

LUNAR INFLUENCE ON FORAGING AND NESTING ACTIVITY OF COMMON POORWILLS (*PHALAENOPTILUS NUTTALLII*)

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ABSTRACT.—Whip-poor-wills (*Caprimulgus vociferus*) forage by sallying from a perch, are active during periods of the night with moonlight, and synchronize hatching with the lunar cycle. In contrast, Common Nighthawks (*Chordeiles minor*) forage during continuous flight and do not increase activity during moonlit periods or synchronize their breeding activities with the lunar cycle. We used data on the foraging activity and nest timing of the Common Poorwill (*Phalaenoptilus nuttallii*) to test the hypothesis that moonlight influences the activity patterns and nest timing of this sallying caprimulgid. If foraging strategy alone influences the response to the lunar cycle, activity by Common Poorwills should be correlated with lunar light levels and hatching should be synchronized with the lunar cycle. Our results support the general prediction that lunar light allows poorwills to forage during periods of the night. However, contrary to expectations, increased foraging activity was correlated only with increasing moon height and not the percent of the moon face illuminated. Furthermore, the nesting cycle was not synchronized with the lunar cycle. We conclude that knowledge of foraging style alone is not sufficient to predict the nature of lunarphilia by goatsuckers. We suggest that habitat choice, duration of twilight, the number of breeding attempts, and the physiological ability to enter torpor also may be important factors mediating lunar influence on foraging activity. Received 19 April 1991, accepted 13 January 1992.

MOONLIGHT depresses nocturnal activity in many animals including crustaceans (e.g. Wolcott and Wolcott 1982), insects (e.g. Williams and Singh 1951), small mammals (e.g. Clarke 1983), bats (e.g. Fenton et al. 1977, Morrison 1978, Reith 1982), and birds (e.g. Watanuki 1986, Nelson 1989). An increased risk of predation often is cited as the reason for this response (Lockard and Owings 1974, Fenton et al. 1977, Morrison 1978, Watanuki 1986, Nelson 1989). In contrast, some birds increase activity during the bright phase of the lunar cycle (e.g. nocturnal singing by both nocturnal and diurnal birds; Cooper 1980, Elliot 1983, Barclay et al. 1985). To date, however, the general influence of moonlight on the behavior of visually orienting nocturnal predators is poorly understood. Intuitively, we would expect an increased level of activity with increased lunar light levels.

The Whip-poor-will (*Caprimulgus vociferus*) is a nocturnal insectivore that exhibits increased locomotory, vocal, and nest-visiting activity during periods of bright moonlight (Mills

1986). Mills (1986) found that the nesting cycles of *Caprimulgus* species are synchronized with the lunar cycle, such that the first two weeks of the nestling period coincide with the period with the most moonlight. Observations of *Caprimulgus* species in North America, Africa, and Europe also indicate that moonlight positively influences singing behavior (Wynne-Edwards 1930, Brauner 1952, Cooper 1980, Jackson 1985), leading Mills (1986) to suggest that caprimulgids are "lunarphilic," meaning that they are limited to foraging crepuscularly (dusk and dawn; Martin 1990) and during periods of the night with moonlight. In contrast to the lunarphilic response of *Caprimulgus* species, Common Nighthawks (*Chordeiles minor*) only forage crepuscularly, and not during the night, regardless of moonlight levels (Aldridge and Brigham 1991, Brigham and Fenton 1991). Furthermore, there is no evidence for synchrony of hatching dates in *C. minor* or *C. acutipennis* nests with the lunar cycle (Mills 1986).

The different foraging styles of *Chordeiles* and *Caprimulgus* could explain the differences in nesting synchrony and activity periods. Whip-poor-wills attack flying insects in upward-directed sallies of short duration from a perch or the ground (a "sit-and-wait" or "sallying" strategy; Mills 1986). Anecdotal evidence suggests

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that other *Caprimulgus* species also use a sit-and-wait/sallying foraging strategy (Bent 1940, Fry et al. 1988). In contrast, *C. minor* and *C. acutipennis* "hawk" flying insects while the birds are engaged in continuous flight (Caccamise 1974, Brigham 1990, Aldridge and Brigham 1991, Brigham and Fenton 1991).

