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BREEDING BIOLOGY OF THE COMMON POORWILL AT THE NORTHERN EDGE OF ITS DISTRIBUTION

RYAN D. CSADA[1] AND R. MARK BRIGHAM
Department of Biology
University of Regina
Regina, Saskatchewan S4S 0A2, Canada

Abstract.—The breeding biology of Common Poorwills (*Phalaenoptilus nuttallii*) was studied from 1989 to 1992 in the Okanagan Valley of British Columbia and 1991 to 1992 in the Cypress Hills of Saskatchewan, Canada. Individuals were captured by luring them into mist nets using song playbacks. Data were collected from a total of 27 nests (from 17 pairs), found by following birds outfitted with radio transmitters. Poorwills arrived from mid-April to late May. Four of five pairs in British Columbia and two of three pairs in Saskatchewan made two nesting attempts each. Poorwills appeared to be monogamous and the pair bond, with one exception, was maintained throughout the breeding season. First clutches were laid from late May to late June and second clutches from early July to early August. Nest initiation was approximately 2 wk earlier in British Columbia than in Saskatchewan. Twenty-six of 27 clutches consisted of two eggs. Both male and female birds shared incubating and brooding responsibilities, although males were found incubating significantly more often, whereas females brooded significantly more. The incubation period was 20–21 d. Hatching success was 63% in British Columbia and 71% in Saskatchewan. The nestling period was 20–22 d. Fledging success was 8% and 30% for British Columbia and Saskatchewan, respectively. Predation appeared to be the most important factor limiting reproductive success.

BIOLOGÍA REPRODUCTIVA DE *PHALAENOPTILUS NUTTALLII* EN EL EXTREMO NORTE DE SU DISTRIBUCIÓN

Sinopsis.—Se estudió la biología reproductiva de *Phalaenoptilus nuttallii* entre 1989 y 1992 en el valle de Okanagan de la Columbia Británica y entre 1991 y 1992 en las lomas Cypress de Saskatchewan, Canadá. Se capturaron los individuos atrayéndolos a las redes con grabaciones de sus cantos. Se coleccionaron datos de 27 nidos (17 parejas), hallados siguiendo aves ceñidas con radiotransmisores. Las aves llegaron desde el medio de abril hasta finales de mayo. Cuatro de cinco parejas en la Columbia Británica y dos de tres parejas en Saskatchewan hicieron dos intentos de anidar cada una. La especie parece ser monógama y la unión de la pareja (cona una excepción) se mantuvo a través de la temporada. Las primeras camadas se colocaron entre finales de mayo y finales de junio y las segundas camadas entre principios de julio y principios de agosto. La construcción de nidos comenzó aproximadamente dos semanas antes en la Columbia Británica que en Saskatchewan. Veintiséis de las 27 camadas consistieron en dos huevos. Tanto el macho como la hembra compartieron las responsabilidades de incubación y crianza, aunque se halló que los machos incubaban más a menudo y las hembras invirtieron más tiempo en la crianza. El período de incubación duró entre 20 y 21 días. El éxito de eclosión fue de 63% en la Columbia Británica y de 71% en Saskatchewan. El período de anidaje duró entre 20 y 22 días. El éxito en producir volantones fue de 8% y 30% en la Columbia Británica y en Saskatchewan respectivamente. Al parecer la depredación fue el factor más importante limitando el éxito reproductivo.

Most of the 77 species in the family Caprimulgidae are nocturnal insectivores. Little is known about their biology in general and their

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[1] *Current address: Biology Department, York University, 4700 Keele Street, North York, Ontario M3J 1P3, Canada.*

breeding biology in particular (Martin 1990). Available data suggest significant variation among species in reproductive strategies. For example, depending on the species, one (e.g., Common Nighthawk [*Chordeiles minor*]; Bent 1940) or two (e.g., European Nightjar [*Caprimulgus europeaus*]; Lack 1930) clutches are laid each year, despite the fact that clutches nearly always consist of two eggs.

The Common Poorwill (*Phalaenoptilus nuttallii*) is a caprimulgid found on high, rolling plains, semi-arid flats and rocky foothills, throughout western North America (Csada and Brigham 1992). The scant data on poorwill breeding biology (e.g., Aldrich 1935, Bent 1940, Orr 1948, Swisher 1978) are largely anecdotal, based on one pair at most, and do not encompass an entire breeding season. There are no detailed reports on male-female interactions (e.g., mating system, brooding or incubating responsibilities) or measurements of reproductive success.

