DAYLIGHT INCUBATION SEX ROLES IN WILSON'S PLOVER[1]

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How do pairs of monogamous birds divide parental effort? They should do so more or less equally, or sexual selection would favor the evolution of polygamy (Trivers 1972). Considering the diversity of sex roles in incubation in monogamous birds (Skutch 1957), incubation would seem to be a relatively small part of total parental effort. However, in those species in which the parents do not feed the young, such as most shorebirds, incubation is a relatively larger part of parental effort and thus more likely to be shared in monogamous species. I studied daylight incubation sex roles in Wilson's Plover (*Charadrius wilsonia*) to see if they were equal in this normally monogamous shorebird. In addition, limited nighttime data provide some clues to incubation sex roles over the 24-hr period in this species. I also examined patterns of variation in incubation sex roles within and among pairs, and I propose a new method for testing the equality of incubation sex roles.

I studied Wilson's Plovers at Matagorda Island, Aransas National Wildlife Refuge, Calhoun County, Texas, from April to June 1980 and in June 1981. I also studied them at Laguna Atascosa National Wildlife Refuge, Cameron County, Texas, from April to July 1979. The data reported here are all from Matagorda Island in 1980. All nests studied were on the bay side of the island, although these plovers also nested on the beach. The typical nest was near a clump of halophytic vegetation on a salt flat, usually near an area of bare soil. However, an equal number of the nests studied were on asphalt or concrete pavement, parts of a former airfield. In these nests the eggs were placed directly on the pavement, usually near a clump of grass.

Sexes were distinguished by the darker breast band and facial marks of the male, criteria which agreed with copulatory position (6 copulations seen) and egg-laying (2 observations). Behavioral data were collected in 1980 with time-lapse movie cameras photographing the nest at 1-min intervals. Data were not collected at night because the large number of flashes per night (about 600) might have caused nest desertion. In 1981, night data were collected at three nests using a time-lapse movie camera, with flash, photographing the nest every 20 min.

The time-lapse films were converted to instantaneous samples of incubation behavior using a film editor with a frame counter, and the proportion of time each sex spent on the nest was calculated over 3.5-hr time periods from 0700 to 2100. These were called "male attentiveness" and "female attentiveness," and they were summed to get "total attentiveness" for each time period. Because total attentiveness was strongly affected by air temperature (Bergstrom 1982), I removed this source of variation by dividing male attentiveness by total attentiveness to get "male share of attentiveness" for each time period. This also yielded a single variable representing sex roles to use in statistical analysis; "female share" equals (1 − male share). "Incubation shift length" was the time between successive nest reliefs. Pair numbers refer to the order in which nests were

found in 1980; each pair was observed for 2 to 6 days, although not all were in the same stage of incubation. Each pair was only studied for part of the incubation period in order to include a larger number of pairs in the sample. "Egg laying" was the time between the laying of the first and third (last) eggs, usually 5 days, and "hatching" was the time between the hatching of the first and third eggs (1 to 2 days). "Incubation" was the intervening 23 to 24 days. Nests were chosen for observation to include a variety of substrate types, locations, and stages of incubation. Air temperature was measured with a thermistor in the shade 5 cm off the ground near the nest, and nest temperature with a thermistor under the eggs; both were recorded with a telethermometer and strip-chart recorder.

Before I tested for the equality of sex roles, I used non-parametric statistical tests (Siegel 1956) to ensure that the samples were homogeneous, using two-tailed probabilities throughout. For two-sample comparisons, I used the Mann-Whitney U-test for independent groups and the Wilcoxon matched pairs test for related groups. For multiple comparisons the tests used were Kruskal-Wallis ANOVA and Friedman ANOVA for independent and related groups respectively. Incubation stages were assumed to be independent because only three pairs were studied during more than one stage. Survivorship analysis (Hull and Nie 1979) was used on the durations of incubation shifts using the Lee-Desu statistic to determine whether the shift durations compared came from the same distribution.

Testing for the equality of sex roles in attentiveness is complicated by the fact that male and female shares of attentiveness are binomial probabilities, and thus are negatively correlated. Because of this, the paired-sample t-test (used for this purpose by Pierotti 1981) is inappropriate because it assumes positive correlation of the samples (Snedecor and Cochran 1967). A one-sample t-test to see if male (or female) share differs from 50%, used by myself (Bergstrom 1981) and others (Coulson and Wooller 1984), is inappropriate for the same reason because the paired-sample t-test is merely a one-sample t-test on differences (Snedecor and Cochran 1967), and both tests give the same results in this case. There are tests of a binomial probability (Snedecor and Cochran 1967:211) but these would require successive independent samples of which bird is on the the nest, and the temporal patterns in my data (see below) make independence within days difficult to assess. I devised a simple alternative: taking the data from one pair for one day as an independent sample, I counted the number of days in which the male was on the nest more than the female. I then used a goodness-of-fit test (log likelihood ratio or G-test) to see if this differed from the expectation under the null hypothesis that this should be half of the total number of days.

