THE INFLUENCE OF MOONLIGHT ON THE BEHAVIOR OF GOATSUCKERS (CAPRIMULGIDAE)

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ABSTRACT.—Whip-poor-wills (*Caprimulgus vociferus*) showed significantly higher levels of locomotory, vocal, and nest activity during twilight and bright moonlight than under moonless conditions. Field observations and nest record card data indicated that *Caprimulgus* species usually synchronize their reproductive cycle with the lunar cycle. Hatching tends to occur during young waxing moons, presumably so that moonlight-enhanced foraging will be at a maximum while the dependent nestlings are an energy burden on the parents. Observations of foraging Whip-poor-wills suggest they are primarily visually oriented, unlike the bats (Chiroptera). *Received 26 March 1985, accepted 17 November 1985.*

MOST nocturnal flying insectivores are echolocating bats (Fenton 1974, 1984; Simmons and Stein 1980), but a significant though unknown proportion (15% by taxa) are non-echolocating birds, most of which are goatsuckers (Caprimulgidae) in the genus *Caprimulgus.*

Most male caprimulgids are conspicuous by their songs, and many accounts have reported increased singing in bright moonlight (e.g. Wynne-Edwards 1930, Brauner 1952, Cooper 1980, Bjorklund and Bjorklund 1983). This suggests that goatsuckers are moon-loving or lunarphilic, unlike the insectivorous bats, which appear to be lunarphobic or lunar-indifferent (Morrison 1978, Bell 1980, Anthony et al. 1981).

The purpose of this study was to see if caprimulgids, especially Whip-poor-wills (*Caprimulgus vociferus*), adjust locomotory (and hence feeding), vocal, and nest activities according to lunar conditions.

MATERIALS AND METHODS

Study site.—I conducted fieldwork near Rideau Lake Narrows (44°43′N, 76°17′W), eastern Ontario, May-July 1983 and 1984. This was a region of marginal farmland, forest, rock outcrops, and many small lakes, where both Whip-poor-wills and Common Nighthawks (*Chordeiles minor*) were common.

Lunar, solar, and meteorological conditions.—Percentages of moon face illuminated (%MFI), moon heights (measured in time), and times of sunrise, sunset, and various solar positions below the horizon are given in the Astronomical Almanac (e.g. Vohden and Smith 1983), as are correction formulae for coordinates. Because lunar light intensity increases with increasing %MFI and moon height (Bowden 1973), I grouped nights into 5 categories based on %MFI at midnight (0%, 1-25%, 26-50%, 51-75%, and 76-100%), and then subdivided them based on moon height (below the horizon, 1-100 min above the horizon, 101-200 min above, and 201-300 min above). Each 30 min during monitoring, I recorded cloud cover and wind strength based on a predetermined subjective scale of 0-3.

Locomotory activity.—Temporal patterns in the locomotory activity of Whip-poor-wills were monitored by radiotelemetry. The radio packages worn by the birds as backpacks averaged 4.9 g. The signals (173.8-174.1 MHz) were detected with a Merlin 12 (Custom Electronics, Urbana, Illinois) receiver operated with a directional 5-element Yagi antenna. Effective range varied from 500 to 1,000 m, and all transmitters performed for the entire field season.

Eleven birds (7 males, 4 females) were outfitted with radios. Two males disappeared and 1 female was found dying from an eye injury a week after being tagged. The 8 remaining birds were each tracked for 43-63 days. All 5 males held territories and all 3 females and 4 of 5 males fledged young while tagged.

Individual pairs were monitored from blinds near their nests. Readings, taken every 4 min, were defined in terms of distance (near, medium, far), as assessed by the intensity of the radio signal and the direction (1 o'clock through 12 o'clock). Any change from the preceding reading in distance or direction qualified as a move. In all, 14,782 telemetry readings were taken.

I distinguished periods of solar influence (twilight) from periods of lunar influence (night) by determining when moonlight (>25% MFI) began to influence activity after dusk and ceased to influence activity before dawn.