Recently (Csada and Brigham 1992), we provided a largely qualitative review of reproduction in poorwills. In this paper we quantify various aspects of poorwill reproductive biology. Our research, which has focused on the use of torpor by free-ranging birds (Brigham 1992; Csada and Brigham, in press; Kissner and Brigham 1993), has taken place at the northern edge of the species' distribution in south-central British Columbia and southwestern Saskatchewan, Canada. Therefore, the results that we report may not reflect the behavior of poorwills in more southerly locations in the United States and Mexico.

METHODS

We studied poorwills during the spring and summer from 1989 to 1992 in the south Okanagan Valley, British Columbia (49°18′N, 119°31′W), and from 1991 to 1992 in the Cypress Hills, Saskatchewan (49°34′N, 109°53′W). On the hills (500–1000 m asl) of the Okanagan Valley, the vegetation pattern consists of open grassy areas intermixed with stands of ponderosa pine (*Pinus ponderosa*; Cannings et al. 1987). In the Cypress Hills, hills (1000–1250 m asl) have alternating patches of short grasses and stands of white spruce (*Picea glauca*) and trembling aspen (*Populus tremuloides*; Kalcounis et al. 1992). Poorwill activity at both sites was centered in open areas and at forest edges on the slopes of the hills.

Surveying for poorwills started on 15 April in British Columbia and 1 May in Saskatchewan and consisted of listening for responses to song playbacks. This was done nightly for approximately 1 h. When a poorwill was heard, we usually attempted to capture it the following evening.

Poorwills were lured into mist nets using song playbacks. Radio transmitters were attached to the backs of birds with an elastic harness slipped over the wings (Brigham 1992). Usually, the second adult of a nesting pair was captured with a hand net at the nest site, located by following the bird with the transmitter. Adult males are distinguished from females by having white tips on the rectrices, approximately twice the length of the buff colored rectrix tips of females (Chapman 1925).

Even with a knowledge of the area where birds roosted, the cryptic plumage of poorwills forced us to rely on telemetry to locate birds precisely. We traced radio-tagged birds every third or fourth day to find roost sites and to check for the presence of nests. Once breeding activity (eggs) was discovered, nests were checked every second or third day. Replacement eggs are defined as those laid in response to the loss of the original ones and a second clutch is defined as one which has followed the successful hatching of a previous one. We assumed that the incubation period was 20–21 d (Bent 1940; this study) and calculated nest initiation dates as 20 d prior to the hatching day of the first egg for those instances in which only hatching dates were known.

Eggs and nestlings were weighed to the nearest 0.1 g using an Ohaus triple beam balance or Pesola spring scale. When nestlings were approximately 1 wk old, they were banded with U.S. Fish and Wildlife aluminum leg bands.

RESULTS

Migration and pair formation.—On the basis of when we first heard calling, poorwills returned from their wintering grounds between mid April and late May (British Columbia: 27 Apr. 1989, 21 Apr. 1990, 7 May 1991, 17 Apr. 1992; Saskatchewan: 27 May 1991, 9 May 1992). Between years in British Columbia, spring arrival varied by up to a month, likely due to weather. It is not known if males and females returned simultaneously.

Birds carrying transmitters left the sites in British Columbia (15 Sep. 1988) and Saskatchewan (22 Sep. 1991) in September. It is not known if departure was as a family unit.

Males appeared to establish territories at the start of the breeding season. Calling males were separated by approximately 500 m. In Saskatchewan, two pairs of nests were separated by 300 m and 400 m, respectively. Territories appeared to be actively defended as the resident male would approach a speaker broadcasting playbacks of other males.

Two birds (one male, one female) banded in British Columbia in 1991 were recaptured in 1992. The female made nesting attempts in both years at sites separated by approximately 1 km, but the male bred only in 1991. In Saskatchewan, a male banded in 1991 was recaptured in 1992. It bred in both years with the nest sites less than 25 m apart. It is not known if the female in British Columbia or the male in Saskatchewan had the same mate in both years.

Nests and eggs.—Typically, there was no semblance of nest building, although a shallow scrape was occasionally made in the bare earth. Eggs were usually laid on bare ground; occasionally on a hard gravel surface, a flat rock or a bed of pine needles. Eggs were often at least partially shaded by bushes (e.g., sagebrush [*Artemisia* spp.]), a log or a rock.

Of the pairs followed for the entire breeding season, four of five in British Columbia and two of three in Saskatchewan made two nesting attempts. As neither member of the nesting pair associated with another

TABLE 1. Mean and extreme laying dates of first and second clutches in British Columbia and Saskatchewan.

	British Columbia	Saskatchewan
First clutch	(n = 6)	(n = 4)
Mean laying date	9 June	20 June
Earliest laying date	31 May	7 June
Latest laying date	18 June	2 July
Second clutch	(n = 4)	(n = 2)
Mean laying date	13 July	29 July
Earliest laying date	6 July	25 July
Latest laying date	23 July	1 August

individual, poorwills appeared to be monogamous and the pair bond (n = 6), with one exception, was maintained throughout the breeding season.