Examining the data for heterogeneity showed a significant temporal pattern. Over all 16 pairs, mean male share of attentiveness was 24% between 0700 and 1030, 13% between 1031 and 1400, 18% between 1401 and 1730, and 41% between 1731 and 2100 (Friedman $\chi^2 = 15.0$, $P < 0.01$). Male share was significantly lower averaged over the first three time periods (18%) than in the last period (Wilcoxon $T = 13$, $n = 13$, $P = 0.02$). For this reason, further analysis of male share was done on data for whole days (all four periods) only (Table 1). Male share

of attentiveness was not affected by air temperature over four ranges (Kruskal-Wallis $H = 6.0$, $P = 0.11$), even though most other aspects of incubation behavior were strongly affected by this variable (Bergstrom 1982).

Male share of attentiveness (Table 1) differed significantly between stages (Kruskal-Wallis $H = 18.2$, $P = 0.0001$). Male share during egg laying (63%) was significantly higher than during incubation (30%) (Mann-Whitney $z = 3.7$, $P = 0.0002$). Total attentiveness was low during egg laying (Table 1), and it consisted mainly of the male shading the eggs during the heat of the day, especially when there was only one egg. Records of nest temperature at one nest showed that there was little warming of the egg at night during this period. Male share was 41% during hatching, also significantly higher than during incubation ($z = 2.3$, $P = 0.02$). Incubation shift length was significantly shorter at hatching (median survivorship: egg laying = 182.8 min, incubation = 83.8 min, hatching = 33.5 min, Lee-Desu $D = 34.3$, $P < 0.0001$). Only data from the incubation stage were used in further analysis, including 14 pairs observed for a total of 48 days or 672 hr.

For the 48 days of data from the incubation stage, males had higher daylight attentiveness than females on only 7 days, much less than the expected 24 days ($G = 26.7$, $P < 0.001$). In addition to doing a larger share of daylight attentiveness, the female had longer incubation shifts than the male in every pair during the incubation stage (median survivorship: females 141.7 min, males 42.9 min, Lee-Desu $D = 17.1$, $P < 0.0001$). This difference in shift lengths could not be due to the fact that females were usually on the nest during the hottest part of the day, since shift lengths for both sexes were slightly but significantly shorter above 33°C (Lee-Desu $D = 9.3$, $P = 0.01$).

The data I collected all indicated that males were on the nest at night. In the time-lapse movies in 1980, the male was usually on the nest at dusk (38/55 days), but the female was usually on the nest at dawn (33/39 days). At three nests studied for one night each in 1981, only the male was on the nest at night, and the female came to the nest shortly before dawn. Two of these pairs (Pairs 5 and 6) had also been studied in 1980 and both had low male share (Table 1). In five nest checks made in 1980 between 2100 and 2200, the male was on the nest in four; in the fifth my attempts to trap on the nest may have disturbed the normal pattern. Total attentiveness was higher at night than during the day, averaging 92% based on records of nest temperature. Thus if only the male was on the nest at night, male and female shares of attentiveness over 24 hr would be nearly equal in most pairs, or with more time on the nest by the male in some (e.g., Pair 2).

Although the female was on the nest more than the male during the day, sex roles varied significantly among pairs in the incubation stage (Kruskal-Wallis $H = 63.9$, df = 12, $P < 0.0001$). However, sex roles were consistent within pairs on different days of three-day samples during incubation (Friedman $\chi^2 = 2.0$, $P = 0.5$). Pair 2 had the highest male share (Table 1), while a renest by the same pair (Pair 26) also had a high male share. Male share was also high in Pairs 21 and 28, the only pairs in which belly-soaking was seen (Bergstrom 1982). Because these pavement nests were far from water (more than 0.5 km), nest relief was necessary for the soaking bird (the female in Pair 21, both sexes in Pair 28) to go and wet its feathers, and this probably resulted in higher male share. Male share ranged from 7% to 30% in other pairs during incubation. Reasons for these differences among pairs are not known; sex roles did not differ between nests on different substrates (soil or pavement; Mann-Whitney $U = 19.5$, $P = 0.58$).

Sex roles during daylight incubation in Wilson's Plover are most similar to those in the Snowy Plover (*C. alexandrinus*). Rittinghaus (1961) found that the female was on the nest more than the male at 10 of 12 nests studied for one day each, with a mean male share of 34%. Male

TABLE 1. Sex roles in daylight attentiveness in Wilson's Plover.

