

## COMMON POORWILL ACTIVITY AND CALLING BEHAVIOR IN RELATION TO MOONLIGHT AND PREDATION

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**ABSTRACT.**—We investigated the influence of lunar and environmental factors on behavior of Common Poorwills (*Phalaenoptilus nuttallii*) in southern Arizona under a diverse set of natural and artificial conditions. Radio-marked poorwills were most active shortly after sunset during the new moon. Movements declined as evening progressed. Activity remained high for several hours after sunset when the moon was full. Poorwills were heard calling from March through October, but most calling occurred between early May and September. Only ambient light was correlated with number of poorwills heard calling. More poorwills responded to playbacks of conspecifics when the moon was full than when it was new. Poorwills did not change their response to conspecifics during full moon when playback of poorwill calls followed playback of Great Horned Owl (*Bubo virginianus*) calls but, during the new moon, fewer birds responded following the owl call. Poorwill behavior is strongly influenced by lunar conditions; their ability to detect and evade predators is important when calling advertises their location. Received 22 May 2006. Accepted 1 September 2006.

The behavioral influence of sunlight on birds is evident, but the influence of moonlight on diurnal and nocturnal birds is less apparent. For example, many nocturnal birds call most actively at dusk in contrast to the well known singing or calling at dawn by diurnal birds (Brauner 1952, Cooper 1981, Ganey 1990). Frequencies of calling, as well as overall activity patterns, are less well known during true night, when moonlight is the primary source of illumination. Some animals that are eaten by owls limit activity during periods when the moon is full (Price et al. 1984, Brown et al. 1988, Kotler et al. 1994, Brigham et al. 1999, Beier 2005, Lang et al. 2006). Bright moonlight coincides with the highest rates of nocturnal predation on Black-vented Shearwaters (*Puffinus opisthomelas*) and Cassin's Auklets (*Ptychoramphus aleuticus*) by Western Gulls (*Larus occidentalis*) (Nelson 1989, Keitt et al. 2004). Predation by Great Black-backed Gulls (*Larus marinus*) on Manx Shearwaters (*Puffinus puffinus*) is also strongly influenced by lunar condition (Brooke 1990). The behavioral effects of different lunar conditions are not universal, however, and other nocturnal animals increase activity when the moon is full and the sky is relatively bright, presumably because visual constraints

are reduced during those periods (Cooper 1981, Mills 1986, Brigham and Barclay 1992, Jetz et al. 2003).

The Caprimulgidae is a circumglobal family of visually acute, crepuscular or nocturnal insectivores for which some aspects of lunar influence have been evaluated. The most commonly studied aspect of caprimulgid biology in the context of lunar illumination is the possible synchrony of breeding with lunar cycle (Jackson 1985, Mills 1986, Brigham and Barclay 1992, Perrins and Crick 1996). The hypothesis that light levels constrain foraging activity has also been proposed (Csada et al. 1992, Bayne and Brigham 1995, Jetz et al. 2003). Common Poorwills (*Phalaenoptilus nuttallii*; hereafter poorwill) are the smallest North American caprimulgid (45–50 g), and are one of the least understood of all North American birds, principally because of their cryptic coloration and nocturnal habits (Csada and Brigham 1992). We studied Common Poorwills under a diverse set of natural and artificial conditions to assess the influence of environmental and lunar factors on their behavior. Specifically, we compared the likelihood of movement by radio-marked birds between the full and new moons, and measured the rate of vocalization under a range of environmental, lunar, and seasonal situations. We also used playbacks of poorwill and Great Horned Owl (*Bubo virginianus*) vocalizations to examine whether the proximity to a potential predator influences calling responses by poorwills.

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## METHODS

We collected data during 1996–1999 at three sites within 100 km of Tucson, Arizona, USA: the National Audubon Society's Appleton-Whittell Research Ranch (31° 36' N, 110° 30' W), central portions of the Buenos Aires National Wildlife Refuge (31° 41' N, 111° 26' W), and the east side of the Tortolita Mountains (32° 32' N, 111° 00' W). All three sites are within the Sonoran desert ecosystem and share environmental and ecological attributes, including an elevation range of 1,000 to 1,550 m, hot days and cool nights, limited rainfall that typically occurs during the summer monsoon, and an abundance of cacti. Poorwills occurred year-round at the Tortolita and Buenos Aires sites; some over-wintered at the Research Ranch site, although most were absent during the coldest months.