A prey-detection constraint is one possible mechanism that would explain how the lunar cycle influences foraging activity and nest timing. The illumination from a full moon does not appear to be enough for nighthawks to detect prey in time to maneuver and attack (Aldridge and Brigham 1991), whereas stationary Whip-poor-wills probably have a smaller detection distance; less light is required in order to react to passing insects. Furthermore, nighthawks forage on small insects that are difficult to detect (Brigham 1990), whereas Whip-poor-wills forage primarily on larger and, thus, more easily detected moths (Bent 1940).

The purpose of our study was to use data on the foraging activity and hatching dates of the Common Poorwill (*Phalaenoptilus nuttallii*) to evaluate whether moonlight influences the activity patterns and nest timing of this caprimulgid. Poorwills ostensibly employ a sit-and-wait foraging strategy (Bent 1940, Cannings et al. 1987), which leads us to predict that foraging activity by poorwills will increase on nights with moonlight, and hatching dates will be synchronized with a particular phase of the lunar cycle.

MATERIALS AND METHODS

Study site.—The study was conducted from April to September 1989 and 1990 in the Okanagan Valley of south-central British Columbia, Canada (49°18'N, 119°31'W). On the side-hills of the valley, where activities of poorwills were centered, the vegetation is predominantly *Pinus ponderosa* (Cannings et al. 1987). In 1989, we affixed radio transmitters to individuals on the eastern side of the valley near Vaseaux Lake. In 1990, we monitored individuals on the western side, 8 km from the town of Oliver. The two study areas were separated by less than 10 km. We predicted that there should be differences between years in the timing of crepuscular foraging periods resulting from the different aspects of the valley slopes relative to the setting and rising sun.

Lunar and solar conditions.—For the most part, we followed Mills (1986) in categorizing nights relative to lunar and solar conditions. Percentage of moonface illuminated (%MFI) and moon heights (MH; measured in minutes) were taken from the Astronomical

Almanac (Anawalt and Boksenberg 1987). The times of solar and lunar rising and setting, and various solar positions below the horizon, were taken from tables calculated for the study site by the Dominion Astrophysical Observatory (Victoria, British Columbia). Mills (1986) showed that the influence of the moon on the behavior of Whip-poor-wills began when the sun was between 10° and 13° below the horizon. We used nautical twilight (the point when the sun is 12° below the horizon) as the cutoff point delineating dusk and dawn (crepuscular) from true "night" periods. To facilitate a direct comparison with Mills' (1986) results, we grouped nights into five categories based on %MFI at midnight (0, 1–25, 26–50, 51–75, and 76–100) and four categories based on MH at midnight (0, 1–100, 101–200, and 200+).

Foraging activity.—Direct observations of foraging behavior by poorwills were made opportunistically along gravel roads on both sides of the valley. Foraging at dusk was observed directly or with binoculars until it was too dark to see or until the birds ceased foraging.

We measured the temporal patterns of poorwill activity using radiotelemetry. Temperature-sensitive radio transmitters (model PD-2T, Holohil Systems Ltd., Woodlawn, Ontario), with an average mass of 2.4 g, were affixed to the birds using an elastic harness slipped over the wings (Brigham 1989). The temperature-sensitive capability allowed us to determine when individuals entered torpor (Brigham, in press). Data for nights when individuals entered torpor were not included in our analysis.

The effective range of the transmitters varied from 1 to 4 km depending upon terrain. The occasional periods when individuals moved out of range were not included in the analysis. We classified the behavior of each individual as moving or stationary at 5-min intervals using a Merlin 12 telemetry receiver (Custom Electronics, Urbana, Illinois) and a five-element Yagi antenna. During each measurement, a minimum of 20 pulses was monitored with movement being defined as any change in either the direction or strength of the signal. Direct observations of radio-tagged birds convinced us that the "movements" we measured using telemetry represented foraging sallies. Pulses from transmitters carried by active individuals were emitted approximately 1.5 s apart and, during a typical movement, two or three signals varied in intensity. This agrees with our observation of sallies lasting up to 5 s.

Thirteen adult birds (6 females and 7 males) were captured and outfitted with transmitters. In all, 10,242 telemetry readings were taken during 107 complete bird-nights and 39 partial nights of monitoring. One complete bird-night is defined as data for a single individual collected from the beginning of foraging at dusk until the end of foraging at dawn. To facilitate between-year comparisons, we tried to collect data on the same dates and for the same number of birds in 1989 and 1990.

