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

by

ALEXANDER MATTHEW MILLS, B.Sc.

A thesis submitted to the Faculty of
Graduate Studies and Research in partial fulfilment
of the requirements for the degree of
Master of Science

Department of Biology
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Ottawa, Ontario.
February 7, 1985

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ABSTRACT

The influence of moonlight on the nocturnal behaviour of goatsuckers (Caprimulgidae) was studied. For the whip-poor-will (Caprimulgus vociferus), radio telemetry, singing patterns, and patterns of activity at nests indicate that twilight and bright moonlight represent periods of peak activity, while moonless conditions are periods of relative inactivity. Cloud doesn't significantly reduce lunar influence.

Species of the genus Caprimulgus usually synchronize their reproductive cycle with the lunar cycle. Egg hatching occurs 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.

In accord with their lunarphilic behaviour, whip-poor-will foraging observations indicate that they are primarily visually-oriented. The lunarphobic or lunar-indifferent activity patterns of the other major group of nocturnal flying insectivores, the bats (Chiroptera), are not surprising, since they are largely non-visual foragers.

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INTRODUCTION

In the past four decades, echolocation in bats (Chiroptera) has been the subject of intensive research (e.g. Griffin 1946, 1958; Suthers 1965; ~~Simmons~~ et al 1979; Simmons and Stein 1980; Fenton 1984). The collective body of knowledge resulting from this work is a testament to the sophistication and implications of bat sonar, and the domination by bats of the nocturnal flying insectivore realm is probably attributable to these echolocation abilities (Fenton 1974). Nonetheless, about 15% of the vertebrate taxa in this realm are another cosmopolitan group, the nocturnal insectivorous birds, organisms that coexist with bats wherever they are found. There is no evidence that these birds echolocate, and consequently the behavioural and ecological differences between the two groups are of interest.

Most nocturnal insectivorous birds are in the Caprimulgidae (Van Tyne and Berger 1976), a family of about 78 species known as goatsuckers or nightjars (Clements 1981). About 90% of the species are in the cosmopolitan subfamily Caprimulginae, while the remainder are in the New World subfamily Chordeilinae (nighthawks). The former tend to use a sallying mode of foraging and are more strictly nocturnal; the latter use a hawking foraging strategy and are more crepuscular (Bent 1940). Sixty percent (46 species) of all caprimulgids are in the genus Caprimulgus, making it the third largest genus of nocturnal flying insectivores in the world (after Myotis and Rhinolophus: Microchiroptera).

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The nocturnal habits and cryptic plumages of Caprimulgids have rendered them difficult to study. The common poor-will (Phalaenoptilus nuttallii) has attracted attention due to its ability to hibernate (Jaeger 1948, 1949; Howell and Bartholomew 1959; Withers 1977), but very little work has been done on the behavioural ecology of goatsuckers. The most conspicuous quality in most species is the loud night-jarring song of the male, and most natural history accounts focus on this aspect of their behaviour or on daytime nest observations. Many accounts have noted an increase in goatsucker song in bright moonlight (e.g. Wynne-Edwards 1930; Newman 1983; Bjorklund and Bjorklund 1983) and Cooper (1980) investigated the relationship systematically. Vocal activity, at least, suggests that goatsuckers are moon-loving or lunarphilic. Though there is little information, the insectivorous bats appear to be lunarphobic or lunar-indifferent (Fenton et al 1977; Bell 1980; Anthony et al 1981).

By direct observation and by inference from their behaviour, my aim was to determine whether goatsuckers are primarily visually-oriented and, if so, to determine to what extent their visual abilities are limited. I predicted that moonlight should influence not only song but also movement, activity at the nest, and reproductive cycles. I established several quantitative indices of activity (locomotory, vocal, and reproductive) for the whip-poor-will (Caprimulgus vociferus) and evaluated these indices in terms of varying light conditions associated with both lunar and solar factors.

MATERIALS AND METHODS

Study Animals

Except for incidental observations on common nighthawks (Chordeiles minor), all field work was done on the whip-poor-will. The whip-poor-will weighs about 60 g and its cryptic plumage of various shades of brown and gray provides excellent camouflage against the ground where it usually roosts. The species' most obvious feature is the male's loud vigorous song consisting of incessantly repeated "whip-poor-will" notes.

Unlike the nighthawks, undisturbed whip-poor-wills are never active when the sun is above the horizon, and they feed by sallying rather than by hawking. Whip-poor-wills breed from central and eastern Canada into Central America (Godfrey 1966) in semi-open forest. They build no nest but lay two eggs on the leaf litter at wood edges.

Other species of Caprimulgus as well as another Chordeiline were used in testing the relationships between the lunar cycle and the reproductive cycle.

Study Site

In 1983, I conducted field work from 10 June to 6 August at a site on the north shore of Big Rideau Lake, Lanark County, Ontario (44°43'N, 76°17'W; 18UE-980514 31 C/9). The rocky surface here produced a patchy forest of red cedar (Juniperus virginiana), oak

(Quercus spp.), basswood (Tilia americana), shagbark hickory (Carya ovata), and maple (Acer spp.), with ground juniper (Juniperus communis) dominating the shrub layer.

Logging of this site the following winter necessitated changing to a new site, 3.5 km away, for the 1984 season. From 15 May to 22 July, 1984, two assistants and I conducted field work at this new site on the south shore of Upper Rideau Lake, United Counties of Leeds and Grenville, Ontario (18UE-970484). This area is mostly old farmland, now partly overgrown with forests of hop hornbeam (Ostrya virginiana), oak, maple, basswood, American beech (Fagus grandifolia), and shagbark hickory. Ground juniper and brambles (Rubus spp.) are common ground cover plants.

We used a third site nearby for solicitation trials.

Lunar, Solar, and Meteorological Information

Sunrise and sunset are formally defined as the time when the sun is 50' of arc below the horizon. These times, with correction formulae for particular latitude/longitude coordinates, are provided in the Astronomical Almanac (e.g. Vohden and Smith 1983) and its various predecessors. Similarly, the times when the sun is 6°, 12°, and 18° below the horizon are also provided with correction formulae for coordinates, and linear interpolation will allow calculation of the time for any other position within this range.

To test whip-poor-will locomotory activity during twilight, each twilight was divided into five categories based on the sun's

position below the horizon: 50° - 4° , 4° - 7° , 7° - 10° , 10° - 13° , and 13° - 16° .

Lunar conditions were defined in terms of percentage moonface illuminated (%MFI) and height of moon above the horizon (measured in min of time). Percentages MFI are available in the Astronomical Almanac, as are correction formulae for longitude coordinates and time of day or night. Times of moonrise and moonset, together with correction formulae for coordinates, are also available in the Astronomical Almanac.