Instances of Whip-poor-will feeding sallies were recorded visually for distance and direction.

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I could tell when Common Nighthawks were active from their distinctive flight calls. I divided the night into 10-min census periods beginning at sunset and ending at sunrise (with an adjustment period midway of 0–9 min), and noted whether nighthawks were heard in each period.

Vocal activity.—The 5 radio-tracked males contributed equally to song activity. For each 10-min census period, I noted whether each monitored male sang 1–10 "Whip-poor-will" units, 11–100 units, 101–1,000 units, or not at all. These were respectively assigned scores of 1, 2, 3, and 0. Song counts were made in 2,865 10-min periods. I used movement results to distinguish twilight 10-min periods from night ones.

I also measured the levels of aggressive response by male Whip-poor-wills to taped song. Five locations along a prescribed route away from the telemetry site were used for solicitation trials. Care was taken to choose quiet times (wind category 0 or 1) and to spread the 15 test times (3 dusk, 3 dawn, 3 darkness, 6 moonlight) over the season to prevent habituation to the tape.

Each trial ($n = 75$) involved 4 repetitions of 15 s of song played at full volume on a portable cassette player followed by 15 s of silence. A positive vocal response required that the local male sing, and a positive visitation response required that the male either fly over the tape or land within about 10 m. A bird could respond after the 1st, 2nd, 3rd, or 4th 15-s presentation (or never), scoring 4, 3, 2, or 1 (or 0), respectively.

Because song tempo (the number of "Whip-poor-will" units per minute of unbroken song) might indicate an individual's level of arousal, I compared tempos under various light conditions.

Reproductive activity.—I monitored 5 successful nests of 4 radio-tagged pairs from blinds about 6 m away. During incubation, I recorded the number of times the incubating bird left the eggs (nest departures), either to feed or to allow a mate to assume incubation duties. After hatching, I recorded the number of times adults fed the nestlings (nest feedings). Nests were monitored for 14,690 min during incubation and for 22,431 min during the nestling period.

To assess the possibility of a synchronized relationship between the lunar month and goatsucker reproductive cycles, I collected 79 *Caprimulgus* nest records (from 38 different years) for which hatching dates were known or calculable. Whip-poor-will records came from Whedon (1906), Bailey (1912), Nauman (1925), Mousley (1937), Tyler (1940), Raynor (1941), Fowle and Fowle (1954), Kilham (1957), the Ontario Nest Records Scheme (ONRS), the Maritimes Nest Records Scheme (MNRS), the North American Nest Records Program (NANRP), and this field study. Other Temperate Zone *Caprimulgus* data came from Hewett (1883), Gurney (1883), Soppitt (1883), Corbin (1910), Lack (1930), and Berry and Bibby (1981) for European Nightjars (*C. europaeus*); from the South African Ornithological Society for *C. rufigena* and *C. pectoralis;* and from Sprunt (1940) and the NANRP for *C. carolinensis.* For the nighthawks (*Chordeiles minor* and *C. acutipennis*), similar data (74 records from 29 yr) came from the NANRP, the ONRS, the MNRS, the Prairie Nest Records Scheme, and the Quebec Nest Records Scheme. These data were pooled by genus.

I defined hatching dates in terms of days after the most recent full moon, and divided the lunar month into 10 3-day periods, such that the new and full moon dates were in the middle of 3-day periods. Periods, then, are days 2–4, 5–7, . . . , 26–28, 29–1. Because the last period is only 83% the length of the others (because the lunar month is actually 29.5 days), expected values in the statistical tests were adjusted accordingly.

Statistical analysis.—For each solar-defined and lunar-defined category, I generated scores for movement (percentage of radio readings that were moves), singing (percentage of theoretical maximum score), and nest departures and nest feedings (numbers per 1,000 observation minutes). Birds temporarily out of range as determined by telemetry and birds on nests were not included in calculating movement and singing scores. A 2 × 2 contingency table for solar and lunar conditions distinguished twilight periods from night periods.

