peak in nest starts (see above). In 1979, nests on gravel roads had significantly higher clutch hatching success than nests on other roads (57% vs 10%, $G = 4.53$, $P < 0.05$). Clutch hatching success was significantly higher on Matagorda Island in 1980 than at Laguna Atascosa in 1979 ($G = 4.42$, $P < 0.05$), and nest survival probability was also significantly higher in 1980 than in 1979 ($G = 8.4$, $P < 0.01$; Dow 1978).

Causes of nest failure.—The known causes of nest failure were mammalian predation, cattle, and flooding. Five failed nests (3 at Matagorda, 2 at Laguna Atascosa) had tracks or scats of coyotes near them. Tracks of a bobcat-sized cat and broken eggs were found near one failed nest at Laguna Atascosa. One 1979 nest, probably deserted after flooding, later

TABLE 2
WILSON'S PLOVER HATCHING SUCCESS IN TEXAS

	Year	
	1979	1980
Nests		
Number found	29	29
Deserted (after human disturbance)	2	1
Outcome unknown	3	2
Hatched one or more chicks	6	14
Failed (no chicks hatched)	18	12
Clutch hatching success[a]	0.25	0.54
Eggs		
Number laid	57	75
Number hatched	17	34
Left in nest after hatching	1	5
Disappeared during incubation	0	8
Egg hatching success	0.30	0.45
Exposure (Mayfield 1961, 1975)		
Nest-days (days all nests at risk)	230	404
Egg-days (days all eggs at risk)	—[b]	1086
Nest survival probability	0.13	0.47
Egg survival probability	1.0	0.83
Hatching probability	0.94	0.87
Overall nesting success[c]	0.12	0.34

[a] Equals no. of nests hatching 1 or more young/total no. of undisturbed nests with known outcome.
[b] Not calculated as partial clutches were not lost in 1979.
[c] Equals the product of the 3 probabilities preceding it.

had eggshells that appeared to be punctured by a bird's beak. Cattle grazed on Matagorda (but not at Laguna Atascosa), and signs of cattle (crushed eggs and prints) were found near five failed nests and one nest that lost an egg there. Three failed nests at Laguna Atascosa were found under water. Small holes such as those made by rodents (Maxson and Oring 1978) were found in two previously deserted eggs in 1979.

At the other 15 nests that failed, there were no eggshells and no tracks. The parents might have removed eggshells after failure, or the eggs may have been eaten by a predator that left no tracks, such as a bird or a snake.

Effect of rain.—Nests tended to fail around the time of rain (2.5 mm/day or more) in both years, but not always from flooding. In 1979, 67% of 18 failures occurred on the 21 days with rain, significantly more than the 14% of failures expected if rain had no effect (14% of the days had rain; $G = 26.1$, $P < 0.001$). In 1980, 33% of 12 failures occurred on the

9 days of rain, significantly more than the expected 9% ($G = 5.15$, $P < 0.05$). Most rains occurred early in the season (especially in 1980), and this probably accounts for the higher nesting success later in the season.

Chicks.—Mean weight at hatching of 18 chicks was 9.3 ± 0.54 g, with a mean culmen length of 6.0 ± 0.13 mm. The chicks stood up and started to walk within 1–2 h of hatching. I saw one family leave the nest: the third and last egg hatched at 06:45, and the family moved off together (after several false starts) at 08:56 the same day.

Family movements.—Most families moved after hatching to a low wet area where the chicks fed in halophytic vegetation, especially saltwort. In some cases there were suitable areas near the nest and the family did not move very far: one in 1979 moved 10–20 m with their chicks, and in 1980 one moved about 30 m with their chicks. Pairs nesting on roads generally moved farther: one male moved his family to a shallow pond about 100 m from the nest. In Virginia, families moved away from the beach to mud flats behind the dunes, about 100 m from their nest site (Bergstrom and Terwilliger 1987).