I calculated %MFI for midnight each night and used that value for the whole night. I defined sampling periods based on %MFI: 0% (below the horizon), 1-25%, 26-50%, 51-75%, and 76-100%. For each of these, I also made subdivisions based on the height of the moon: below the horizon, 1-100 min above the horizon, 101-200 min above, 201-300 min above, and 301-400 min above. Because low %MFI moons tend to be up during the day while high %MFI moons tend to be up during the night and because of the sine nature of the curve describing %MFI, certain categories defined by this system are rarer than others (some are non-existent). Also, this means that most high moons are also high %MFI moons, though the converse is not true. The full moon was above the horizon for about 524 min in 1983 and for about 508 min in 1984.

Moons increasing %MFI over consecutive nights are known as waxing moons, while those decreasing %MFI over consecutive nights are known as waning moons. The lunar cycle (new moon to new moon) lasts 29.53 days.

Each half-hour during monitoring, I recorded cloud cover and wind strength based on a predetermined subjective scale of 0, 1, 2,

or 3. For analysis, values of 0 and 1 were considered clear or calm, while values of 2 and 3 were considered cloudy or windy. Moon brightness is not just a function of height, percentage illuminated, and cloud, but the other factors like distance of the moon, nature of the part illuminated, and humidity I've considered negligible.

For each index of activity I looked at (locomotory, vocal, and reproductive), conditions could be described in terms of position of the sun below the horizon (during twilight), of %MFI and height of the moon above the horizon (during the night), of wind, and of cloud.

Locomotory Activity

To investigate temporal patterns in the locomotory activity of whip-poor-wills I used radio telemetry. The tags used consisted of the radio circuitry, a lithium battery, a 12 cm whip antenna, and a harness; 1984 tags averaged 4.9 (range 4.8 to 5.1) g, whereas 1983 tags averaged about 5.8 g. The harness consisted of two elastic hairbands knotted together in a figure-eight pattern. When birds were outfitted with the tags, the hair bands were slipped over the wings, one per wing, so that the bird wore the package as a backpack (Fig. 1).

The transmitters were designed to transmit in the 173.800 to 174.075 MHz range. Signals were picked up with a Merlin 12 (Custom Electronics, Urbana) radio receiver operated with a directional 5-element Yagi antenna. Each radio-tag transmitted at a unique frequency and consequently each bird could be identified

by using the channel selector on the receiver. Effective transmitter range varied from 500 to 1000 m and their effective life exceeded the duration of the field season (i.e. over two months).

I induced males into mist nets at night by playing tapes of territorial song, and I captured females by day by flushing them from nests into mist nets. The time of hitting the net to the time of being released with a radiopackage was usually about 1 min.

Individual whip-poor-will pairs were monitored from blinds set up about 5 m from each pair's nest. Readings taken every 4 min were arbitrarily defined in terms of distance (near, medium, far) as assessed by the intensity of the radio signal, and direction (1 o'clock through 12 o'clock). I was interested in whether or not the bird had moved in the preceding 4 min, and any change in distance or direction qualified as a move. A bird moving during the reading, as evidenced by a panning signal direction or an obvious irregularity in signal intensity (a function of the whip antenna), also counted as a move.

In deriving movement scores, the number of moves for all birds for each solar-defined or lunar-defined context was divided by the number of possible moves (the number of readings taken). Birds on nests and birds temporarily out of range were not included in the calculations.

Common nighthawks were present in small numbers at the study site and we could tell if they were active only when their distinctive flight calls were heard overhead. I divided the night up into 10-min census periods beginning at sunset and ending at

sunrise (with an adjustment period midway of 0 to 9 min). We merely noted whether or not we heard nighthawks in each 10-min period.

Vocal Activity

Territorial behaviour was primarily investigated by censussing the singing of the males whose nests we were monitoring. Identification of the singer could be confirmed by location, distinctive song pattern, and telemetry. I divided the night up into 10-min census periods as described for nighthawks above. For each period, we noted whether the monitored male sang 1-10 "whip-poor-will" units, 11-100 units, 101-1000 units, or not at all. These were respectively attributed scores of 1, 2, 3, and 0.

In deriving vocal scores, the individual scores were summed for each solar-defined or lunar-defined context and divided by the possible maximum (3 times the number of 10-min periods each bird was monitored for). Birds on nests and birds temporarily out of range as determined by telemetry were not included in the calculations.

For each 10-min period, we also noted whether or not the resident female sang. (Females sing a much less vigorous, "scratchy," and little-repeated song).

To complement the data collected while monitoring the singing of territorial birds, I also measured the levels of aggressive response of male whip-poor-wills to taped song, similar to the method used by Ickes and Ficken (1970). A prescribed route away from the telemetry site was chosen, and 5 locations along this

route were used for solicitation trials. Care was taken to choose quiet times (winds of 0 or 1 on the 0-3 scale) and to keep the 15 test times (75 trials) spread out over the season so that acclimation to the tape would not be a serious problem.

Each trial involved four repeats of 15 s of song played at full volume on a portable cassette player followed by 15 s of silence. Consequently, each test lasted 2 min. Vocal and visitation responses were the two modes of response measured. A positive response for the former required that the local male sing, and for the latter a positive response required that the bird either fly over the tape or come in and land within about 10 m. A respondent could respond never (score 0) or after any of the four 15 s presentations; responses after the first, second, third, and fourth presentations respectively merited scores of 4, 3, 2, and 1. For each trial, a score of 4 was the maximum in both vocal and visitation response; i.e., scores were not additive.

Thinking that song tempo--the number of "whip-poor-will" units per minute of unbroken song--might indicate an individual's level of arousal, I made comparisons between the tempos of birds before being subjected to intrusion (taped song) and after, as well as comparisons for individual birds under various light conditions.

Reproductive Activity

We found the nests of radio-tagged pairs and monitored activity from blinds about 5 m away. In 1983, the one nesting female was equipped with a LED light-tag of similar design and weight to the radio-tag.

We measured nest activity during incubation by recording the number of times the incubating bird left the nest (nest departures), either to feed or to allow a mate to assume incubation duties. After the eggs hatched, we measured activity by recording the number of times adults fed the young (nest feedings). When an adult visited the nestlings, we assumed that it fed them; the feeding cries of the young by about the third day of life or direct observation usually confirmed this.

In deriving reproductive activity scores, the numbers of departures or the numbers of feedings for all nests were summed for each solar-defined or lunar-defined context and were expressed as a rate (number per 1000 min of nest monitoring).