Pair #	Male share (%)[2]	Stage[3]	Total attentiveness (%)	n (days)
1	79	E	53	2
2	51	I	70	5
3	28	I	79	2
5	15	I	83	5
6	7	I	85	3
10	10	I	82	3
11	17	I	80	3
16	16	I	86	4
17	16	I	70	1
17	78	H	87	1
18	56	E	74	2
18	21	I	84	1
18	44	H	77	3
19	59	E	74	1
19	30	I	83	5
21	46	I	84	4
22	13	I	74	3
25	23	H	80	3
26[1]	45	I	77	6
28	38	I	79	3

[1] Renest by Pair 2.
[2] Percent of total attentiveness that was done by the male.
[3] E = egg laying (ca. 5 days), I = incubation (23–24 days), H = hatching (1–2 days).

attentiveness was highest late in the day. In Japan, male share of attentiveness was 86% during egg laying and hatching, while male share dropped to 15–16% during incubation, when the male was probably on the nest at night (Nakazawa 1979). In the Killdeer (*C. vociferus*, Mundahl 1982) and the Piping Plover (*C. melodus*, Cairns 1982) daylight attentiveness was shared roughly equally during incubation. However, male share of attentiveness during egg laying was about 80% in Killdeer (when total attentiveness was low), and five Killdeers trapped on the nest at night during incubation were all males (Mundahl 1982). Data on nighttime incubation are needed for all plovers.

Male plovers may do more of the erratic attentiveness during egg laying because females need to do extra foraging at this time. The increase in male share of attentiveness at hatching could be caused by two behaviors seen in Wilson's Plover: (1) eggshells are removed immediately after hatching, usually at nest relief, and (2) sometimes one parent broods the chick(s) near the nest while the other incubates the remaining egg(s) (Bergstrom 1982). The reduction in incubation shift length at hatching may also be associated with one or both of these behaviors. Eggshell removal is very common in ground-nesting birds, but the separate brooding has not been reported for other plovers.

Explanations of daily incubation sex role patterns focus either on proximate factors (Wallman et al. 1979) or on ultimate factors, primarily parental effort (Miller 1977, Mundahl 1982). Examining the proximate factors first, I found that Wilson's Plover males will incubate alone (although with reduced total attentiveness compared to pairs); and in one female, attentiveness was a normal amount for a pair (75%) for one day in the absence of the male (Bergstrom 1981). Thus the 24-hr pattern is not caused by fixed sex-typical circadian cycles in incubation, nor could it be caused by fixed cycles in other behaviors. The variability in sex roles among pairs and consistency within pairs (also found in Ringed Turtle-Doves, *Streptopelia risoria*) may indicate that cooperative interactions between members of a pair determine the division of labor (Wallman et al. 1979). Nest relief in Wilson's Plover was unusual in that normally one bird left several minutes before the other

bird arrived, and no calls were given (Bergstrom 1982). Thus the communication required for this cooperation must occur away from the nest, perhaps at the feeding ground.

Three ultimate explanations focus on the fact that a 24-hr pattern, with the sexes incubating at different times of day, could make the parental effort per unit time on the nest unequal in the two sexes. Females can recover energy spent on eggs most efficiently if males are on the nest when food is most available, allowing females to feed at those times (Miller 1977). The energetic costs of incubation probably differ between night and day, and this would affect the parental effort per unit time on the nest (Miller 1977), but these costs are known only for arctic shorebirds. The risk of predation while incubating may differ between night and day (Mundahl 1982), but very few data are available on this point. None of these three hypotheses are exclusive, but measurements of daily patterns of (1) food availability, (2) costs of incubation, and (3) predation rates could be used to test their predictions.

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VIREO: PROCEDURES AND SERVICES FOR THE ORNITHOLOGICAL COMMUNITY[1]

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In 1979 the Academy of Natural Sciences founded Visual Resources for Ornithology, VIREO, as a photographic analog of the traditional skin collection. The specific aim of the program is to make bird photographs available to ornithologists for research and teaching. Toward this end, during the six years since its founding VIREO has built a collection of over 90,000 photographs. At the same time, we have developed and implemented curatorial procedures to ensure the long-term safety of the collection. This article briefly describes basic principles governing the program and summarizes VIREO services now available to the ornithological community.

Why archive ornithological photographs? Photography plays a central role in the study of birds. Photographs document facts, reveal detail, convey information, and portray habitats and methods as well as the birds themselves. Yet of the countless bird photographs that have been taken during the last hundred years, relatively few are available for scientific study or teaching. Most lie buried in small boxes on dusty shelves in forgotten closets, functionally inaccessible even to the photographer after a few years.

Bringing disparate collections together into a central archive enables access to these photographs. Centralization has the additional beneficial effect of bringing the photographs into proper storage conditions. While some films