Poorwills were captured at night either using mist nets in conjunction with playbacks of territorial calls or with a spotlight and long-handled net (Swenson and Swenson 1977, Jackson 1984, Brigham 1992). A few birds were captured or recaptured during daylight by flushing them into mist nets placed near roosts. Captured birds were banded with a USGS metal band and fitted with a temperature-sensitive radio transmitter (2 models that differed in mass and range were used: Model PD-2T, 2.8 g and 1–4 km range, and Model BD-2GT, 1.7 g and 0.5–2 km range; Holohil Systems Inc., Carp, ON, Canada). Transmitters were affixed using an elastic harness slipped over the wings (Brigham 1992, Hill et al. 1999).

*Likelihood of Activity.*—Radio-marked poorwills were monitored remotely using a Lotek SRX 400 Telemetry Receiver (Lotek Engineering Inc., Newmarket, ON, Canada) to assess activity patterns by quantifying variation in signal strength. Activity can be inferred because signal strength of successive radio pulses varies widely when radio-marked animals are active due to rapid changes in orientation of the transmitting antenna (Sutter et al. 1996, Brigham et al. 1999).

We evaluated the relationship between time of night, lunar illumination, and movement by poorwills using telemetry data from 5-min periods exactly 1, 3, and 5 hrs past sunset on nights for which there was either a full moon

(>95% of the moon's face illuminated; 82 bird-nights from 6 males, 5 females, and 2 unknown gender juveniles) or no moon (<5% of the moon's face illuminated; 92 bird-nights from 9 males, 4 females, and 2 unknown gender juveniles). We only used data from birds that were euthermic (i.e., not torpid based on body temperature above 30° C) and for which there was either movement or inactivity in at least one of the 5-min periods. We inferred that movement had occurred when the standard deviation of the intensity of three signals recorded by the Lotek receiver was >10. This value was derived from comparisons of variation in signal strength when movement or inactivity by birds could be observed directly (cf. Sutter et al. 1996, Brigham et al. 1999). We used Chi-square tests to evaluate whether there were differences in the number of times that movement occurred during each 5-min period, for the two different lunar conditions.

*Environmental Influences on Vocalization.*—We examined the influence of climatic, lunar, and seasonal variables on poorwill vocalization by conducting night-time counts of calling poorwills at established points in the three study sites. Counts were made on 89 survey nights between June 1996 and January 1999, although effort varied seasonally and between sites. Most surveys, especially during spring and summer, were at 7 to 10 day intervals, but logistics meant that five were separated from a prior survey by only 2 to 4 days and 10 were separated by 2 weeks to 10 months. Two counts were done on 55 of 89 survey nights with 1–3 hrs separating each count making for 144 total counts. Poorwills were counted at the Research Ranch and Buenos Aires sites at nine points: three, each separated by 1 km, along each of three narrow and lightly-used dirt roads. Counts at the Tortolita Mountains site consisted of either five individual points or two sets of three points; in both cases points were separated by 1 km or more (logistics at Tortolita required two separate routes).

Calling poorwills were counted at each point for 3 min during which time CPW, who conducted all counts, remained in darkness and silent (playbacks of poorwill calls were not used). The number of calling birds was assigned based on differing direction and distance of calls and temporal overlap in calling

(i.e., 2 or more birds calling at the same time). Counts were started at least 1 hr after sunset and completed in 1–2 hrs. No counts were conducted during civil twilight (when the sun is 0° to 6° below the horizon), even though poorwills called frequently during this time, so that solar light did not complicate our interpretation of the influence of lunar illumination. No counts were conducted when it rained.

We recorded environmental variables twice (Tortolita Mountains) or three (Research Ranch and Buenos Aires) times during each survey, and averaged them to establish overall count conditions. We measured ambient light levels, temperature, relative humidity, average wind speed, and percent cloud cover. Wind speed and/or relative humidity were not measured during 49 counts. A Beseler PM2L Color Analyzer (Charles Beseler Co., Linden, NJ, USA) was used to measure ambient light levels (Hecker and Brigham 1999). This device generates a unit-less measure of light intensity to facilitate setting exposure times for film printing. It works at light intensities at which many light meters are ineffective. We used a Cole-Parmer thermistor thermometer (Model 8402-00; Cole-Parmer Instrument Co., Vernon Hills, IL, USA) to measure ambient temperature and a General Eastern thermo-hygrometer (Model 880, General Eastern Instruments, Woburn, MA, USA) to measure relative humidity. We measured wind speed ( $\pm 3$  km/hr) over a 3–4 min period with a Kestrel wind meter (NK Electronics, Chester, PA, USA), which averaged measurements taken at 1-sec intervals. Percent cloud cover was visually estimated.