To assess the possibility of a synchronized relationship between lunar cycle and the reproductive cycle of goatsuckers, I collected nest records for which hatching dates of the first egg were known or calculable within two days' certainty. For the whip-poor-will, these records came from this field study, from the Ontario Nest Records Scheme (ONRS) (Royal Ontario Museum, Toronto), the Maritimes Nest Records Scheme (MNRS) (Canadian Wildlife Service, Sackville), the North American Nest Records Program (NANRP) (Cornell University, Ithaca), and the literature (Whedon 1906; Bailey 1912; Nauman 1925; Mousley 1937; Tyler 1940; Raynor 1941; Fowle and Fowle 1954; Kilham 1957). Data for the nightjars (Caprimulgus spp.) came from Hewett (1883), Gurney (1883), Soppitt (1883), Corbin (1910), Lack (1930), and Berry and Bibby (1981) for C. europaeus and from the South African Ornithological Society (SAOS) for C. rufigena and C. pectoralis. Chuck-will's-widow (C.

carolinensis) data came from Sprunt (1940) and the NANRP. For the nighthawks (Chordeiles spp.), similar data came from the NANRP, the ONRS, the MNRS, the Prairie Nest Records Scheme (Manitoba Museum of Man and Nature, Winnipeg), and the Quebec Nest Records Scheme (National Museums of Canada, Ottawa) for C. minor and from the NANRP for C. acutipennis. These data were pooled by genus (Caprimulgus and Chordeiles).

Three control groups were also prepared. These included similar data from the ONRS and NANRP for a non-insectivorous nocturnal bird, the American woodcock (Scolopax minor), and for a diurnal bird, the vesper sparrow (Pooecetes gramineus), as well as a data set generated from random numbers.

If laying dates only were known, I calculated hatching dates by adding a certain number of days to the laying of the first egg (19 for the whip-poor-will (pers. obs.), 20 for the chuck-will's-widow (H. Harrison 1975), 19 for C. europaeus (Berry and Bibby 1981), 16 for C. rufigena (SAOS), and 17 for C. pectoralis (SAOS)); or the last egg (19 for the nighthawks (NANRP), 18 for the woodcock (NANRP), and 13 for the vesper sparrow (NANRP).

I defined hatching dates in terms of days since the most recent full moon. To ensure that expected values were at least five, the lunar month was divided into six 5-day periods, such that the new moon and the full moon dates were in the middle of 5-day periods. Thus, the 5-day periods are days 3-7, 8-12, 13-17, 18-22, 23-27, and 28-2. Since this last period is only 90% the length of the others (since the lunar cycle is really only 29.5 days), expected values in the statistical tests were adjusted accordingly.

Dates for lunar phases for the various years were extracted from the Astronomical Almanac and its various predecessors.

Feeding Observations

All instances of feeding we witnessed were recorded for date, time, sally distance, sally direction (angle above horizon), perch height, and perch description. Stomach contents records on labels of museum specimens were collated.

Migration Schedules

To see if lunar conditions influence whip-poor-will migration, arrival dates for the whip-poor-will in eastern Ontario were extracted from the records of the Kingston Field Naturalists and The Ottawa Field-Naturalists' Club. As for the hatching date data, arrival dates were defined in terms of days since the most recent full moon. The same 5-day periods were used.

Data Pooling and Statistical Analysis

For telemetry, singing, nest departures, and nest feedings, data were pooled for all birds, regardless of sex, and for all nests. I felt my sample population was too small to divide it based on sex, and I noticed no difference between locomotory responses of males and of females. For each solar-defined or lunar-defined context (sometimes with wind and cloud factors considered), then, one score has been calculated.

To test the influence of %MFI, height of moon, wind, and cloud on night scores, scores were subjected to multiple linear regression and correlation analysis (weighted according to variations in sample size) using dummy variables for the various %MFI, height, cloud, and wind categories.

When serial pairwise t-tests or χ^2 -tests were used, I applied the Bonferonni procedure (Miller 1966) in correcting alpha levels. Where possible, results of statistical tests are presented in figures and tables and not in the text.

RESULTS

General Information

Three males were outfitted with radio tags in mid-June, 1983, and between 17 May and 8 June 1984, four males and four females were similarly outfitted. Two of the 1983 males promptly disappeared, and one 1984 female was found dying a week after being outfitted, having suffered an eye injury. Consequently, telemetry data were derived from the activities of eight birds, five males and three females. These were each tracked for anywhere from 43 to 63 days. All five males held territories and all three females and four of five males successfully raised young while radio-tagged. In all, 14,782 telemetry readings were taken.

Data for singing activity came from the five radio-tracked males, each bird contributing about a fifth to the total sample. In all, song counts were made in 2,865 10-min periods.

Seven nests were found, but two were deserted. In one case this was because the female died; in the other the female abandoned the nest where we captured her but re-nested nine days later. Nest data then, come from five nests (four pairs), all of which successfully fledged young. During incubation, nests were monitored for a total of 14,690 min, and during the nestling period the figure was 22,431 min.

In all, 80 all-night man-vigils and 78 part-night man-vigils produced this data base.

The locomotory, vocal, and reproductive indices used to assess whip-poor-will activity were subjected to similar analyses, and except for minor details, the results of each are similar as well. Where the results of vocal and reproductive indices echo those of the locomotory index, I report only the essentials, and focus on the peculiarities of each index.

Locomotory Activity

For further analysis, I first distinguished periods of solar influence (twilight) from periods of lunar influence (night). On moonless nights, whip-poor-will activity appeared to end when the sun was about 13° below the horizon; this pattern was mirrored in the morning. To verify this observation, I pooled all data for the period when the sun was 10° to 13° below the horizon into two categories: moonless and moonlit ($>25\%$ MFI). I did the same for the period during which the sun was 13° to 16° below the horizon (Fig. 2). Comparison showed that moonlight had no influence on the activity levels in the 10° to 13° period, but it significantly enhanced activity during the 13° to 16° period. The moonless 13° to 16° activity level is still marginally higher than the moonless night average, so twilight conditions suitable for whip-poor-will activity may end slightly after (dusk) or begin slightly before (dawn) the 13° figure. Nonetheless, 13° as a threshold value is about as sensitive a measure possible. I will call the periods when the sun is between $50'$ and 13° below the horizon "crepuscular twilight."

At the other extreme, activity appeared to begin (dusk) and end (dawn) when the sun was a few degrees below the horizon. The dusk mean time occurred when the sun was $2.8 \pm 1.0^\circ$ below the horizon ($n=76$ evenings), while the dawn mean time occurred when the sun was $3.6 \pm 1.0^\circ$ below the horizon ($n=61$ mornings). These two solar positions reflecting activity thresholds are different ($t=5.2$; $d.f.=135$; $P<.001$).