One bird carrying a transmitter was killed by an unknown predator, and the signals for three other individuals stopped abruptly and suspiciously, suggesting that predation had occurred. For six pairs where one or both individuals carried a transmitter during the breeding season, five pairs made nesting attempts, and of those, four laid two clutches. Of the seven nesting attempts that we followed to completion, three resulted in young reaching fledging age.

Nesting cycles.—We collected poorwill nesting records for which hatching dates were known, or could be calculated, to test the possibility of a synchronized relationship with the lunar cycle. We classified each nesting record in terms of the number of days between hatching and the most recent full moon. Due to a small sample size of hatching dates, we divided the lunar month into five six-day periods (corrected to reflect a lunar month of 29.5 days) instead of the 10 three-day periods used by Mills (1986). Nine nesting records were from our own data and the remainder were from the British Columbia Provincial Museum or the Cornell Laboratory of Ornithology.

Statistical analysis.—Means are reported along with ± 1 SD. For each night, we generated scores for movement (percentage of telemetry readings that were moves) by individuals and assigned them to dusk, dawn or true-night periods. Scores for night periods were assigned to one of the categories for both %MFI and MH variables. Movement proportions were arcsin transformed before analysis by one-way ANOVA. Where ANOVA was significant, Tukey's multiple-comparison tests (Zar 1984) were used. The null hypothesis was rejected for alpha values of less than 0.05.

RESULTS

On 12 nights, we observed 258 instances of poorwills foraging by sallying from the ground to a maximum of 3 m in the air. In all cases, flights lasted less than 5 s. On average, individuals made 5.0 ± 1.7 attacks per min. We never observed poorwills flying continuously while foraging.

Foraging activity always occurred during both dusk and dawn periods on nights when individuals did not enter torpor. The beginning of foraging at dusk and end of foraging at dawn was correlated with the time of sunset ($r_s = 0.88$, $n = 134$, $P < 0.001$) and sunrise ($r_s = 0.71$, $n = 79$, $P < 0.001$), respectively. There was no difference between males and females for either 1989 or 1990 in the time after sunset when foraging began ($F = 0.02$, $df = 1$ and 61 , $P > 0.80$; and $F = 3.25$, $df = 1$ and 55 , $P > 0.05$, respectively). However, with data for the sexes pooled, there was a significant difference between years

(1989, $\bar{x} = 34.1 \pm 24.3$ min after sunset vs. 1990 $\bar{x} = 23.5 \pm 9.6$ min; $F = 8.39$, $df = 1$ and 131 , $P < 0.001$). Neither males nor females differed significantly between years in the time (relative to sunrise) when foraging ended at dawn ($F = 2.66$, $df = 1$ and 38 , $P > 0.1$, and $F = 3.79$, $df = 1$ and 35 , $P > 0.05$, respectively). However, as was the case for dusk bouts, there was a significant difference between years with the sexes pooled (1989 $\bar{x} = 56.3 \pm 26.3$ min before sunrise vs. 1990 $\bar{x} = 39.6 \pm 12.6$; $F = 12.36$, $df = 1$ and 77 , $P < 0.001$).

Analysis of crepuscular and night activity data were pooled by sex and, because there were no significant differences between 1989 and 1990 in activity levels for any of the lunar conditions ($P > 0.20$ in all cases), the data were also pooled for the two years. There were significant differences in activity levels with respect to the lunar condition defined in terms of %MFI ($F = 7.4$, $df = 1$ and 105 , $P < 0.001$; Fig. 1) and MH ($F = 9.4$, $df = 1$ and 105 , $P < 0.001$; Fig. 2). However, these differences did not occur in the expected stepwise fashion. Partial correlation analysis between activity and %MFI (controlled for MH) was not significant ($r = -0.01$, $n = 113$, $P > 0.5$), but activity and MH (controlled for %MFI) were correlated ($r = 0.31$, $n = 113$, $P < 0.01$). It may be that MH is a better predictor of light levels, because moons with a high %MFI are as likely to be low in the sky as high, while all high moons have a high %MFI. If nights were simply divided into dusk, dawn, bright moonlit, and dark-night (on the basis of MH) categories, activity did decrease significantly in the expected stepwise fashion ($F = 85.0$, $df = 1$ and 301 , $P < 0.001$; Fig. 3).

We found no evidence for a relationship between lunar phase and hatching date (Fig. 4). Hatching dates were distributed randomly throughout the lunar month ($X^2 = 1.21$, $df = 1$ and 4 , $P > 0.50$).