Eggs were laid on consecutive days for the four clutches observed. First-clutch eggs were laid between late May and early June in British Columbia and mid to late June in Saskatchewan (Table 1). On three occasions, first-clutch eggs disappeared and replacement eggs were laid within 1 wk. Second clutches were laid in early to mid July in British Columbia and between late July and early August in Saskatchewan (Table 1). A new site, usually within 100 m of the first, was used for the second clutch. On two occasions, the female laid and began incubating a second clutch while the male continued to feed the young of the first.

Eggs were generally white, sometimes with a pinkish tinge (especially right after being laid) and darker spots at the larger end. Both the pinkish tinge and spots faded as incubation progressed. Two eggs were laid in 26 of the 27 nesting attempts by the 17 pairs observed. One nest had only one egg; a second egg was likely taken by a predator.

Incubation began with the laying of the first egg and, for four clutches that were followed from initiation to hatching, lasted 20 d for three clutches and 21 d for one clutch. Both males and females have brood patches and shared incubating responsibilities. On seven occasions a nest was checked once during the day and once at night to determine which member of the pair was incubating or brooding. In all instances, the bird that was incubating or brooding during the day was relieved of this responsibility for the night by its mate. In the daytime period, on the basis of the number of times that incubating or brooding birds were flushed, males did significantly more incubating (43 times for males vs. 17 for females) whereas females did significantly more brooding (seven times for males vs. 28 for females; 2 × 2 contingency table: $\chi^2 = 21.6$, $P < 0.01$). Exchanges of incubation or brooding, when eggs or chicks were left unprotected for short periods of time, appeared to start at dusk and last until dawn. These exchanges did not occur during the daytime.

Hatching and nestlings.—Eggs hatched on consecutive days, usually early in the morning. In all cases, pieces of eggshell were removed or consumed by adults within hours of the chicks' hatching.

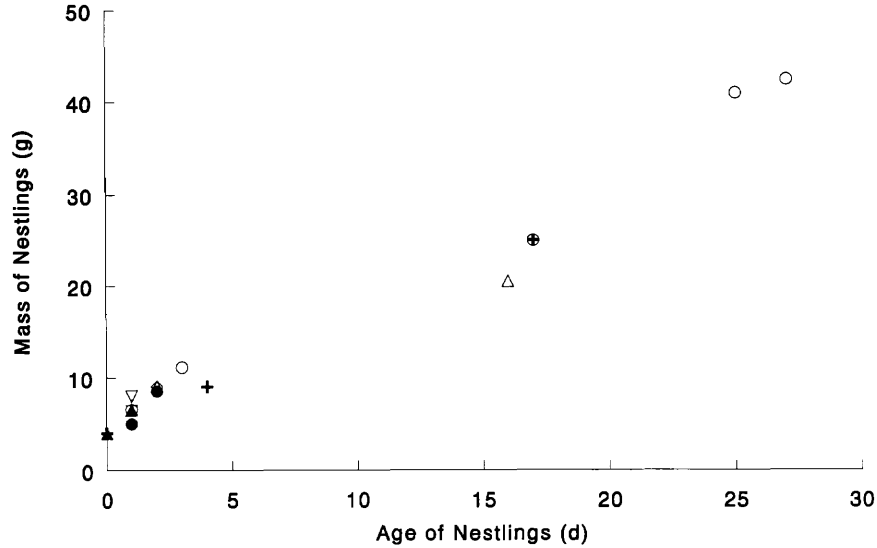

FIGURE 1. Growth rate of poorwill chicks in British Columbia. Each chick (n = 8) is represented by a different symbol.

The hatching success (number of eggs hatched per number of eggs laid) for 19 complete clutches in British Columbia was 63% (24/38) and for seven complete clutches in Saskatchewan was 71% (10/14). The one incomplete clutch (one egg) was abandoned. Nineteen eggs from 10 nests did not hatch, either abandoned (9) or for unknown (presumably predation) reasons (10). Eight of the abandoned eggs were from first clutches.

At hatching, chicks had open eyes and were thinly covered with a pale buff colored down. Their wings were about one-third grown, feet were almost adult size, and the rectrices were just emerging. Young could vocalize at this time.

Both males and females brooded, beginning with hatching of the first egg. The adults moved the young, or they moved themselves, every few days in the nestling period. In all six instances in Saskatchewan, the distance moved was approximately 1 m.