Multiple regression analysis of the night telemetry data for %MFI, moon height, and cloud cover indicates that the %MFI factor by itself can adequately predict activity levels ($F_5=72.1$; $d.f.=1,21$; $P<.005$), though moon height and %MFI influences are difficult to separate since they themselves are highly correlated ($r=.87$). Increasing %MFI or increasing moon height results in increases of activity (Fig. 3). The coefficients of determination (derived from partial correlation coefficients) shown in Table 1a indicate that cloud, unlike %MFI and moon height, is not a significant factor.

All twilight telemetry data were pooled into cloud periods and clear periods. Cloud had no influence on the amounts of movement ($\chi^2=1.4$; $d.f.=1$; $.30>P>.20$) and did not advance the onset of movement in the evening ($\chi^2=7.7$; $d.f.=4$; $.20>P>.10$) or delay the cessation of movement in the morning ($\chi^2=2.1$; $d.f.=4$; $.80>P>.70$).

Comparing dusk and dawn scores reveals that there is significantly more movement at dusk (42.9% of 3329 radio readings were moves) than at dawn (38.2% of 2594) ($\chi^2=13.2$; $d.f.=1$; $P<.0005$). Patterns of activity for dusk and dawn are the same when considered in terms of solar position, but are different when

considered in terms of temporal sequence (Fig. 4). That is, dusk patterns are mirrored at dawn.

Finally, I compared activity scores among dusk, dawn, darkness (no moon), bright moonlight by %MFI (>75%), and bright moonlight by height (>200 min above the horizon). Since peak twilight activity occurs when the sun is between approximately 4° and 13° below the horizon (Fig. 4), dusk and dawn scores used in this analysis were derived from those periods. Each of the five contexts is statistically unique, with the twilight and moonlight scores all being greater than those in darkness (Fig. 5).

We noted nighthawks at the study site on 89 occasions. Seventy-five of these were during crepuscular twilight, leaving only 14 sightings during the night. Twelve of these sightings occurred when the moon was up, a significant departure from random (binomial probability; $P=.014$). Ten of the 12 moonlight sightings were made in periods of 76% or more MFI. Though nighthawks tend to be crepuscular, moonlight enhances night activity.

Vocal Activity

Since crepuscular twilight lasts almost 100 min at the summer solstice at 44°N , I used the first ten 10-min census periods in the evening and the last ten in the morning as twilight periods, while all other 10-min periods were considered night periods.

The %MFI factor can by itself predict amounts of night singing ($F_{1,16}=24.8$; $d.f.=1,16$; $P<.005$), according to multiple regression analysis of %MFI, moon height, and wind. Wind is not a significant

coefficient of determination, whereas %MFI and moon height are highly significant (Table 1b). As for movement, the greater the %MFI or the higher the moon, the more singing there is (Fig. 6).

Fig. 7 presents singing scores for dusk and dawn. Unlike the patterns indicated in locomotory activity, the dusk-dawn patterns are the same when considered in terms of temporal sequence but are different when considered in terms of position of the sun. There is more song at dawn (33.6% of theoretical maximum score for 538 10-min periods) than at dusk (25.8% for 642 periods) ($\chi^2=25.6$; d.f.=1; $P<.0005$).

I compared singing levels among dusk, dawn, darkness, bright moonlight by %MFI, and bright moonlight by height (as for telemetry scores), and found twilight levels comparable to those of bright moonlight (Fig. 8). For dusk and dawn, I used peak periods of the third through ninth 10-min periods; this approximates the period when the sun is between 4° and 13° below the horizon.

Females were heard singing on 45 occasions; only eight of these were not in twilight periods. Seven of these eight occurred when the moon was up (always 51% or more MFI), and though this is indicative of agreement with other results presented so far, it is not statistically different from random (binomial probability; $P=.074$).

Fig. 9 shows the vocal and visitation responses to solicitation for dusk, dawn, moonlight (>50% MFI) and darkness expressed as percentages of theoretical maxima. Analysis of variance indicates a non-random pattern in vocal response, but a random pattern in visitation response. The latter, however, is probably related to the fact that visiting the tape by a respondent

is a relatively rare event, something not adequately assessed by inferential statistics; note that in all three nights that solicitations were made in darkness, not one bird ($n=15$) responded by visiting the tape. Ten of the 12 other test times (moonlight and twilight) had at least one bird (and usually more) respond by visiting the tape. For the vocal responses, SNK tests indicate that among the dusk, dawn, and moonlight scores there are no significant differences, while darkness scores are significantly less than those at dusk, dawn, or in moonlight. Thus, vocal response (and probably locomotory response) as an indicator of potential aggressiveness suggests that conditions of darkness are relatively unsuitable for aggressive encounters.

I assume that there are no seasonal effects complicating the solicitation data. Most trials took place in June and even the moonlight ones as late as 12 July elicited strong vocal response. Radio-tagged birds elsewhere were still having singing contests with neighbours in mid-July.

I found no evidence that song tempo is indicative of level of aggressiveness. Five of the six birds used to investigate this sped up after hearing taped songs, but the difference between the means was not significant ($t=.9$; $d.f.=10$; $.20 > P > .10$).

One male on the study site in 1984 did not replace a mate that had died in late May. This unmated condition induced more singing in this individual, and only he provided enough opportunity to look at differences in tempo among the various lunar-defined and solar-defined contexts. His mean tempos for twilight ($n=10$), bright moonlight ($>75\%$ MFI; $n=9$), and darkness ($n=5$) were 51.8, 50.5, and

39.2 song units per minute, respectively. The twilight and moonlight tempos are not statistically different, but both are significantly greater than the darkness tempo (Bonferonni t-test; $P < .02$). Tempos measured from this bird as dawn approached on 2 July (Fig. 10) also indicate an increase in tempo as light levels increase.

Reproductive Activity

Monitoring departures from the nest during incubation (Fig. 11) and feedings of the nestlings later (Fig. 12) indicates increasing activity levels with increasing %MFI and increasing moon height. Multiple regression analyses for %MFI and moon height indicate that %MFI can adequately predict numbers of departures ($F_S = 7.3$; d.f.=1,8; $P < .05$) and numbers of feedings of the nestlings ($F_S = 6.2$; d.f.=1,8; $P < .05$). Coefficients of determination are shown in Table 1c and 1d.

Figures 13 and 14 graphically present departures from the nest and feedings of the nestlings, respectively, for dusk, dawn, bright moonlight by %MFI, bright moonlight by height, and darkness. Twilight and moonlight scores are not statistically different for departures; for feedings of the nestlings, there are significantly higher levels at dusk than at dawn or in moonlight.