Night scores were subjected to multiple regression and correlation analysis using dummy variables for the various categories and weighted according to sample size. Factors were %MFI, moon height, and cloud (0–1 clear, 2–3 cloudy) for movement; %MFI, moon height, and wind (0–1 calm, 2–3 windy) for song; and %MFI and moon height for nest activity.

Differences among twilight, bright moonlight, and darkness scores were tested using a Bonferroni Chi-square (Miller 1966). Vocal and visitation responses to taped song were analyzed for variance (ANOVA), and between-category scores were tested by the Student-Newman-Keuls procedure (SNK) (Sokal and Rohlf 1981). Song tempo measures were subjected to a Bonferroni t-test (Miller 1966), and a Chi-square test was used to test the data for synchrony between the lunar month and the reproductive cycle.

RESULTS

Locomotory activity.—On moonless nights Whip-poor-will activity appeared to end (dusk) and begin (dawn) when the sun was about 13° below the horizon. A contingency table for moonless and moonlit (>25% MFI) conditions verified this pattern for the periods when the sun was 10–13° and 13–16° below the horizon (Fig. 1). Moonlight influenced activity only when the sun was more than 13° below. At the

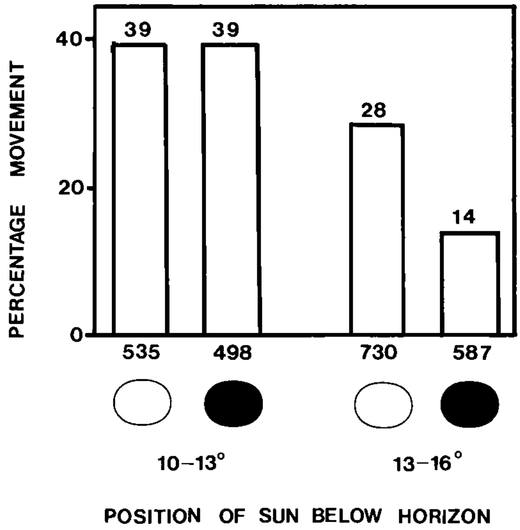

Fig. 1. The influence of moonlight on Whip-poor-will locomotory activity during the twilight-night transition. Percentage movement is the percentage of telemetry readings taken (total readings are given below each column) that were moves. Open circles represent moonlight conditions (>25% moon face illuminated) and closed circles represent moonless conditions. There was no lunar influence when the sun was 10-13° below the horizon, but the influence of the moon was significant for the 13-16° position ($\chi^2 = 35.5$, df = 1, $P < 0.005$).

other extreme, activity began (dusk) and ceased (dawn) when the sun was a few degrees below the horizon (Mills 1985). I will call the periods when the sun is between 4° and 13° below the horizon "crepuscular twilight."

Analysis of night telemetry data indicated that %MFI by itself was an adequate predictor of activity levels (Fig. 2A). Moon height appears to be a better predictor, but this is misleading due to the high correlation ($r = 0.87$) between moon height and %MFI. The latter is actually the better indicator because moons with high %MFI are as likely to be low in the sky as high, while all high moons have high %MFI. The coefficients of determination (derived from partial correlation coefficients) indicated that cloud cover, unlike %MFI and moon height, was not a significant factor (Table 1).

I compared activity levels among dusk, dawn, bright moonlight by %MFI (>75%), bright moonlight by height (>200 min above the horizon), and darkness (no moon). Because twilight activity occurred primarily during crepuscular twilight, dusk and dawn activity levels were derived from those periods. Each of the 5 contexts was unique statistically, with moonlight and twilight scores being greater than darkness scores (Fig. 3A).

I witnessed 60 sallies in 27 instances of Whip-poor-will feeding. Sallies were short ($\bar{x} = 2.2 \pm 0.1$ m) and were usually upward rather than outward ($\bar{x} = 71 \pm 4°$).

Nighthawks were recorded in 89 10-min periods. Seventy-five of these were during crepuscular twilight, and only 14 during the night. Twelve of the 14 occurred when the moon was up, a significant departure from random ($P = 0.014$; binomial probability). Ten of the 12 moonlight sightings were made in periods of 76% or more MFI.