DISCUSSION

Our data confirm that Common Poorwills, like Whip-poor-wills, are sit-and-wait predators. Furthermore, poorwill activity patterns are affected by both solar and lunar light levels. As we expected, the times of initiation and cessation of activity were correlated with the times of sunset and sunrise. There was a difference in the timing of crepuscular activity periods for birds inhabiting different sides of the valley.

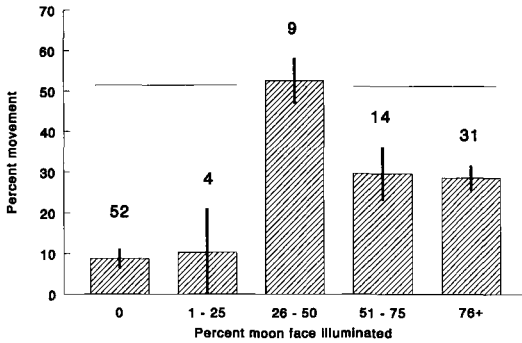


Fig. 1. Proportion (untransformed) of telemetry fixes (classified as movements) related to percentage of moon face illuminated (%MFI). Data pooled for all nights and all individuals. Error bars represent ± 1 SE. Horizontal bars indicate activity levels not significantly different (Tukey's test). Numbers above bars are number of bird-nights.

The earlier start to activity by poorwills on the west slope could be because this slope is shaded earlier than the eastern side of the valley as the sun sets. However, if the onset and cessation of foraging is controlled by light levels alone, we would have expected the reverse pattern to occur at sunrise, with the birds on the west slope, which is lit by the rising sun first, ceasing activity first. This did not occur, suggesting that crepuscular light levels alone do not control activity periods. Our impression was that the wet, cool spring of 1990 resulted in lower flying-insect abundance. Low prey abundance may have forced poorwills to forage for longer pe-

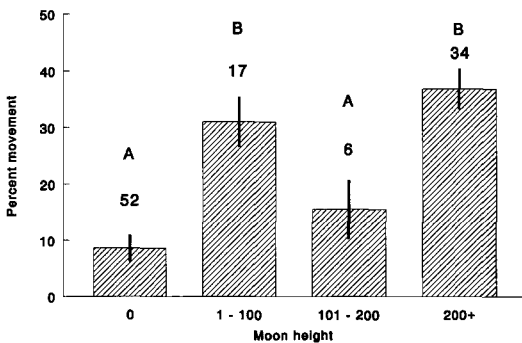


Fig. 2. Proportion (untransformed) of telemetry fixes (classified as movements) related to moon height (MH). Data pooled for all nights and all individuals. Error bars ± 1 SE. Categories denoted by same letter are not significantly different (Tukey's test). Numbers above bars are number of bird-nights.

riods in 1990 in order to meet energy requirements.

As predicted, poorwill foraging activity increased on nights with bright moonlight versus nights with none. Unlike Mills' (1986) results for Whip-poor-wills, however, we found no correlation between activity and %MFI, although there was a correlation with MH. This suggests that some lunar light is necessary to allow activity but, above a threshold level, other factors also are important. Alternatively, differences in habitat complexity may account for the difference in activity patterns relative to lunar light levels by different species. Poorwills are found in relatively open habitats (Bent 1940) in which the illumination provided by a moon low in the sky may provide enough light for foraging. In relatively closed habitats, like those inhabited by Whip-poor-wills, a high and thus bright moon may be required for sustained nocturnal activity.

The duration of crepuscular twilight might account for the differences in activity between Whip-poor-wills and Common Poorwills. Poorwill activity levels are highest during twilight periods at dusk and dawn, indicating the importance of these periods to the birds. The length of twilight during the summer increases with distance from the equator and, because our study site is 5° higher in latitude relative to the Ontario site used by Mills' (1986) Whip-poor-wills, Common Poorwills in the Okanagan have more twilight time available for foraging. This may reduce the importance of the night foraging period and, thus, the influence of lunar condition. The pattern of lunarphilia by goatsuckers may be strongest near the equator, where twilight is the shortest and the importance of truly nocturnal foraging may be the greatest (Mills 1986).