Parents appeared to defend an area around the chicks if there were other Wilson's Plovers nearby. One male in 1979 did Parallel Run displays (Bergstrom 1988) with another male tending chicks nearby at the edge of the same pond. Another male in 1979, while he still had eggs, did Parallel Run displays with a male that had chicks nearby, and his mate sometimes did the display to the other male also (Bergstrom 1988).

During the day, one parent stayed near the chicks while the other parent was out of sight. The attentive parent did not follow, call to, or lead the chicks, but 50–80% of its time was spent alert, displaying or brooding (Bergstrom 1981). Both in Texas and Virginia, when not being brooded, chicks spent almost all of their time hidden in vegetation, presumably feeding. When the parents changed roles they often called to each other loudly with *Tweet* calls (Bergstrom 1988), in sharp contrast to the normally silent nest relief (see above). When the family moved from one area to another, often in the evening, I always saw both parents with the chicks.

I was unable to follow broods until fledging because of their mobility and cryptic behavior. There were indications of chick mortality (e.g., the only families seen with three chicks had young chicks), but it was not possible to estimate chick survival. Time to fledging is not known (the reference in Johnsgard 1981 to Tomkins 1944 on this subject is wrong: 21 days was only a minimum possible time given by Tomkins).

Adoption.—I saw one 1980 pair with three chicks the day after hatching, on 14 May. I banded two of the chicks, and then the parents led them down a road away from their nest. I next saw the parents on 19 May and they behaved as if they had no chicks. Their second nest was near their first (see above) and was started about 26 May. I did not see the banded chicks again until 3 June, when one of them was being attended and brooded by an unbanded male. This male defended an area around the chick adjacent to the territory of its parents, using Parallel Run displays (Bergstrom 1988). The adoption probably occurred before 19 May, and it could have been caused in part by the banding of the chicks.

Adoption might result from the attraction to chicks of unrelated females, a phenomenon I saw in Texas and Virginia. On 2 occasions, after I had banded and released a chick, or visited a nest containing a chick, an unrelated female approached the chick and tried to brood it.

DISCUSSION

Two functions have been proposed for the tendency of plovers to nest near objects: nest concealment by disruption of its outline (Bunni 1959, Graul 1975), and use as a windbreak (Tomkins 1944). Vegetation near nests may have the same function in Texas, where objects are uncommon. At Mono Lake, Snowy Plovers nesting beside scarce objects had lower hatching success than pairs nesting elsewhere (Page et al. 1985). A windbreak would help keep eggs from rolling out of the nest in Texas, and the vegetation near nests tended to be in the direction of the prevailing winds. Most of the vegetatation was not tall enough to function as a sunscreen.

Although Wilson's Plovers nesting in Texas seem to have a breeding season long enough to allow double-brooding, no cases were found there. Double-brooded plovers usually have either single-parent incubation (as in Mountain Plovers [*C. montanus*], Graul 1973) or single-parent brood care (as in Snowy Plovers, Warriner et al. 1986). Both of these are rare in Wilson's Plover (Bergstrom 1981).

Laying intervals in Wilson's Plovers were similar to those in other plovers, except Killdeers (*C. vociferus*), which laid more rapidly (Bunni 1959, Cairns 1982, Graul 1975, Rittinghaus 1961, Warriner et al. 1986). This difference is not related to clutch size nor to the weight of the eggs or the clutch relative to female body weight (Graul 1973:88), as Killdeers are not distinct from this group in any of these variables.

The defense of the chicks, but not the nest site or a fixed feeding area, has also been reported in Snowy (Rittinghaus 1961, Boyd 1972) and Mountain plovers (Graul 1975). In plovers in which a relatively fixed feeding area is defended near water (Piping Plovers, [Cairns 1977], and Killdeers, [Lenington 1980]), the nesting territory is often used for brooding at night. However, as family movements within a species probably vary with the proximity of feeding areas to the nest site, it is not clear whether these are consistent species differences.

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