Vocal activity.—Singing was a function of %MFI and moon height (Fig. 2B). The %MFI factor alone could predict amounts of night singing. Wind was not a significant determinant, whereas %MFI and moon height were highly significant (Table 1).

I compared singing levels among dusk, dawn, bright moonlight by %MFI, bright moonlight by height, and darkness, and found twilight levels comparable to those of bright moonlight (Fig. 3B). For dusk and dawn, I used peak periods of the third through ninth 10-min periods; this approximates crepuscular twilight.

Responses to taped song for dusk, dawn, moonlight (>50% MFI), and darkness are shown in Fig. 4. Only vocal responses indicated a nonrandom pattern (ANOVA $F_s = 4.79$, df = 3,11, $P < 0.05$), even though males never responded by visitation in darkness (ANOVA $F_s = 2.73$, df = 3,11, $0.05 < P < 0.10$). The overall response suggests that darkness is unsuitable for aggressive encounters.

An unmated male at the study site that sang more than the mated birds had mean tempos of 51.8 song units per min for twilight ($n = 10$), 50.5 for bright moonlight (>75% MFI; $n = 9$), and 39.2 for darkness ($n = 5$). Twilight and moonlight tempos were significantly greater than the darkness tempo (Bonferroni *t*-test, $P < 0.02$).

Reproductive activity.—Nest departures during incubation (Fig. 2C) and nest feedings later (Fig. 2D) indicated that activity levels increased with increasing %MFI and moon height. Percentage of MFI alone adequately predicted numbers of departures and numbers of feedings. Coefficients of determination are shown in Table 1.

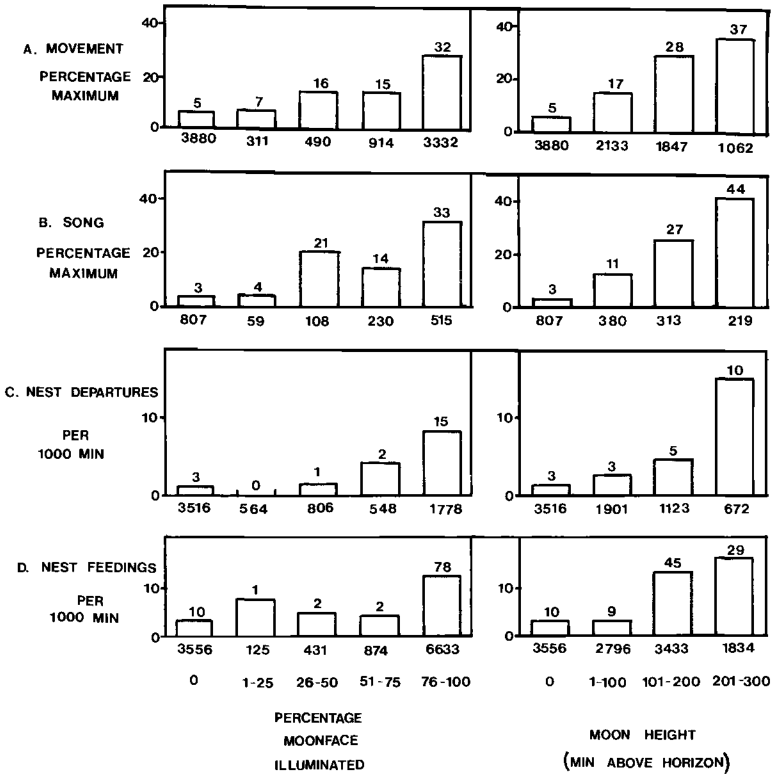

Fig. 2. The influence of percentage of moon face illuminated and moon height on Whip-poor-will movement (A), song (B), nest departures (C), and nest feedings (D) during the night. Sample sizes are shown below each column. Because departures and feedings are relatively rare events, numbers above columns in C and D are gross scores.

