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Nocturnal Nest Attendance of Killdeers: More Than Meets the Eye

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Parental effort in shorebirds has been the subject of a number of studies (Norton 1972, Maxson and Oring 1980, Bergstrom 1981, 1986, Cairns 1982, Byrkjedal 1985, Carter and Montgomerie 1987, Brunton 1988a, b). However, except for shorebirds that breed in areas with 24-h daylight (i.e. arctic regions), nocturnal parental behavior has been sadly neglected (but see Thibault and McNeil 1995a). In temperate regions, researchers have assumed that, if a bird is on the nest at dusk and at dawn, it stays there through the night (Maxson and Oring 1980, Brunton 1988a, b). This may be due to an historical assumption that shorebirds feed only during daylight. However, recent studies have demonstrated that shorebirds are active during nighttime hours (see review by McNeil 1991), suggesting that nocturnal parental behavior might be more variable than previously presumed.

In this paper we report on the nest attendance of radiomarked Killdeers (*Charadrius vociferus*) breeding in the Great Basin of western North America. The breeding behavior of Killdeers has been the focus of numerous studies (Pickwell 1930, Nickell 1943, Bunni 1959, Mace 1971, Lenington 1980, Mundahl 1982, Brunton 1988a, b). Nevertheless, almost nothing has been published concerning their nocturnal nest-attendance patterns. Of nine nests visited at night, only males were observed incubating (Mundahl 1982, Brunton 1988a). We examined the question of whether or not nocturnal incubation was performed exclusively by males.

Methods.—Work was conducted from June to August 1994 at the Jay Dow, Sr. Wetlands (JDW), a wetlands research facility operated by the University of Nevada, Reno. JDW is located at the southern end of Honey Lake in northeastern California and encompasses approximately 540 ha. Habitat includes 14 freshwater ponds surrounded by Great Basin desert dominated by sagebrush (*Artemisia* sp.) and greasewood (*Sarcobatus* sp.). As many as 100 pairs of Killdeers breed annually at these wetlands. Most birds are individually color banded.

All Killdeers were trapped on nests with automatic nest traps. Birds were individually marked with UV-resistant color bands and a metal U. S. Fish and Wildlife Service band. Killdeers were sexed based on plumage characteristics (males typically have darker markings in the face and forehead, more red in feathers on the back, and a redder eye ring relative to females) and breeding behavior (position of copulating bird and degree of alarming behavior which is greater in males; Mundahl 1982, L. Oring unpubl. data).

We glued 2.65-g radio transmitters (Model PD-2, Holohil Systems, Woodlawn, Ontario) to the lower backs of adult Killdeers (17 males, 15 females) using techniques described by Warnock and Warnock (1993). Radio transmitters weighed approximately 0.03% of a Killdeer's total mass. Positions of birds were determined by a combination of triangulation and visual resighting using a truck equipped with null system antennas. All Killdeer habitat was accessible by road. We often got initial bearings on birds and then used radio strength to determine locations. Nest attendance was determined by direct observation, or a Killdeer was assumed to be attending a nest if the radio signal came from the direction of the nest and the radio signal did not vary for a minimum of 10 s.

We monitored all nocturnal nesting radiomarked Killdeers from 2100 to 0000 PST in order to determine whether the bird was incubating. In order to evaluate nocturnal nest attendance in more detail, we conducted 10 all-night observations (2000–0600) of four incubating Killdeer pairs carrying radio transmitters. For these observations, we parked our radio truck within 200 m of a nest at an angle where we could unambiguously determine if a bird was on the nest based upon radio-signal strength, modulation and direction. If the radio signal was erratic, or coming from an angle away from the nest, we assumed the bird was not incubating. For all-night observations, the incubation period was divided into an early (1 to 12 days after clutch completion) and a late (13 days to hatching; mean incubation period = 24 days; Brunton 1988a) period.

Results.—Twenty-nine breeding Killdeers were tracked from 3 to 63 days (median = 26 days $\pm$ SD of 17.5). We collected 96 nocturnal locations on 22 different nesting birds. For the period between 2100 and 0000, 50% of the locations of males (no. observations per bird, $\bar{x} = 4.3 \pm 1.9$, $n = 12$ birds) were from the nest, while 27% of female locations (no. observations per bird, $\bar{x} = 4.4 \pm 3.1$, $n = 10$ birds) were from the nest.