When adults exchanged places at the nest (starting at dusk), the arriving adult regurgitated insects to both young. The brooding bird occasionally foraged nearby and also fed the young. We could not determine the amount of food brought per trip, rate of feeding or distribution of food among the chicks. Both adults and nestlings defecated at the edges of or in the nest. Adults were not observed to eat or remove fecal sacs.

Newly hatched chicks weighed approximately 4 g and fledged at a mass of about 40 g (Fig. 1). Asymmetric chick masses, due to time-of-hatching differences, were maintained for at least 14 d after hatching. The two fledglings followed exceeded the mean adult mass (47.2 ± 6

[SD] g for males [$n = 15$] and 49.5 ± 6.3 for females [$n = 10$]; Csada and Brigham 1992) by approximately 10%. The nestling period, for the two broods followed to fledging, was 20 and 21 d, respectively.

The young of one brood associated (e.g., roosted) with the male parent for at least 10 d after fledging while the female parent laid and incubated a second clutch. It is not known at what age the fledglings were last fed by adults.

Reproductive success.—The minimum fledging success (chicks fledged per number of eggs hatched) was 8% (2/24) in British Columbia and 30% (3/10) in Saskatchewan. The fate of six chicks in British Columbia and three in Saskatchewan, all near fledging age, is unknown. If these chicks did fledge, the fledging success was 33% and 60% for British Columbia and Saskatchewan, respectively.

Nestling loss was due to abandonment (2) and predation (18). Sixty-seven percent (12/18) of the predation events occurred in the week after hatching. Although we have no direct evidence, we believe that mammals (possibly coyotes [*Canis latrans*], foxes [*Vulpes fulva*] and skunks [*Mephitis mephitis*]) and snakes (rattlesnakes [*Crotalus viridis*] or gopher snakes [*Pituophis melanoleucus*]) were likely predators of both eggs and young.

DISCUSSION

Where comparable, our data largely agree with earlier observations (Aldrich 1935, Bent 1940, Orr 1948) that poorwills are monogamous, with both males and females sharing incubating and brooding responsibilities. We found, however, that males did significantly more incubating and females did significantly more brooding. Our data suggest that pair bonds tend to be maintained for at least one breeding season.

Adults move the young, or the young move themselves, frequently during the nestling stage and these movements appear to be of two types (Swenson and Hendricks 1983). Short movements (approximately 1 m) may be a thermoregulatory response (e.g., avoiding wet areas: Swisher 1978) or to improve concealment from predators. Long movements (greater than 3 m) reported in other studies (Evans 1967, Swenson and Hendricks 1983) may be an anti-predator defense triggered by disturbance (e.g., handling).

Predation seems to be the most important factor in limiting fledging success. At least 18 of the 35 chicks were consumed by a predator. Sixty-seven percent of this predation occurred in the first week after hatching. In our experience, parents on nests usually do not flush until an intruder is close (less than 3 m). Adults do not flush until the intruder is closer still as the chicks grow older. This may make younger chicks more vulnerable to predation.

Our results show that the start of the breeding season for poorwills varies between populations. Individuals in British Columbia tend to lay first-clutch eggs approximately 2 wk earlier than birds in Saskatchewan, which breed at a higher elevation. Although we know of no published data, we expect that individuals in more southerly populations will also make two nesting attempts each year, but lay eggs even earlier. We predict that these individuals would have a higher reproductive success because environmental conditions tend to be less extreme (e.g., shorter periods of low temperature and or high precipitation), resulting in lower energy demands, at lower latitudes.

Poorwills, unlike Whip-poor-wills (*Caprimulgus vociferus*; Mills 1986), do not synchronize hatching dates with the lunar cycle such that the first 2 wk of the nesting period coincide with the period with the most moonlight (Brigham and Barclay 1992). This may be because poorwills attempt two clutches each breeding season, whereas Mills (1986) found only one pair of double-brooded Whip-poor-wills of the eight he studied. If only one nesting attempt is made, there is a greater probability of adjusting the laying date to allow synchrony with the lunar cycle. Poorwills may be forced to choose between laying one clutch to attempt to synchronize nesting with the lunar cycle to maximize foraging time when energy demand is highest and laying two clutches with first eggs being laid as early as possible to increase the possibility of having enough time to complete both successfully. It appears that poorwills at both our study sites choose the latter of the above options.

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ERRATUM

Survival rates of flightless Mountain Plovers (*Charadrius montanus*) are similar to those reported 20 yr ago, implying that recent declines in continental populations of this species are attributable either to longer-term declines in nesting productivity or to phenomena occurring at non-breeding locales, as concluded by B. J. Miller and F. L. Knopf (1993: 505, J. Field Ornithol. 64:500–506) but erroneously rejected in the abstract (1993:500) of that paper.

Brian J. Miller and Fritz L. Knopf