Most birds called during the warmer months and we included for our analysis the 92 counts between 5 May and 3 September, during which time 80% of all calling occurred. Forty-seven of the 92 counts included in our analysis were at the Research Ranch, 42 at Buenos Aires, and 3 at Tortolita Mountains. We assumed there was no site specific lunar effect. The maximum number of birds heard at each point along each route within any year was used as an estimate of year- and site-specific bird maximums. The number of calls detected during any count were standardized against the maximums and our analysis was based on the percentage of the maximum

number of birds calling, not the number of birds specifically. We used two separate backward stepwise multiple regressions to assess the importance of environmental variables. First, for all 92 counts with light, temperature, and percent cloud cover as variables, and second, for the smaller sample of 43 counts for which data on relative humidity and wind speed were also available.

*Influence of Owls on Vocalization.*—We assessed the influence of owls on calling behavior by poorwills by measuring the response to playbacks of poorwill calls both with and without the implied presence of a Great Horned Owl (these owls are common nocturnal predators and were heard in all 3 study areas). We surveyed for calling poorwills (independently from the counts described) using two playback treatments to discern the effect of potential owl presence on poorwill calling behavior under differing light levels. Playbacks were conducted at 1.6-km intervals on dirt road systems at the Research Ranch and Tortolita Mountains sites, as well as on lightly traveled dirt roads on the east side of the Rincon Mountains, 50 km east of Tucson (32° 07' N, 110° 28' W), on desert flats near Black Mountain, 60 km north of Tucson (32° 49' N, 110° 57' W), and on the west side of the Silverbell Mountains, 55 km west of Tucson (32° 26' N, 111° 30' W). At each stop, we waited in silence and darkness for 30 sec and then played a treatment tape. The test was conducted between 6 June and 11 July 1998 on calm or nearly calm nights with little or no cloud cover, beginning at least 90 min after sunset. The test usually took several hours and was not repeated on the same evening. Three routes were surveyed twice, once during the full moon and again during no moon, and two were surveyed three times each, twice during a full moon (separated temporally by 1 month) and once when there was no moon.

We randomly assigned a treatment to each stop prior to surveys, but with the condition that each set of two stops included each treatment. Counts were based on response to two playbacks treatments: poorwill only (15 sec poorwill, 60 sec silence, 15 sec poorwill) and poorwill, Great Horned Owl, poorwill (15 sec poorwill, 60 sec silence, 15 sec Great Horned Owl, 15 sec poorwill). The treatment variation thus occurred in the second call sequence. Re-

cordings used in treatments were taken from a standard collection of bird songs (Peterson Field Guides: Western Bird Songs, Houghton Mifflin Co., Boston, MA, USA). Complete 90–120 sec treatment tapes were created so that switching of tapes during counts was unnecessary. We used a portable cassette player, set at 3/4 maximum volume and judged that poorwills within ~300 m responded.

We measured the number of responding birds and calling intensity during the 60-sec interval following playback of the initial call and again during the 60-sec interval following playback of the treatment call(s). The number of birds calling was based on the direction and distance of calls, and overlap in calling. To characterize intensity, we counted the total number of calls, regardless of the number of birds calling, and assigned a categorical value based on six categories: (0) no calls, (1) 1–5 calls, (2) 6–10 calls, (3) 11–20 calls, (4) 21–30 calls, and (5) 31+ calls. Categorical values were used to minimize potential errors in counting when calling was particularly intense. We completed 12 surveys with a total of 168 individual stops, 84 for each treatment. Stops at which no poorwills were heard (29 in total), were eliminated from our analysis. We initially compared the full versus new moon results prior to the treatment playback (i.e., the numerical and categorical response to the first poorwill call only). A subsequent analysis to assess treatment effects was based on the per point change in number of birds or calls from the 60-sec period after the first playback to the 60-sec period after the second playback. Preliminary analysis indicated that data for both survey treatments were not normally distributed (Shapiro-Wilks'  $W$  with associated  $P < 0.01$ ); therefore, we used a non-parametric Mann-Whitney  $U$ -test for all comparisons.