Nest departure and nest feeding activity, respectively, for dusk, dawn, bright moonlight by %MFI, bright moonlight by height, and darkness are presented in Fig. 3C and D. Twilight and moonlight levels were not statistically different for departures. There were significantly higher levels at dusk than at dawn or in moonlight for nest feedings. In both cases, darkness scores were significantly the smallest.

I examined the relationship between lunar

TABLE 1. Coefficients of determination from multiple partial correlation analyses for amount of movement, amount of song, numbers of nest departures, and numbers of nest feedings during the night. % MFI = percentage of moon face illuminated.

	Factor correlated with score	Coefficient of determination	F_s	df	P
Movement	% MFI	0.77	72.1	1,21	<0.005
	Moon height	0.83	101.2		<0.005
	Cloud	0.04	0.9		>0.25
Song	% MFI	0.61	24.8	1,16	<0.005
	Moon height	0.77	54.9		<0.005
	Wind	0.01	0.1		>0.25
Nest departures	% MFI	0.48	7.3	1,8	<0.05
	Moon height	0.66	15.3		<0.005
Nest feedings	% MFI	0.44	6.4	1,8	<0.05
	Moon height	0.77	27.5		<0.005

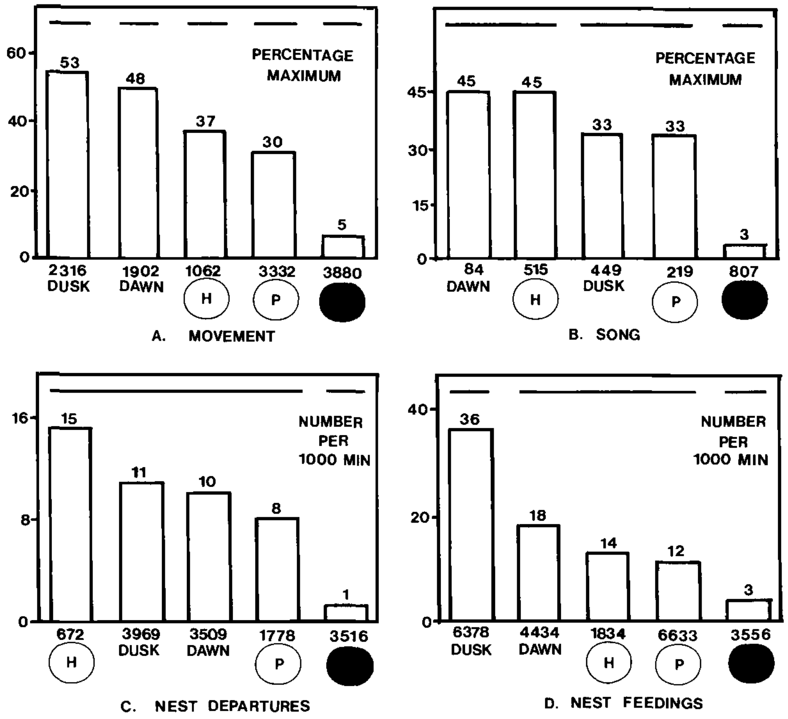

Fig. 3. Comparisons of Whip-poor-will activities during dusk, dawn, bright moonlight by percentage of moon face illuminated (P), bright moonlight by height (H), and darkness (closed circles). Sample sizes are shown below each column. Breaks in lines above histograms indicate statistical differences (Bonferroni Chi-square test; $P < 0.05$).

phase and hatching date for *Caprimulgus, Chordeiles*, and a random-number data set (Fig. 5). Only *Caprimulgus* exhibited a synchrony between the reproductive and lunar cycles (χ^2, df = 9; Fig. 5). Hatching was centered around 10 days before a full moon, a time when a waxing moon is about 25% illuminated.

The young I observed usually made their first flights in their third week, and the youngest I saw make a feeding sally was 18 or 19 days old. Although the young fed themselves by age 30 days, they still accepted food from the parents. According to Harrison (1975), European Nightjars are independent at age 31-34 days.

