Male Incubation in Wilson's Plover (*Charadrius wilsonia*)

PETER W. BERGSTROM
Committee on Evolutionary Biology, University of Chicago, 1103 E. 57th Street, Chicago, Illinois 60637 USA

Male incubation, defined as exclusive incubation by the male, is thought to be a necessary step in the evolution of polyandry from monogamy in birds. When the female has time to gather more food, she can lay clutches more rapidly, which may be an advantage under certain conditions (Emlen and Oring 1977, Graul 1973). Polyandry is then possible if the female can mate with other males for successive clutches.

This is the first report of male incubation in Wilson's Plover (*Charadrius wilsonia*), a strictly monogamous shorebird (Tomkins 1944 and unpubl. data). Males incubated alone at three nests for a total of 31 days of incubation, documented by 215 h of behavioral samples at these three nests. At 14 other nests in 1980, the males' average share of daylight incubation was 27% (range 7–44%), which is significantly less than 50% ($t = 5.21$, df = 13, $P = 0.0002$, using arcsine transformation).

Nesting behavior of Wilson's Plover was studied during two breeding seasons at two locations on the coast of Texas. In 1979, 450 h of behavioral observations were made at 15 nests at Laguna Atascosa National Wildlife Refuge, Cameron County, Texas. Focal-animal samples (Altmann 1974) were made on both parents at a nest, dividing their behavior into feeding, displaying (including all social behavior), preening, incubating, alert standing, and out of sight. Data were analyzed using the CRESCAT system (Kaye 1977). In 1980, time-lapse movie samples at 1-min intervals were made of 900 h of parental behavior at 15 nests on Matagorda Island, Aransas National Wildlife Refuge, Calhoun County, Texas. The movies were analyzed with an editor with a frame counter. Using time checks on the film, single frames were converted to instantaneous samples (Altmann 1974) of behavior at the nest. Behavior was classified as sitting on eggs, standing over eggs, standing near nest, or out of sight. Nests were numbered consecutively each year, and pair number corresponded to nest number (e.g. Nest 29-79 was the 29th nest found in 1979, and male 29-79 was the male incubating on that nest). At least one parent was color banded at each nest, and the sexes could always be distinguished by plumage. Incubation period was 25–26 days, and active nests were found between 5 April (young chicks seen 1 May) and 17 July. Data presented here show incubation time, defined as the estimated percentage of daylight hours spent incubating, by each parent and by males alone after female disappearance. Incubation time was transformed using the arcsine transformation (Winer 1971) for all statistical tests.

In 1979, males incubated alone at the last two active nests of the season, 26-79 and 29-79. Female 26-79 disappeared between day 10 and day 18 of incubation, while I was not watching the nest. From 28 June (day 18) onward, I watched this nest for 52 h during all periods of the day and saw only the male incubating. All three eggs hatched in this nest on 6 July, and the chicks were led away by the male and not seen again.

For comparative purposes, average incubation time, as the percentage of time spent incubating, is shown in Fig. 1a for 9 nests at which both parents incubated. The females were on the nest about 60% of the time, and the males about 20% of the time, between 0700 and 1730. Between 1731 and 2100, the females' incubation time decreased and the males' increased, so that each was about 40%. Total incubation time for the day was 76%. Figure 1b shows incubation time for Nest 26-79, before and after female disappearance. Total incubation time for this nest before disappearance was 89%, and male incubation time was 28%, but after disappearance the male incubated 73% of the time, which is similar to the average for pairs.

At Nest 29-79, the female was seen on the nest on the afternoons of days 7, 9, and 11 of incubation, but not on the afternoon of day 10 (1 July). She was not seen on or near the nest during 97.5 h of observation between days 14 and 26 of incubation. Figure 1c shows incubation time for this nest before and after female disappearance. During 9.5 h of observation prior to her disappearance, total incubation time was 65% and male incubation time was 41% (data available only for 1401–2100). After her disappearance, the male's incubation time increased to 60% during this period, but he had had unusually low incubation time between 0700–1030 and 1731–2100. He made long trips away from the nest at these times, presumably to feed. Because this nest also hatched successfully, on 17 July, none of his absences led to a lethal heating of the eggs.