## RESULTS

**Likelihood of Activity.**—We used data from 135 activity records (59 full moon, 76 new moon) for the period 1 hr past sunset, 112 (56 full moon, 56 new moon) for 3 hrs past sunset, and 97 (48 full moon, 49 new moon) for 5 hrs past sunset to examine poorwill movements. The likelihood that a bird was active during full moon was similar in the three time periods with movement occurring in 70% (1 hr),

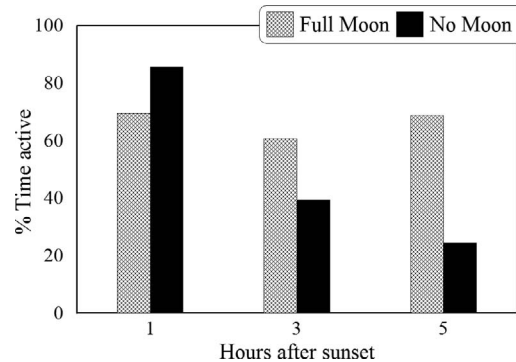


FIG. 1. Likelihood of activity by Common Poorwills during 5-min periods 1, 3, and 5 hrs after sunset in southern Arizona. There were between 97 and 135 sampling periods within each time period, and activity differs within each ( $\chi^2$  tests, all  $P < 0.05$ ).

61% (3 hrs), and 69% (5 hrs) of each. The likelihood of activity decreased over time during the new moon with movements occurring in 86, 39, and 25% of the three periods, respectively (Fig. 1). Birds were more likely to be active 3 and 5 hrs past sunset when the moon was full versus when it was new ( $\chi^2_1 = 5.1$ ,  $P = 0.023$  and  $\chi^2_1 = 19.1$ ,  $P < 0.001$ , respectively). The situation was reversed, however, 1 hr past sunset, when activity was more common during the new than the full moon ( $\chi^2_1 = 5.1$ ,  $P = 0.024$ ).

**Environmental Influences on Vocalizations.**—Poorwills in southern Arizona called throughout an extended period from March through October (Fig. 2). Most calling occurred during the summer months. The central 50 and 80% of all calls were recorded between 27 May and 29 July, and 5 May and 9 September, respectively. Ambient light levels significantly predicted poorwill calling, whether based on the data from 92 counts for which only light, temperature, and cloud cover were analyzed ( $F_{1,89} = 92.2$ ,  $R^2 = 0.509$ ,  $P < 0.001$ ,  $\beta_{\text{Light}} = 0.71$ ; Fig. 3), or based on the data from 43 counts that also included relative humidity and wind speed ( $F_{1,41} = 49.1$ ,  $R^2 = 0.545$ ,  $P < 0.001$ ,  $\beta_{\text{Light}} = 0.74$ ). No other environmental variable measured was significantly related to the number of calling birds, regardless of the data set used.

**Influence of Owls on Vocalizations.**—The effect of moonlight on calling was also evident from playback surveys whose purpose

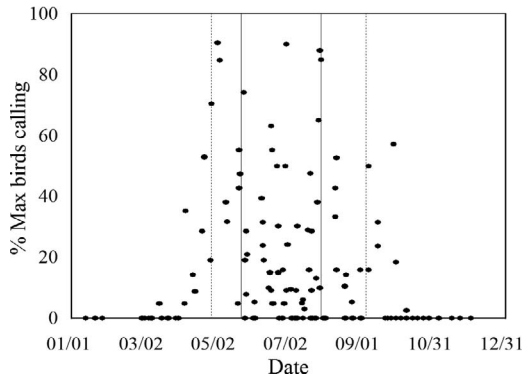


FIG. 2. Seasonality of calling by Common Poorwills in southern Arizona from point count surveys without playback of a poorwill call. Solid lines encompass the central 50% of all calls, and stippled lines the central 80%.