DISCUSSION

Lunarphilia in goatsuckers.—My result indicates that conditions most suitable for foraging and territorial behavior occur during twilight and periods of bright moonlight. Moonlight also enhanced goatsucker song.

Caprimulgids are not known to echolocate, and birds that do apparently use echolocation only for orientation in caves (Griffin and Thompson 1982, Fenton 1984). The use of acoustic cues for finding food is well documented in some nocturnal predators such as owls and bats (Payne 1971, Konishi 1973, Bell 1982), but a captive Common Poorwill (*Phalaenoptilus nuttallii*) feeding on flying moths did not respond until an insect came into the visual field (Brauner 1953). My field observations of upward-directed sallies suggest that Whip-poor-wills find food by exploiting backlit insect targets.

Goatsucker eyes have numerous elongated rods as well as tapeta lucida, which indicates extreme light sensitivity (Nicol et al. 1974). Nonetheless, reduced foraging in darkness probably is due to visual constraints rather than to changes in insect availability.

Most insects are lunarphobic (Williams and Singh 1951, Bowden and Church 1973), and only a few are lunarphilic (Kerfoot 1967, Jahn 1982) or lunar-indifferent (Blair 1982, Snow 1982). Moths, apparently the favorite food of Whip-poor-wills (Tyler 1940) and Common

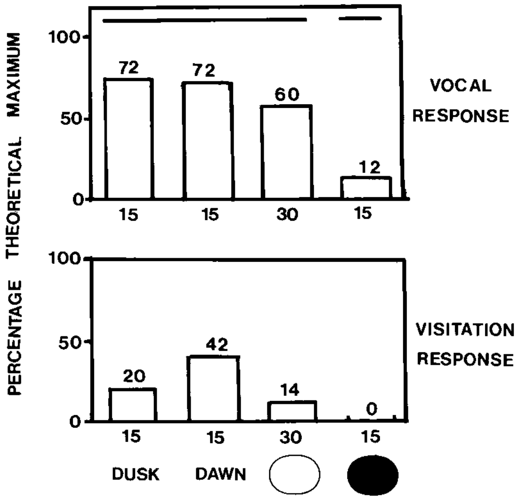

Fig. 4. Vocal and visitation responses of male Whip-poor-will territory holders to intrusion (taped song). Percentage theoretical maximum is the strength of the response based on the scoring system. Open circle represents moonlight conditions (>50% MFI) and closed circle represents darkness. Numbers of test trials are shown below each column. Break in the line above vocal response columns indicates statistical differences (SNK test).

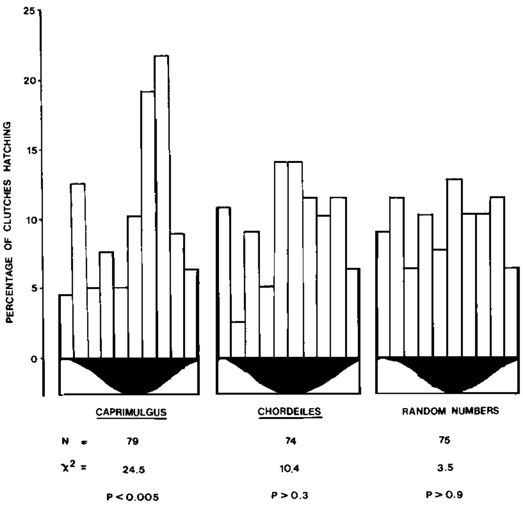

Fig. 5. Relationships between lunar phase and hatching date (N = number of clutches) for *Caprimulgus*, *Chordeiles*, and a data set generated from random numbers. Lunar cycle is indicated by contrasting sine wave below each histogram.

Poorwills (Brauner 1952), are mostly lunarphobic (Morton et al. 1981, De Abreu 1982, Banerjee and Mondal 1983, Stradling et al. 1983). Evidently, for improved foraging success, increased light levels in moonlight more than compensate for reduction in insect numbers.