Data from separate all-night nest watches revealed that 78% of the observations (no. observations per bird, $\bar{x} = 9.7 \pm 7.0$, $n = 58$) of six male Killdeers between 2100 and 0300 were from the nest. While males generally incubated during the night, members

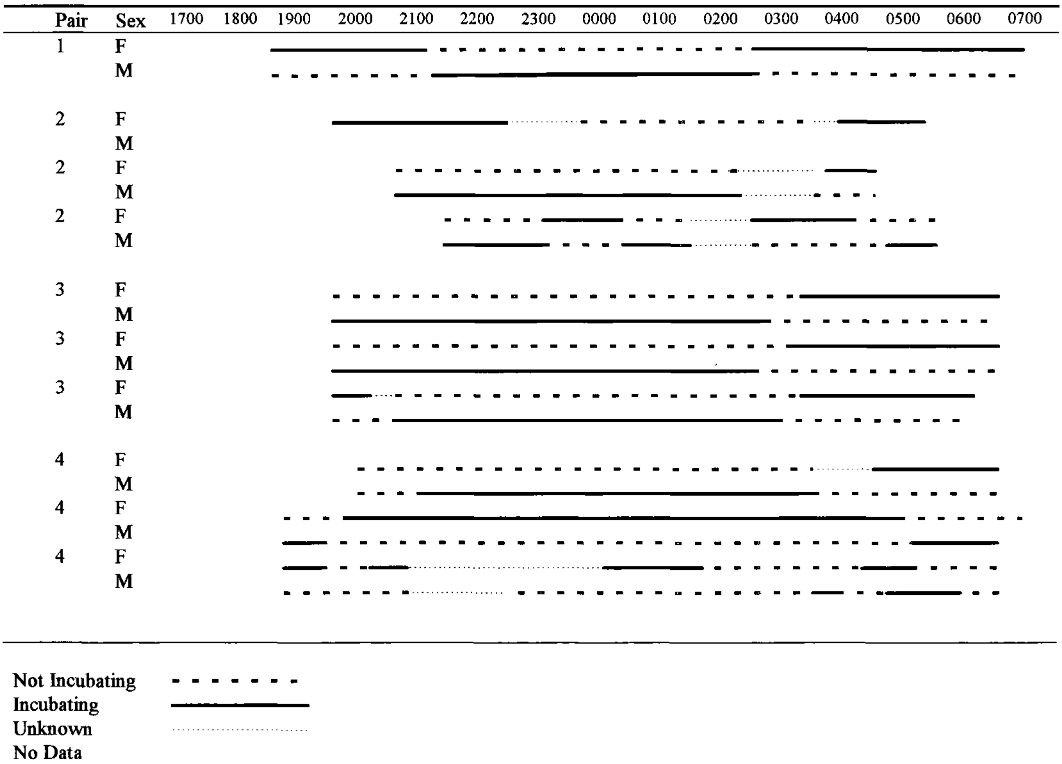

Fig. 1. Time frame of nocturnal nest attendance of four radiomarked pairs (M, male; F, female) of Killdeers at Jay Dow, Sr. Wetlands during June–July 1994. Dates of observations: (pair 1) 11 July; (2) 16, 20, 23 July; (3) 30 June, 2, 5 July; and (4) 5, 8, 11 July.

of one pair reversed this pattern on two different nights (pair 4; Fig. 1). Mate switches at the nest in the evening generally took place at or just prior to darkness (2000–2100), and morning switches occurred just prior to or at the first light of day (0300–0400; Fig. 1). Weather during these nocturnal observations was basically clear (occasional clouds) and calm, and the temperature rarely fell below 13°C.

Discussion.—Allocation of parental effort in Killdeers is variable, especially with respect to incubation duties. Brunton (1988a) observed higher diurnal nest attendance by Killdeers in the last 12 days of incubation, and males spent significantly more of this time incubating. Nocturnal incubation duties in Killdeers also may be affected by stage of incubation, but we did not have sufficient data to explore this issue. In Wilson's Plovers (*C. wilsonia*), males spend more time incubating in the night in the last 12 days of incubation than in the first 12 days (Thibault and McNeil 1995a). In our study, only two of the 10 all-night observations on Killdeers were done on pairs in early incubation. In one case, the male did the majority of nocturnal incubation and, in the other, the female did.

Previously, investigators studying Killdeers have observed only males on nests at night. This was not the case at JDW. Males contributed most of the nocturnal incubation effort; however, one male was observed to incubate through one night, while his mate incubated the majority of two other nights (pair 4, Fig. 1). Among plovers, males tend to adopt the primary parental role. In at least *Charadrius*, this appears to include accepting the bulk of nocturnal incubation. For example, male Wilson's Plovers in Texas and Venezuela appear to be the primary nocturnal incubators (Bergstrom 1986, Thibault and McNeil 1995a, b). Also in Snowy Plovers (*C. alexandrinus*), 90% of the birds incubating at dusk are males, and males are believed to provide the majority of nighttime incubation (Warriner et al. 1986). In both of the above species, females do the majority of daytime incubation. On the other hand, in the more northerly Greater Golden-Plovers (*Pluvialis apricaria*), males incubate during the day and females during the night (Byrkjedal 1985).