Seventy-nine Caprimulgus hatching dates for two North American, two African, and one European species representing 38 different years were collected. Similarly, 74 Chordeiles, 43 American woodcock, and 53 vesper sparrow hatching dates

representing 29, 14, and 21 years respectively were collected. The large numbers of years in each case allays concern about season effects.

Grouped results shown in Fig. 15 have been standardized. Only Caprimulgus shows a distribution significantly different from random, indicating that it is the only one of the five that exhibits a synchrony between reproductive cycle and lunar cycle. Hatching is clustered around 20 days after the most recent full moon, a time at which a waxing moon is about 25% illuminated. Grouping the data in any of the four other 5-day period combinations doesn't alter the results; only Caprimulgus differs significantly from random, and hatching is clustered around three weeks after the most recent full moon.

Of the five whip-poor-will pairs I studied, only one definitely laid a second clutch after hatching a first (began 14 days later), so it isn't possible to measure the possible relationship between lunar phase and the timing of multiple clutches. Two of the other four pairs didn't have a chance to lay a second clutch after hatching a first, since in one case the female died and in another the first clutch was deserted just before hatching. Also, one of the remaining two cases was of a nest in July (the latest ever for Ontario), so it itself may have been a second clutch.

Where we could tell, the young usually made their first flights in their third week, and the youngest one we saw make a feeding sally was 18 or 19 days old. However, in one of the nests there was a tremendous difference between the two young (which is

not unusual for birds laying only two eggs), and the second young took about five weeks to reach the stage the first one had reached in three. Also, though the young were feeding themselves by 30 days, they were still accepting food from the parents as well.

Feeding Observations

Over the course of the study, we witnessed 27 instances of feeding amounting to 60 sallies. Sallies were short and were usually upward rather than outward (Table 2). We noticed no evidence of sallies being most often directed towards the brightest part of the sky.

Most sallies we witnessed were at dusk, but this probably reflects a bias due to our own visual limitations.

Migration Schedules

Forty-four whip-poor-will arrival dates for eastern Ontario since 1885 were found. The large number allays concern about season effects. Grouped results shown in Fig. 16 reveal a random pattern, suggesting that arrival date is not related to moon phase.

DISCUSSION

Lunarphilia in Goatsuckers Manifested in Movement

Radio telemetry has been used in many studies of vertebrate behaviour. Among those with bird subjects, researchers usually claim no or negligible influence (Imboden 1975; Siegfried et al 1977; Raim 1978; Martin and Bider 1978; Royall and Bray 1980) although a few have found significant differences in the behaviours of tagged and non-tagged individuals (Ramakka 1972; Greenwood and Sargeant 1973; Dufty 1982). I found no evidence to suggest that the tags seriously influenced whip-poor-will behaviour; all five monitored males held territories and survived the duration of the study and all three females successfully fledged young. If the tags did reduce locomotory activity, I assume that the influence was uniform over all light conditions.

The nocturnal whip-poor-will moves more in bright moonlight and twilight than in periods of relative darkness, and the essentially crepuscular common nighthawk, when active at night, is more active in bright moonlight. Brauner (1952) showed that poor-wills were active for longer periods if there was a significant amount of moonlight as twilight merged into night; however, it's not clear what his measure of activity was. If goatsuckers are visually-oriented predators, lunarphilia is not surprising. In full moon conditions, there can be over 200 times the amount of

ambient light that there is under moonless conditions (Bowden 1973).

In addition to their large eyes, goatsuckers have tapeta lucida, typical of nocturnal animals, that give them a strong reflected eyeshine (Van Rossem 1927; Nicol et al 1974). Furthermore, in goatsuckers as in owls, the rods are more numerous than cones and are particularly long and thin (Welty 1975). Brauner (1953) observed a captive poor-will feeding on flying moths and noted that the bird did not respond until the insect came into the visual field. That some nocturnal predators like bats and owls partly depend on hearing for finding food is well documented (Payne 1971; Konishi 1973; Bell 1982), but it remains to be seen if goatsuckers do the same. Caprimulgids are not known to echolocate, and those birds that do (Apodidae, Collocalia; Steatornithidae, Steatornis) appear to use echolocation only for orientation in caves (Griffin 1954; Medway 1967; Fenton 1975; Griffin and Thompson 1982).

Despite the importance of vision and consequent importance of moonlight, whip-poor-wills do move at night when there is no moon, but they do not move very much. Though the reduction in movement is doubtless primarily due to reduced foraging profitability, it is also manifested in terms of territorial behaviour. In the solicitation experiments, territorial males often investigated the tape in the moonlight trials but never in the darkness trials.

Since night feeding rates of the nestlings increase with increasing moonlight and since these periods are coincident with periods of most movement, movement is at least partly related to

foraging. My observations of whip-poor-will feeding behaviour are in agreement with those reported by others (e.g. Tyler 1940), in that the usual method of feeding is by sallying out from perches after specific targets. We saw birds sallying from perches at ground level and above, and Sutton and Burleigh (1940) reported a record of a whip-poor-will feeding at over 20 m. There is some evidence based on personal observation and on stomach contents (Tyler 1940; de Kiriline Lawrence 1974) that these birds sometimes glean from ground or foliage, and in one case an assistant saw a flying bird deviate from its course as hawking species do.

Insects in many orders are consumed by whip-poor-wills (Tyler 1940; Royal Ontario Museum labels), and chuck-will's-widows are known to occasionally eat small birds (Sprunt 1940) and to sally after bats (Denton 1967). I saw whip-poor-wills sallying after and eating tiny insects, but they also eat the large saturniid moths (Lepidoptera) (Tyler 1940). Eaton (in Tyler 1940) collected a whip-poor-will at dusk and found 36 large moths in the stomach. At the study site, the most common June insects were caddisflies (Trichoptera), but I don't know the extent to which they were used by the birds as a food source.

Morse (1971) pointed out the importance of considering insect activity patterns in space and time when considering patterns of insectivorous birds. The fact that whip-poor-wills feed less in darkness than in twilight or bright moonlight suggests that there is less foraging opportunity in darkness. Although I have so far attributed this lessening of foraging opportunity to visual

limitations, the possibility of an insufficient insect supply should not be overlooked.

The influence of moonlight on insect activity patterns is complex, and problems are compounded by sampling biases. With this caveat in mind, the general consensus among entomologists is that most insects are lunarphobic (Williams and Singh 1951; Bowden and Church 1973), though some taxa are lunarphilic or lunar-indifferent (Table 3).

This variety of responses suggests that under any given lunar circumstances at least some taxa are available. This, in combination with the catholic diet of the whip-poor-will and the almost uniform lunarphobic response of moths--apparently the whip-poor-will's favourite food--supports the claim that increased activity of the birds in moonlight is certainly related to visually-oriented opportunity and not to insect availability.