The weak territorial responses of Whip-poor-wills in darkness may occur simply because darkness is relatively unsuitable for territorial encounters. It is also possible that temporary torpor occurs during the dark periods of the night because birds exhibit short-term body temperature fluctuations (Siegfried et al. 1975, McNab 1983) and because goatsuckers readily enter torpor (Bartholomew et al. 1962, Ligon 1970, Withers 1977).

For *Caprimulgus*, the first 2 weeks after egg hatching are the most sensitive for nestling survival (Fig. 5), although the fifth and sixth weeks one lunar month later, when the young gain independence, also may be important. I suggest that selection has favored parents that synchronize the first 2 weeks of the nestlings' lives with the greatest amount of moonlight for foraging. As the lunar month enters the following dark half, the developing independence of the young alleviates the burden on the parents, and as the cycle enters the next bright half, the improved foraging conditions allow the young to become completely independent.

The hatching of clutches at times other than those of maximal moonlight may be due to the inexperience of young parents (Perrins 1970) or to failures of first clutches. After a nest fails, the parents may not wait the better part of a lunar cycle to begin again, especially at temperate latitudes where the breeding season is short. *Chordeiles* probably show no tendency to synchronize the reproductive cycle with the lunar month because they are partially diurnal.

Data for 7 pairs of double-brooded European Nightjars (Lack 1930) indicate a mean of 31.3 ± 0.4 days from first egg to first egg. The one double-brooded Whip-poor-will pair in my study began clutches 33 days apart. These figures are consistent with the possibility that consecutive broods are one lunar month (29.5 days) apart so that both broods are in phase with lunar cycling, although this could be fortuitous. American Goldfinches (*Carduelis tristis*) average 33.7 days (Stokes 1950) and Cedar Waxwings (*Bombycilla cedrorum*) 29.8 days (Putnam 1949) between consecutive clutches. However, the young of the first goatsucker clutch are still dependent (the male assumed responsibility in Lack's cases and in mine) when the second clutch is laid, indicating there is some urgency in starting the second clutch.

Chapin and Wing (1959) suggested that Sooty Terns (*Sterna fuscata*) on Ascension Island used the moon as a regulator and began a breeding cycle every 10 lunar months. Their data were reinterpreted by Ashmole (1963), who rejected the lunar hypothesis. Other than in terns and goatsuckers, lunar influence on avian reproductive cycles is generally ignored (Murton and Westwood 1977).

At the equator, crepuscular twilight lasts at most for 39 min, while at my study site it lasts as long as 84 min. Therefore, the potential for exploitation of twilight by lunarphilic species decreases nearer the equator, while that for moonlight (because of longer nights) increases. Patterns of lunarphilia may be strongest in equatorial regions.

Bats and nocturnal birds.—Worldwide there are almost 700 species of animal-eating bats, mostly insectivorous (Fenton 1982). Nocturnal obligate insectivorous birds comprise 91 species in 3 families (Clements 1981): potoos (Nyctibiidae), owlet-nightjars (Aegothelidae), and goatsuckers. Some of the approximately 140 owl species and probably some of the 13 frogmouth species (Podargidae) also eat flying insects at night. Only about 15% of the world's vertebrate nocturnal flying insectivore taxa are birds.

The general lunarphobia or lunar-indifference exhibited by most insectivorous bats is not surprising, because the majority uses echolocation in at least part of the food detection process (Fenton 1982). Echolocation, by circumventing the need for light, may seem superior to vision as a method of prey detection. Fenton and Fleming (1976) suggested this holds only for small insectivores, however, and costs of echolocation such as warning sonar-sensitive potential prey (Miller and Oleson 1979, Fenton and Fullard 1979) and atmospheric attenuation (Griffin 1971) may favor vision in some cases.

Evidence for interactions between birds and bats is scarce. Shields and Bildstein (1979) found that vespertilionid bats appeared to dominate Common Nighthawks in aggressive encounters at a food source localized at a light. Most flying insects probably are not defensible as food, however (Brown 1964). This, and the subdivision of the nocturnal flying insectivore niche through differences in size, foraging strategies, and sensory modalities, may reduce the potential for bird-bat competition.

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