We found no synchrony between the lunar cycle and the hatching dates of poorwill nests; it appears that a sallying strategy of foraging and the lunar cycle are not as closely linked as we expected. However, the number of breeding attempts made during the summer is a potentially complicating factor. In the Okanagan, two of five poorwill pairs made a second breeding attempt after chicks reached fledging age. Two other pairs produced a second clutch after chicks (< 7 days old) were preyed upon. Mills (1986) found only one pair of double-brooded Whip-poor-wills of the eight pairs he studied. If only one nesting attempt is made, there probably is

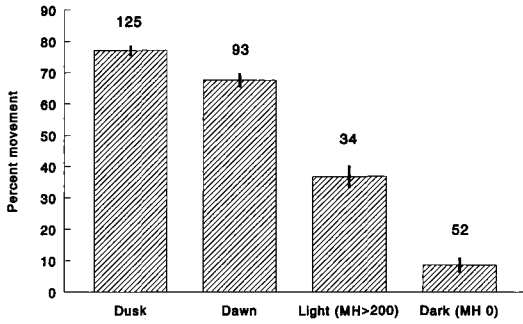


Fig. 3. Proportion (untransformed) of telemetry fixes (classified as movements) during dusk, dawn, light (MH >200), and dark-night (MH 0) periods. Data pooled for all nights and all individuals. Error bars represent ± 1 SE. Activity levels are significantly different among all categories (Tukey's test). Numbers above bars are number of bird-nights.

a greater possibility of adjusting the laying date to allow synchrony with the lunar cycle, whereas to complete two breeding cycles likely requires egg laying to begin as early as conditions allow, regardless of the lunar cycle. Poorwills could be faced with the tradeoff of: attempting to synchronize nesting with the lunar cycle to maximize foraging time when energy demand is highest, but at the cost of reducing the probability of successfully completing a second breeding attempt; or laying as early as possible, but with the cost of coping with high energy demands of chicks during periods with little or no moonlight.

One feature of the biology of poorwills that markedly influences activity during periods of food shortage is the ability to enter torpor, which has been well documented for food-deprived captive birds (Marshall 1955, Bartholomew et

al. 1957, Howell and Bartholomew 1959, Austin and Bradley 1969, Ligon 1970, Withers 1977). Free-ranging birds in our study also used this strategy (Brigham, in press). There is no published information on the use of torpor by captive or free-ranging Whip-poor-wills. If the ability to enter torpor significantly alters the influence of lunar light on foraging, we would predict that Whip-poor-wills may not be capable of entering torpor. It is not intuitively apparent, however, how the ability to enter torpor might affect foraging activity during most of the summer, a period when torpor was not used by Common Poorwills.

Brauner (1952) found that poorwills are vocally most active on nights with moonlight, but concluded the poorwills are "not active through the night when undisturbed, regardless of the lunar condition." This conclusion is not supported by our telemetry data. We suggest that singing should not be used as an index of activity because, unlike foraging, singing can occur regardless of light levels. Although singing by Whip-poor-wills is more common during periods with moonlight (Mills 1986), our impression was that the vast majority of vocal behavior by Common Poorwills occurred in crepuscular periods (e.g. Brauner 1952).

In summary, our study supports the general prediction that lunar light allows a sallying goatsucker, the Common Poorwill, to forage during light periods of the night. However, contrary to our expectations, increased foraging activity was correlated with MH only and not with %MFI, nor was the nesting cycle synchronized with the lunar cycle. Thus, knowledge of foraging style alone is not sufficient to predict the nature of lunarphilia in goatsuckers. Habitat choice, duration of twilight, number of breeding attempts, and the physiological ability to enter torpor also may be important factors affecting foraging activity.

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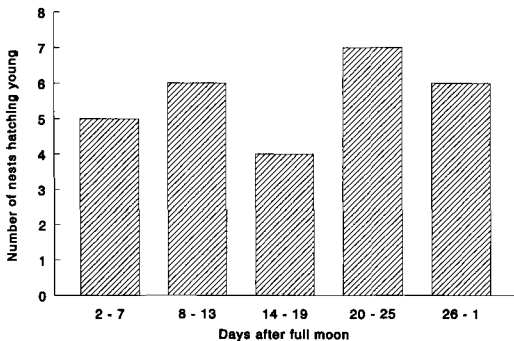


Fig. 4. Relationship between lunar phase and hatching date for Common Poorwills.

C. Brigham, R. L. Mackey, M. C. Firman, L. S. Johnson and three anonymous reviewers greatly improved earlier versions of the manuscript.

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