Nighthawks tend to feed on smaller insect fare than whip-poor-wills (Gross 1940; Caccamise 1974), though the biomass consumed can be just as great or greater (Blem 1972). The fact that we rarely noted nighthawks between dusk and dawn is not surprising. Unlike whip-poor-wills, they are often active before sunset, and occasionally in mid-day. Caccamise (1974) found that nighthawks sometimes consume large amounts of food well before sunset.

Lunarphilia in Goatsuckers Manifested in Song

Whip-poor-wills sing more and at faster tempos in bright moonlight and twilight than in periods of relative darkness. High

levels of song, therefore, are coincident with high levels of movement. This is consistent with many anecdotal accounts that claim that goatsuckers regularly travel song perch routes circumscribing their territories (Bolles 1912; Coale 1920; Hersey 1923; Tyler 1940; de Kiriline Lawrence 1974; Cadbury 1981), and with reports that goatsuckers begin singing as soon as they become active (Wynne-Edwards 1930; Orr 1948; Brauner 1952).

Most ecological or behavioural work centering on goatsuckers has focussed on song (Wynne-Edwards 1930; Brauner 1952; Mengel and Jenkinson 1971; Mengel et al 1972; Cooper 1980; Cadbury 1981; Bjorklund and Bjorklund 1983), and in several cases the relationship between lunar circumstances and song has been considered. Cooper (1980) used call counts along a prescribed route through whip-poor-will and chuck-will's-widow territories and tested the influence of seven variables (date, sine date, temperature, humidity, visibility, wind velocity, and moon phase) on song; only moon phase and calendar date showed significant correlations with numbers of singing birds. For moon phase and numbers of singing birds, Cooper found a significant positive correlation, though only the whip-poor-will correlation was significantly different from zero when the two species were treated independently. These data weren't used to test for moon height as a contributing factor.

It has been shown for the whip-poor-will (Cleaves 1945; Bjorklund and Bjorklund 1983), the chuck-will's-widow (Sprunt 1940; Mengel and Jenkinson 1971), the European nightjar (Wynne-Edwards 1930), the fiery-necked nightjar (C. pectoralis) (A. Mills; unpubl.

data), and the poor-will (Brauner 1952), that moonlight enhances song. Cadbury (1981) discounted moonlight as an enhancing factor for the European nightjar, but he monitored only at twilight.

Though they didn't define the term, Bjorklund and Bjorklund (1983) also pointed out that moonlight enhances the vigour of whip-poor-will song. If they mean tempo, then this is in agreement with my findings. Mengel and Jenkinson (1971) rejected Harper's (1938) claim that song tempo in the chuck-will's-widow is related to temperature and Bjorklund and Bjorklund (1983) noted no influence of temperature on whip-poor-will song. Stoner (1920) and Bjorklund and Bjorklund (1983) both reported that wind does decrease whip-poor-will vocal activity.

It has been known for many decades that light is only one important factor related to the onset of dawn song in diurnal birds (Schwan 1920). Reproductive stage and date are also important, as are a variety of endogenous rhythms (Daan 1976). Fowle and Fowle (1954) noticed that whip-poor-will song commencement at dusk could more accurately be predicted by clock time than by a particular light level. I found that the times of song cessation at dawn relative to light levels differed from those of song commencement at dusk, and I also found that the patterns of song amount at dawn were different from those at dusk regarding light levels. Light measures at any time between sunset and sunrise are obviously not the only determinants of the amount of song activity.

Several workers have discussed the question of why passerine birds sing more at dawn than at dusk (e.g. Kacelnick and Krebs 1983; Montgomerie 1984). My data indicate the same pattern for the nocturnal whip-poor-will and consequently suggest that low acoustic

attenuation (Henwood and Fabrick 1979), low foraging profitability at dawn (Avery and Krebs 1984) or possibly the threat of overnight invasion (Kacelnick and Krebs 1983) may be the contributing factors; the notion that males sing more after long fasts to indicate good physical condition is not supported. Adult whip-poor-wills move more and feed the young more at dusk, supporting the idea of lower foraging profitability at dawn.

Moonlight influences singing activity of diurnal passerines. Wright (1913) found that moonlight advances song commencement for some species at dawn, and R.M.R. Barclay (pers. comm.) and I (unpubl. data) have noted a higher incidence of night song among a variety of North American passerines when there is moonlight.

Vocal responses to taped solicitations are weaker in darkness than in moonlight or twilight, even though ability to sing should not be directly influenced by light levels. If vocal response indicates a bird's willingness to make a locomotory response, then the weak vocal response in darkness is understandable. An alternative explanation may be that temporary torpor occurs during the dark periods of the night, it being well known that many birds exhibit body temperature fluctuations over 24-hour periods (Siegfried et al 1975; McNab 1983) and that goatsuckers readily enter torpor (Bartholomew et al 1962; Withers 1977; Ligon 1970).

Lunarphilia in Goatsuckers Manifested in Breeding

Adult whip-poor-wills leave the nest more and feed the nestlings more in bright moonlight and in twilight than in periods of relative darkness. Goatsuckers of the genus Caprimulgus

synchronize their reproductive schedules with lunar phase and they may also synchronize their migration schedules with lunar phase. Chordeiles, being less strictly nocturnal, does not synchronize reproductive with lunar cycles.

Many accounts chronicling changes and circumstances at goatsucker nests exist (Whedon 1906; Dubois 1911; Nauman 1925; Lack 1930; Aldrich 1935; Mousley 1937; Tyler 1940; Raynor 1941; Orr 1948; Fowle and Fowle 1954; Kilham 1957; Moulton 1957; Berry 1979; Berry and Bibby 1981), but only Raynor (1941) and Orr (1948) include observations during the birds' activity periods. Of those, only Raynor made non-twilight observations (one night), but he couldn't draw any conclusions about lunar influence.

The correlations between bright moon and nest departures and between bright moon and feedings of the nestlings are strong evidence of lunar influence. The evident synchrony between reproductive and lunar schedules, however, is even more telling of lunar influence and appears to be unique among birds; Murton and Westwood's (1977) "Avian Breeding Cycles" doesn't even mention moonlight. A similar situation has been presented by Chapin and Wing (1959), however, who showed that for 18 consecutive years the colony of sooty terns (Sterna fuscata) on Ascension Island (8°S, 14°W) began a breeding cycle every 10 lunar months. They believed that the moon was used by the birds only as a regulator in an equatorial region where the potential for solar cues was minimal, and pointed out that after the birds had gathered at the island the production of eggs, incubation, and the gathering of food for the chicks all went ahead regardless of lunar phase. In this case then

(unlike Caprimulgus), the moon is important only as a zeitgeber and not for any direct reasons.