Male 29-79 was seen with his chicks a few times after their hatching. He led them to one of the few marshes remaining in the area, where he defended a territory around the chicks at the edge of the water. Table 1 shows time budgets for two intact pairs with young chicks, and for male 29-79 when his chicks were 2 days old. Male 29-79 fed more near the chicks, was alert less and displayed less near the chicks,

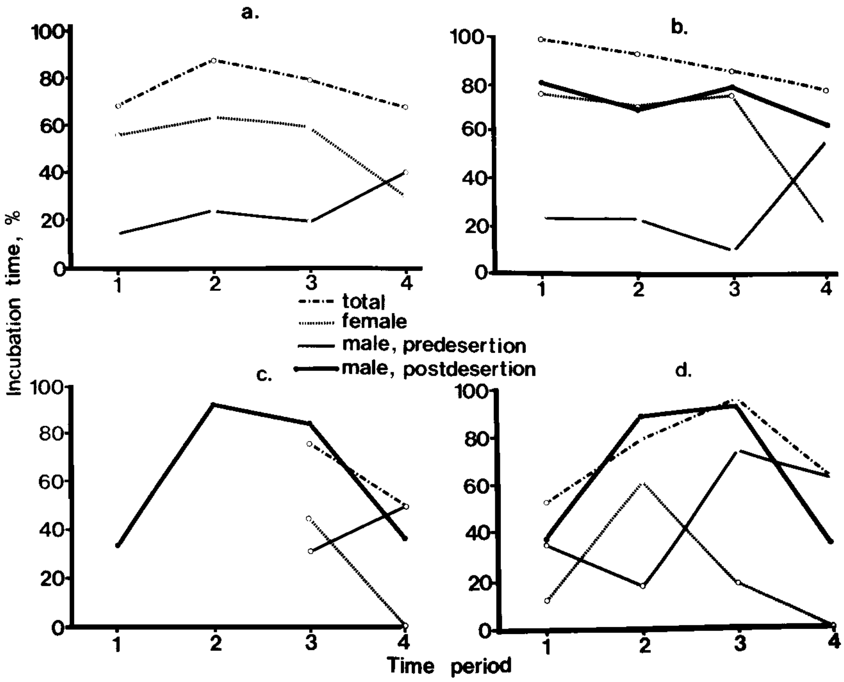

Fig. 1. Incubation time (percentage of time spent incubating) for Wilson's Plover. Time period 1 = 0700–1030, 2 = 1031–1400, 3 = 1401–1730, 4 = 1731–2100. **a**: Average times for nine nests at which both parents incubated (1979). **b**: Nest 26-79 before and after female disappearance. **c**: Nest 29-79 before female disappearance (1401–2100 only) and after disappearance. **d**: Nest 29-80 before and after female disappearance.

and was out of sight more than the total for intact pairs. He spent only 21% of the sample attending the chicks (alert, display, and brood), compared to 50–80% for the intact pairs. This reduction in time spent attending the chicks may have been the result of his incubating alone for 12 days.

One case of male incubation occurred on Matagorda Island in 1980. At Nest 29-80, the female was trapped and experimentally removed from the nest on the morning of day 17 of incubation (12 June) and returned on the morning of day 18. She did not come to the nest during the rest of day 18 and was not seen again. In time-lapse samples made throughout days 22–24 of incubation, the male incubated alone. Hatching began the next day, 20 June, and all three eggs hatched. Figure 1d shows incubation time for this nest on day 16, before removal, and for the male alone on days 22–24 of incubation. (Incubation time at the start of day 16 was somewhat reduced, as it was at most nests, by the recent placing of the camera.) Male 29-80 had higher incubation time than most males prior to the female's disappearance, and his incubation time after disappearance was almost identical to that of male 29-79 when he was alone (Fig. 1c). Before female removal, total daily incubation time was 71%, and male incubation time was 48%. The male alone incubated 58% of the time on day 22 (which had a camera-placement effect similar to that on day 16).