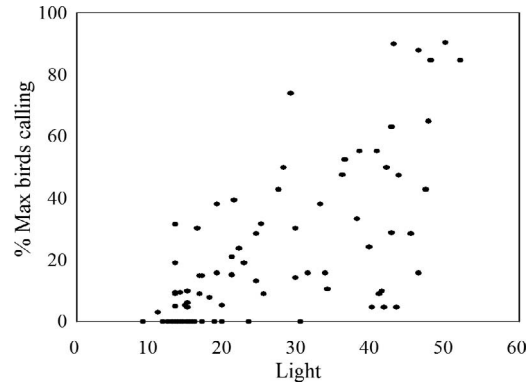


FIG. 3. Relationship between ambient light at night and calling by Common Poorwills during spring and summer in southern Arizona without playback of a poorwill call. Light levels are unit-less measurements from a photographic light meter, with "10" representative of no moon and little light, and "50" of a full moon and bright conditions.

was to evaluate the effect of owl calls on poorwill vocalizing. Poorwills responded in significantly greater numbers and more intensely during full moons versus new moons after playback of the first poorwill call. The number of birds responding during the new moon averaged only 38% of the number calling during the full moon (mean of 0.59 birds at each point vs. 1.55 birds;  $Z_{54,85} = 5.66$ ,  $P < 0.001$ ). The categorical number of calls detected during the new moon averaged 52% of the number heard during full moon (1.57 vs. 3.02;  $Z_{54,85} = 4.51$ ,  $P < 0.001$ ).

There was no significant difference in the change in calling response following playback of the second treatment call(s) during the full moon either in number of birds responding or intensity of calling. The number of responding poorwills increased 16% (from 1.64 to 1.90 birds) per point following the poorwill only treatment during the full moon from the period after the first call to the period after the second. Calling increased 14% (from 1.47 to 1.67 birds) after the Great Horned Owl then poorwill treatment ( $Z_{42,43} = 0.14$ ,  $P > 0.1$ ). The number of calls increased 21% (from 3.05 to 3.69) after the poorwill only treatment, and 11% (from 3.00 to 3.33) following the Great Horned Owl then poorwill treatment ( $Z_{42,43} = 0.85$ ,  $P > 0.1$ ). In contrast, there was a significant difference in the change in response by poorwills when the moon was new, both in the number of birds responding and the categorical intensity of calling. The number of

responding poorwills following the poorwill only treatment during the new moon increased 59% (from 0.56 to 0.89 birds) after the second call compared to after the first call, but decreased 11% (from 0.63 to 0.56 birds) after the Great Horned Owl then poorwill treatment ( $Z_{27,27} = 2.42$ ,  $P = 0.016$ ). Categorically, the number of calls increased 35% (from 1.59 to 2.15) after the poorwill only treatment, but decreased 4% (from 1.56 to 1.48) following the Great Horned Owl then poorwill treatment ( $Z_{27,27} = 2.19$ ,  $P = 0.029$ ).

## DISCUSSION

The intensity of night-time lunar illumination varies by more than a hundred-fold depending on phase (Austin et al. 1976). Consequently, it is not surprising that lunar phase should influence behavior of nocturnal animals, especially those that orient visually, although the direction of this influence may not be obvious. In the absence of extenuating factors, visually-oriented nocturnal predators like poorwills should concentrate foraging activity during bright moonlight but vocalize more frequently when there is little moonlight, when foraging should be least efficient (Brigham and Barclay 1992, Csada et al. 1992, Bayne and Brigham 1995). Chuckwill's-widows (*Caprimulgus carolinensis*) and Whip-poor-wills (*C. vociferus*) call with greater frequency during moonlit conditions, how-

ever, and lunar illumination is the only environmental factor correlated with calling during the breeding season (Cooper 1981, Mills 1986, Ganey 1990). Poorwills in our study vocalized most actively during the full moon and lunar illumination was the only environmental variable we measured with which the number of birds heard calling was correlated. In addition, poorwills tended to be more active (which we interpret as foraging) during full moon, although the number of flying insect prey depended principally on temperature and was independent of ambient light (Woods 2002). Consequently, increased activity by poorwills during the brightest periods was not related to increased prey density, and vice versa.