The patterns revealed in Fig. 15 suggest that for the breeding cycle of Caprimulgus there is a most sensitive time in the lunar cycle, regarding the welfare of the young. It is difficult to tell from nest observations, however, when the most stressful period in breeding occurs. Because the parents feed the young by regurgitation, the amount of feeding is not necessarily directly related to the number of feedings per night, unlike the case with most passerines. We also found it difficult to say when fledging occurs because independence is attained quite gradually. Though not precocial, whip-poor-wills are not altricial either. Within a few days after hatching, the young usually have moved or have been moved a meter or more from the initial nest position. Thereafter, the nest position tends to change daily (Mousley 1937; Tyler 1940; Raynor 1941; Orr 1948; Fowle and Fowle 1954), due at least partly to independent movements by the young. C. Harrison (1975) gives 16-18 days as the time of first flight for the European nightjar, and in this study I found it impossible to capture a volant 18 day old whip-poor-will.

With these considerations in mind, the pattern in Fig. 15 suggests that for Caprimulgus the first two weeks after egg hatching are the most sensitive for nestling survival, although it is possible that the fifth and sixth weeks one lunar month later are the most sensitive, since this is when the young gain independence. Natural selection has favoured those parents that

time reproduction to synchronize the first two weeks of the nestlings' lives with the periods of best foraging opportunity regarding moonlight. As the lunar cycle enters the following dark half, the developing independence of the young alleviates the burden on the parents. As the lunar cycle enters the next bright half, the improved foraging conditions should allow the young to become completely independent. European nightjars are independent at 31-34 days (C. Harrison 1975).

The hatching of clutches at times other than the "ideal" may be due to inexperience of young parents (Perrins 1970) or more likely to predation or failure of a first clutch. After a nest fails, the parents may not wait the better part of a lunar cycle to begin again, especially where the species live at temperate latitudes where the breeding season is short.

Fowle and Fowle (1954) and Raynor (1941) each gave daily weight measures for one nest; Raynor's clutch hatched four days after the full moon and the Fowles' 17 days after. The two are thus out of phase, but no differences are obvious; both sets of young exhibited patterns of decreasing gain:weight ratios with time. Only a large sample would be sensitive enough to assess the differences, if any, between new moon hatching and full moon hatching clutches.

Lack (1930) showed that the European nightjar is sometimes double-brooded and the data for the seven pairs presented by him indicate a mean time between the hatch of the first clutch and the laying of the first egg of the second clutch of $12.3 \pm .4$ days. If

you add to this figure the standard incubation period of 19 days, we have a between-clutch time of 31.3 days or almost exactly one lunar cycle (29.5 days). This allows consecutive clutches both to be in phase with the lunar cycle. For my one double-brooded whip-poor-will pair the between-clutch time was 33 days, reasonably in agreement with the one lunar cycle per clutch hypothesis. Obviously, this approximately 30-day period between clutches could be fortuitous. However, the young of the first clutch are still dependent (the male assumed responsibility in both Lack's cases and mine) when the second clutch is laid, indicating that there is some urgency in getting the second clutch begun.

Berry and Bibby (1981) listed 11 instances for European nightjar pairs where they knew the date of male arrival in the spring and the date when the first egg was laid. The mean time between the two events was 17.2 ± 1.4 days. This suggests that males tend to arrive during the new moon, since the birds tend to lay their clutches at the time of the full moon and since there are just over two weeks between new moon and full moon. In 1984, the time between the arrival of the first male whip-poor-wills and the first egg of five nests was 14 days. However, I found no statistical evidence that migration times are influenced by moon phase (Fig. 16), though the arrival dates available were derived from casual observations only. Since foraging profitability is low during the dark phases of the moon, it makes most sense to use this time migrating, rather than those periods that offer the best foraging opportunities.

The considerations relating to laying date, nestling independence, and double-broodedness lead to the idealized picture shown in Fig. 17.

Patterns of Lunar Influence in Other Animals

There are many examples of lunar influence in marine organisms, particularly invertebrates. In most cases, evidence for bimodal activity patterns through one lunar cycle is presented (e.g. Hastings 1981; Middaugh 1981; Tsai et al 1981; Iliffe and Pearse 1982; Cohen and Brockmann 1983; Doherty 1983) and since there are usually two spring tides (dramatic high tides) in each lunar cycle, these manifestations of lunar influence in marine situations are certainly related to the influence of tides and not to the influence of illumination.

As for insects, vertebrates exhibit a variety of responses to moonlight (Table 4). Most studies have focussed on small rodents, a group that is invariably lunarphobic. In a surprising number of studies of nocturnal animal activity patterns, the influence of moonlight hasn't been considered at all. Examples include bats (Brown 1968), northern flying squirrels (Glaucomys sabrinus) (Ferron 1983), northern saw-whet owls (Aegolius acadicus) (Forbes and Warner 1974), and barred owls (Strix varia) (Nicholls and Warner 1972). Sick and Teixeira (1981) showed that several species of typically diurnal hummingbirds (Trochilidae) and tyrant flycatchers (Tyrannidae) become active at night in the presence of bright artificial illumination.

Considering all of the patterns shown in Table 4, it appears that predators are lunarphilic and prey are lunarphobic. Obviously, many organisms are both predators and prey, and sometimes the response to moonlight can be ambiguously interpreted. Trillmich and Mohren's (1981) seals, land bound in moonlight, may be responding as predators or as prey. Whip-poor-wills are potential prey for nocturnal predators, but the costs of avoiding predation by being lunarphobic (poor foraging opportunities) are far outweighed by the benefits of being lunarphilic (excellent foraging opportunities). The lunarphobia in non-insectivorous bats is usually attributed to predator avoidance (Morrison 1980), though Turner (1975) related reduction in vampire bat (Desmodus rotundus) activity to activity patterns of its victims.

For the whip-poor-will, twilight is just as important an activity period as bright moonlight, and this is probably also the case for all lunarphilic organisms. At the whip-poor-will study site (44°N), crepuscular twilight at the summer solstice lasts 94.5 min. At the equator, however, where other goatsuckers as well as other lunarphilic organisms live, crepuscular twilight lasts 52.5 min at the most (summer and winter solstices). This means that breeding crepuscular creatures at 44°N experience twilight conditions for about 1.8 times as long as crepuscular creatures at the equator. For visually-oriented nocturnal birds, it is reasonable to assume then that the moon is an even more significant factor in equatorial regions where twilight is brief.