With Killdeers at JDW, mate switching sometimes occurred at regular intervals through the night (pair 2; Fig. 1). Reasons for this variability remain unknown. However, in White-rumped Sandpipers (*Calidris fuscicollis*) and Wilson's Plovers, weather has been shown to greatly influence incubation behavior (Carter and Montgomerie 1987, Thibault and McNeil 1995a). Weather has a large influence on diurnal incubation patterns of Killdeers. During daylight hours, especially on hot days, two parents are more effective in keeping egg temperatures at viable levels. Grant (1982) noted that male and female Killdeers at the Salton Sea, California switched nest attendance every 10 to 15 min to belly-soak when temperatures grew hot (see also Schardien and Jackson 1979). Temperature of incubated eggs increases with increasing ambient temperature, and eggs exposed to temperatures over 40°C risk embryonic damage (Grant 1982). Ambient daytime temperatures at our study site frequently rose over 38°C, and belly-soaking Killdeers were commonly observed in 1994. Female Killdeers at our study site were more likely to incubate during daylight hours; however, 36% of our nesting locations (n = 83) of male Killdeers from 0600 to 1600 came from the nest (unpubl. data).

Killdeers typically are classified as obligate, biparental breeders. However, the flexibility of incubation strategies presented here suggests the value of comparative studies of the allocation of parental effort. Given the wide range of environments and latitudes (subarctic to the tropics) in which Killdeers breed, comparative breeding studies on this species would undoubtedly add to knowledge of the evolution of shorebird mating systems. Nocturnal incubation by Killdeers, conducted mainly by males, is more variable than previously thought. Therefore, comparative studies must include analyses of nocturnal behavior.

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Literature Cited

BERGSTROM, P. W. 1981. Male incubation in Wilson's Plover (*Charadrius wilsonia*). Auk 98:835–838.

BERGSTROM, P. W. 1986. Daylight incubation sex roles in Wilson's Plover. Condor 88:113–115.

BRUNTON, D. H. 1988a. Energy expenditure in reproductive effort of male and female Killdeer (*Charadrius vociferus*). Auk 105:553–564.

BRUNTON, D. H. 1988b. Sexual differences in reproductive effort: Time-activity budgets of monogamous Killdeer, *Charadrius vociferus*. Anim. Behav. 36:705–717.

BUNNI, M. 1959. The Killdeer, *Charadrius v. vociferus* Linnaeus, in the breeding season: Ecology, behavior, and the development of homiothermism. Ph.D. dissertation, Univ. Michigan, Ann Arbor.

BYRKJEDAL, I. 1985. Time-activity budget for breeding Greater Golden Plovers in Norwegian mountains. Wilson Bull. 97:486–501.

CAIRNS, W. E. 1982. Biology and behavior of breeding Piping Plovers. Wilson Bull. 94:531–545.

CARTER, R. V., AND R. D. MONTGOMERIE. 1985. The influence of weather on incubation scheduling of the White-rumped Sandpiper (*Calidris fuscicollis*): A uniparental incubator in a cold environment. Behaviour 95:261–289.

CARTER, R. V., AND R. D. MONTGOMERIE. 1987. Day-to-day variation in nest attentiveness of White-rumped Sandpipers. Condor 89:252–260.

GRANT, G. S. 1982. Avian incubation: Egg temperature, nest humidity, and behavioral thermoregulation in a hot environment. Ornithol. Monogr. 30.

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

MACE, T. R. 1971. Nest dispersion and productivity of Killdeers, *Charadrius vociferus*. M.Sc. thesis, Univ. Minnesota, St. Paul.

MAXSON, S. J., AND L. W. ORING. 1980. Breeding season time and energy budgets of the polyandrous Spotted Sandpiper. Behaviour 74:200–263.

MCNEIL, R. 1991. Nocturnality in shorebirds. Pages 1098–1104 *in* Acta XX Congressus Internationalis Orithologici (B. D. Bell, Ed.). Christchurch, New Zealand, 1990. New Zealand Ornithol. Congr. Trust Board, Wellington.

MUNDAHL, J. T. 1982. Role specialization in the parental and territorial behavior of the Killdeer. Wilson Bull. 94:515–530.

NICKELL, W. P. 1943. Observations on the nesting of the Killdeer. Wilson Bull. 55:23–28.

NORTON, D. W. 1972. Incubation schedules of four species of calidrine sandpipers at Barrow, Alaska. Condor 74:164–176.

PICKWELL, G. 1930. The sex of the incubating Killdeer. Auk 47:499–506.

SCHARDIEN, B. J., AND J. A. JACKSON. 1979. Belly-soaking as a thermoregulatory mechanism in nesting Killdeers. Auk 96:604–606.

THIBAULT, M., AND R. MCNEIL. 1995a. Day- and night-time parental investment by incubating Wilson's Plovers in a tropical environment. Can. J. Zool. 73:879–886.

THIBAULT, M., AND R. MCNEIL. 1995b. Predator-prey relationship between Wilson's Plovers and fiddler crabs in northeastern Venezuela. Wilson Bull. 107:73–80.

WARNOCK, N., AND S. WARNOCK. 1993. Attachment of radio-transmitters to sandpipers: Review and methods. Wader Study Group Bull. 70:28–30.

WARRINER, J. S., J. C. WARRINER, G. W. PAGE, AND L. E. STENZEL. 1986. Mating system and reproductive success of a small population of polygamous Snowy Plovers. Wilson Bull. 98:15–37.

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