One other removal experiment was done in 1980. The male was removed from Nest 21-80 on the morning of day 16 (9 June) of incubation and returned on the morning of day 17. The female's incubation time was 75% during the removal period. The male began incubating at 1703 on day 17, and he was on the nest 42% of the time between then and nightfall, with no incubation by the female after 1703. This is a normal male incubation time for this period (Fig. 1a), but the female usually incubates as well. Each of the removed birds lost 10 g (15% of their body weight) during 24 h of captivity, so it is surprising that male 21-80 undertook a normal load of incubation only 9 h after his release. I made 15.5 h of focal-animal samples on pair 21-80 on days 21–23 of incubation, and average daily incubation time for the pair after removal was 81%, compared to 88% before removal. Female incubation time was 66%,

TABLE 1. Time budgets (percentage of sample spent in various activities) for two intact pairs with young chicks, and male 29-79 with young chicks.

Nest	Sex	Alert	Display	Brood	Feed	Other[a]	OOS[b]	*n*[c]
21-79	M	10	8	0	0	2	80	315
	F	34	49	0	1	0	16	
Unknown	M	21	6	0	4	6	63	613
	F	30	1	0	12	10	47	
29-79	M[d]	5	5	11	33	9	37	125

[a] Fly, preen, and rest.

[b] Out of sight, usually away from chicks.

[c] Sample size in minutes.

[d] Female out of sight throughout sample.

compared to 49% before the removal. One egg disappeared from this nest during days 21–23, one egg hatched, and one egg was left in the nest. The two eggs in the nest on day 24 floated high in water, indicating both were close to hatching.

Males of many species of shorebirds in which both sexes incubate are reported to take an increasing share of incubation as it proceeds, and this has been shown statistically for the Least Sandpiper (*Calidris minutilla*) (Miller 1977). Exclusive male incubation, however, has only been documented in a few species of monogamous shorebirds. The best-documented case of male incubation is the Killdeer (*Charadrius vociferus*). In a study of 39 Killdeer nests, Bunni (1959) reported exclusive male incubation at three nests, lasting for 2, 9, and 11 days per nest before hatching. All three were second nests at the end of the breeding season, which appears to be when male incubation occurs in Wilson's Plover. Male incubation sometimes occurs for briefer periods before hatching in the Least Sandpiper (Miller 1977) and in the Dunlin (*Calidris alpina*) (Soikkeli 1967). Only one parent incubates at most nests of the polygamous Mountain Plover (*Charadrius montanus*), and this species has a diurnal incubation pattern (Graul 1975: Fig. 4) very similar to that of males 29-79 and 29-80 (Fig. 1c, 1d).

Male incubation leads to female emancipation and the possibility of additional clutches, but it does not follow that male incubation is the result of selection for female emancipation. Other selective pressures could produce male incubation, and selection for female emancipation might begin after male incubation existed. One hypothesis is that the female deserts because she is in worse condition than the male due to the stress of egg laying, and her chance of survival would decrease if she didn't desert (Graul 1973, Ashkenazie and Safriel 1979). This hypothesis has not been tested directly on known pairs, but Ashkenazie and Safriel (1979) showed that random samples of female Semipalmated Sandpipers (*Calidris pusilla*) decreased in weight more rapidly than similar samples of males as the season progressed. They also estimated that females had 15% higher energy requirements than males during the breeding season, due mainly to egg laying.

Another hypothesis is that there is an advantage to uniparental care at the end of the breeding season. An increase in the local food supply caused by the removal of one of the parents has been proposed by Pitelka (1959) as a possible advantage of uniparental care. This theory predicts that either sex could desert, but only females appear to desert in Wilson's Plover and Killdeer. These two hypotheses are not mutually exclusive, however. There could be an advantage to the female in deserting and an advantage to the reproductive success of the pair in uniparental care. No data are available to isolate these hypotheses, and they are difficult to test separately, because both are related to the food supply.

Male incubation in Killdeer is thought to follow female desertion (Bunni 1959), but the possibility that missing females died rather than deserting cannot be ruled out, because the females were not seen after they stopped incubating. However, there were three other broods of Wilson's Plovers seen at the end of the breeding season in 1979 in addition to 26-79 and 29-79, and all three were also cared for by lone males. Because these were the only cases of mate loss seen that year, I suspect that they were the result of desertion rather than the coincidence of five female deaths. Female desertion after hatching is common in several monogamous shorebirds, including the Killdeer (Lenington 1980).