Jetz et al. (2003) found a strong relationship between lunar cycle and timing of foraging activity by Standard-winged (*Macrodipteryx longipennis*) and Long-tailed (*Caprimulgus climacurus*) nightjars in equatorial West Africa. They noted that foraging was concentrated during the crepuscular period during all phases of the lunar cycle but increased significantly around new moon. They also detected a small but significant increase in abundance of some larger insects during full moon periods which correlated with increased foraging during periods of the night with lunar light. In cooler more seasonal subtropical environments, temperature as well as light levels strongly affects activity patterns of Freckled Nightjars (*Caprimulgus tristigma*; R. A. M. Ashdown and A. E. McKechnie, unpubl. data). Unfortunately, calling behavior was not evaluated in either of these studies.

Peaks in calling occur for some nocturnal birds throughout the breeding season, and are often attributed to different breeding stages (e.g., Clark and Anderson 1997). We found no seasonal peaks in calling, possibly because of the cyclic influence of lunar phase on calling frequency. Poorwills are known to call persistently (Bent 1940, Gabrielson and Jewett 1940, Bailey and Niedrach 1965, this study), and we heard birds call in every month but January. These observations support the hypothesis that individuals are inclined to call frequently where they occur as year-round residents, regardless of breeding stage, but in locations where they are migratory, calling tends to cease in late summer (Kalcounis et

al. 1992). These results suggest a trade-off exists between frequent calling and efficient foraging, assuming that calling reduces foraging efficiency. The extent to which vocalizing may restrict foraging by caprimulgids is uncertain, but males deplete fat reserves during the breeding season whereas females, which probably call infrequently, do not (Csada and Brigham 1992, Thomas et al. 1996). Energetic shortfalls resulting from forgoing feeding when prey are most visible are probably minimized since full moons are above the horizon for the most time. Consequently, more foraging time is available when the moon is relatively full. During new moon, activity was highest shortly after sunset and diminished as evening progressed, whereas during full moon, activity levels were consistent throughout late evening (cf. Brauner 1952). These contrasting patterns suggest that during new moons, poorwills must forage with greater intensity at and just past twilight, since low light levels will reduce foraging efficiency and may increase predation risk later in the night.

Why are poorwills more vocal during periods of high lunar illumination? In addition to the offsetting increase in time available for foraging, the ease with which males can move within and defend their territories is likely enhanced by relatively bright conditions. Our results suggest the ability to detect and evade predators is also important when calling advertises location. This explanation is supported by the higher intensity of calling in response to conspecific calls following owl playbacks during the full moon, but an apparent reluctance to respond under similar circumstances during the new moon. Other relatively small nocturnal birds that are especially vocal when the moon is bright also have acute vision and rely heavily on vision to forage (e.g., Whip-poor-will). We surmise that visual acuity influences timing or extent to which smaller nocturnal animals vocalize at night. For nocturnal animals that may less easily detect and out-manuever predators, the increased risk of predation during the full moon selects for less activity. Gerbils (*Gerbillus* spp.) and other desert rodents, as well as Australian Owlet-Nightjars (*Aegotheles cristatus*), adjust foraging patterns to avoid bright moonlight and are all preyed upon by owls (Price et al. 1984, Brown et al. 1988, Kotler et al.

1994, Brigham et al. 1999). Notably, one male radio-marked poorwill was killed by an owl (*Otus* sp.) in our study. The bird was taken under relatively dim conditions when the moon was in its first quarter and setting. Whether specific predators and or predator foraging strategies are the major selective pressures which have shaped the differences in response to lunar conditions between caprimulgids and some rodents, remains to be understood.

Future research is needed with an emphasis on explaining the role of lunar illumination on behavior of other birds that are active at night, including those that are generally considered diurnal (e.g., Johnson et al. 2003). The lunar cycle is relatively short in comparison with the overall breeding season for most birds, and consideration of this variable could provide insight into foraging strategies and timing of breeding. Knowledge of the lunar phase and its effect on both foraging by and predation risk on nocturnal birds may also be an important consideration for surveying nocturnal species (Ganey 1990, Downs 1998). Additionally, our study sites were relatively distant from large urban centers and the light pollution associated with them. Light pollution could relieve some dependence on moonlight for efficient foraging by predators but, as a consequence, enhance predation pressure on their prey (Buchanan 2005, Frank 2005, Lloyd 2005). Perhaps more importantly, the loss of cyclic variation in nocturnal illumination may disrupt behaviors that evolved in association with regular fluctuation between bright and dark periods (Rich and Longcore 2005). Additional research into the impact of light pollution on the behavior of nocturnal animals is essential, considering the extent to which it has altered the night sky in many developed regions.

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