In conclusion, the absence of one parent caused the remaining parent (three males and one female) to increase its incubation time significantly (paired $t = -3.34$, df $= 3$, $P = 0.022$), but it also caused a significant decrease in total incubation time at the nest (paired $t = 3.52$, df $= 3$, $P = 0.019$), apparently without reducing hatching success. Thus, the division of labor during incubation in Wilson's Plover is highly flexible, allowing the male to do all the incubation for up to 12 days (male 29-79) and the female to do all the incubation for at least 1.3 days (female 21-80). This flexibility preadapts this species for the evolution of polygamy, especially polyandry (Emlen and Oring 1977). Sequential polyandry and simultaneous polygyny have been reported in the Snowy Plover (*Charadrius alexandrinus*) (Warriner and Warriner 1978), and sequential polyandry and possible polygyny have been reported in the Mountain Plover (Graul 1973). In addition, the results show that in the morning and evening, incubation time can be as low as 34% (Fig. 1c, 1d) without causing hatching failure. The question of why pairs normally incubate more than this minimum will be addressed in a future paper (Bergstrom in prep.).

Male incubation should be looked for in other monogamous shorebirds at the end of the breeding season, because it could have been overlooked in earlier studies. To test hypotheses about male incubation, estimates of changes in food availability through the breeding season are needed, as are successive weighings of known pairs through the breeding season and data on breeding success of lone males and pairs. Ideally, data on the fates of absent females should be collected.

I thank my advisor, A. R. Kiester, and the staffs of Laguna Atascosa National Wildlife Refuge and Aransas National Wildlife Refuge for assistance in the field. This research was supported by a University Unendowed Fellowship from the University of Chicago, a NSF Graduate Fellowship, and by grants from the Henry Hinds Fund of the University of Chicago, the Eli A. Nierman Foundation, the E. Alexander Bergstrom Research Fund, the Frank A. Chapman Memorial Fund of the American Museum of Natural History, and the Alexander Bache Fund of the National Academy of Sciences. Computer time was provided by the University of Chicago Computation Center. J. W. Fitzpatrick, D. Schemske, A. R. Kiester, J. R. Walters, W. Graul, L. Oring, and S. Still made helpful comments on earlier versions of the manuscript.

LITERATURE CITED

ALTMANN, J. 1974. Observational study of behavior: sampling methods. Behaviour 49: 227–267.

ASHKENAZIE, S., & U. SAFRIEL. 1979. Time-energy budget of the Semipalmated Sandpiper *Calidris pusilla* at Barrow, Alaska. Ecology 60: 783–799.

BUNNI, M. 1959. The Killdeer, *Charadrius v. vociferus* Linnaeus, in the breeding season: ecology, behavior, and the development of homoiothermism. Unpublished D.Sc. thesis, Ann Arbor, Michigan, Univ. Michigan.

EMLEN, S. T., & L. W. ORING. 1977. Ecology, sexual selection, and the evolution of mating systems. Science 197: 215–223.

GRAUL, W. 1973. Adaptive aspects of the Mountain Plover social system. Living Bird 12: 69–94.

———. 1975. Breeding biology of the Mountain Plover. Wilson Bull. 87: 6–31.

KAYE, K. 1977. CRESCAT: software system for the analysis of sequential or real-time data. Chicago, Univ. Chicago Computation Center.

LENINGTON, S. 1980. Bi-parental care in Killdeer: an adaptive hypothesis. Wilson Bull. 92: 8–20.

MILLER, E. 1977. Breeding biology of the Least Sandpiper, *Calidris minutilla* (Vieill.), on Sable Island, Nova Scotia. Unpublished Ph.D. dissertation, Halifax, Nova Scotia, Dalhousie Univ.

PITELKA, F. A. 1959. Numbers, breeding schedule, and territoriality in Pectoral Sandpipers of northern Alaska. Condor 61: 233–264.

SOIKKELI, M. 1967. Breeding cycle and population dynamics of the Dunlin (*Calidris alpina*). Ann. Zool. Fennica 4: 158–198.

TOMKINS, I. R. 1944. Wilson's Plover in its summer home. Auk 61: 259–269.

WARRINER, J., & R. WARRINER. 1978. Pajaro's Plovers. Point Reyes Bird Observatory 45: 4–5.

WINER, B. 1971. Statistical principles in experimental design, 2nd ed. New York, McGraw-Hill Book Co.

Received 23 October 1980, accepted 12 May 1981.