Many lunarphobic creatures are active in twilight when illumination is sometimes greater than in moonlight. Owings and Handa (1975) have suggested that the key difference is that

predators can make use of moon shadows, of which there is no equivalent during twilight. In support of this, they showed that the presence of shadows significantly improves capture success in burrowing owls (Athene cunicularia).

Bats and Birds as Nocturnal Flying Insectivores

Worldwide there are almost 700 species of animal-eating bats, most of which feed predominantly on insects (Fenton 1983). Nocturnal obligate insectivorous birds comprise three families, the potoos (Nyctibiidae), the owlet-nightjars (Aegothelidae), and the goatsuckers. According to Clements (1981), the number of species in these three families is 91, 46 of which are in the genus Caprimulgus. Some of the world's approximately 140 species of owls, and probably some of the 13 species of frogmouths (Podargidae) as well, sometimes eat flying insects at night. Probably about 15% of the world's nocturnal flying insectivore taxa are birds.

Among bat biologists, the general consensus is that insectivorous bats are lunarphobic, but Morrison (1978) pointed out that the data from mist-netting that have promoted this idea could be as easily interpreted as increased visibility of the net in moonlight instead of the usual explanation of reduced bat activity. Anthony et al (1981) found that little brown bats (Myotis lucifugus: Vespertilionidae) were lunar-indifferent regarding time spent in roosts, and Bell (1980) noted no quantitative effect of moonlight on several desert vespertilionids. Fenton et al (1977) found that Scotophilus viridis (Vespertilionidae) foraged within

the canopy on a clear moonlit night but above the canopy on a subsequent cloudy night. At the present time, no general conclusion can be drawn about the influence of moonlight on insectivorous bats.

Two differences of ecological and behavioural importance between insectivorous bats and the nocturnal insectivorous birds are obvious. All insectivorous bats can echolocate and most if not all use echolocation in at least part of the food acquisition process (Fenton 1982). There is no evidence that the nocturnal insectivorous birds use echolocation. Second, all nocturnal birds weigh more than 30 g while most bats (>85% in any fauna) weigh less than 30 g (Fenton 1974). These two differences combine to suggest that echolocation is a more efficient mode of prey detection for small insectivores while vision is more efficient for larger ones (Fenton and Fleming 1976).

That many insects are sensitive to bat echolocation calls is now well established (Roeder and Treat 1960; Miller and Oleson 1979; Fenton and Fullard 1979), and this cost of echolocation in reducing bat foraging success has been discussed by Fenton (1980). In addition, the utility of echolocation is severely limited by range (Griffin 1971). Visually-oriented insectivores such as goatsuckers don't suffer these problems, and the problem of alerting prey may be especially important when one considers that moths, apparently the favourite food of whip-poor-wills (Tyler 1940; de Kiriline Lawrence 1974) and a favourite of poor-wills (Brauner 1952) are especially sensitive to echolocation calls and are thus especially evasive in the presence of foraging bats.

Evidence for competitive interactions between birds and bats is scarce. Apart from anecdotal reports of apparent interactions, only Shields and Bildstein (1979) have treated the question systematically. They investigated the foraging behaviour and interactions of vespertilionid bats and common nighthawks at a food source localized at a light. They found that the bats appeared to dominate the birds in aggressive encounters. In addition, the nighthawks appeared to expend more energy in foraging when bats were present, and the bats were less restricted to the light. In contrast, Fenton et al (1980) witnessed no interactions between the same groups at a riverine food source. At the whip-poor-will study site, we netted long-eared bats (Myotis septentrionalis: Vespertilionidae) at dusk and saw foraging hoary bats (Lasiurus cinereus: Vespertilionidae) at dusk and dawn, but no bird-bat interactions were noted. In short, there is some potential for bird-bat competition, but this is probably reduced by the indefendability of flying insects as a food source (Brown 1964), and by subdivision of the nocturnal flying insectivore niche through size differences, sensory differences, foraging strategy differences, and food preference differences.

Conclusions

The evidence presented indicates that whip-poor-wills in particular and goatsuckers in general are distinctly lunarphilic. Though this is the first study investigating lunar influence on several behavioural attributes of birds, its evidence is added to a number of studies of both vertebrates and invertebrates whose data

argue for a variety of lunarphilic, lunarphobic, and lunar-indifferent patterns. Lunarphilia in goatsuckers indicates that they are visually-oriented predators inhabiting a niche where they use nocturnal insects as food but require sufficient light to secure that resource.

SUMMARY

1. Twilight conditions suitable for whip-poor-will activity occur when the sun is between approximately 3° and 13° below the horizon.
2. During the night, whip-poor-wills move more, sing more, leave the nest more, and feed the young more with increasing %MFI (percentage moonface illuminated) and increasing moon height.
3. Twilight levels of whip-poor-will movement, singing, and activity at the nest are similar to those of bright moonlight at night.
4. Whip-poor-will song tempo is faster in bright moonlight and in twilight than in darkness.
5. Cloud cover doesn't significantly reduce whip-poor-will movement and wind doesn't reduce amount of song.
6. Common nighthawks are primarily crepuscular but when active at night they are most active in moonlight.
7. Species of the genus Caprimulgus synchronize their breeding cycle with the lunar cycle, with clutches tending to hatch during young waxing moons.

8. There is no evidence that whip-poor-will migration schedules are influenced by lunar cycling.
9. Whip-poor-wills usually capture prey by making short sallies from perches for specific targets. Sallies are directed more upward than outward.

TABLES AND FIGURES

Table 1.

Coefficients of determination derived from multiple partial correlation analyses for amount of movement (a), amount of song (b), numbers of nest departures (c), and numbers of nest feedings (d) during the night.

Table 1.

	Factor Correlated with Score	Coefficient of Determination	F _s	Degrees of Freedom	Significance
(a) Movement	%MFI moon height cloud	.77 .83 .04	72.1 101.2 .9	1, 21	P<.005 P<.005 P> .25
(b) Song	%MFI moon height wind	.61 .77 .01	24.8 54.9 .1	1, 16	P<.005 P<.005 P> .25
(c) Nest Leavings	%MFI moon height	.48 .66	7.3 15.3	1, 8	P< .05 P<.005
(d) Nest Feedings	%MFI moon height	.44 .77	6.4 27.5	1, 8	P< .05 P<.005

Table 2.

Distances, angles, and perch heights for whip-poor-will feeding sally observations. Sally perches had varying degrees of canopy cover.

Table 2.

	Sample Size	Mean
Estimated Distance	59	$2.2 \pm .1$ m
Estimated Angle Above Horizontal	39	$71 \pm 4^\circ$
Perch Height	26	$2.2 \pm .6$ m

Table 3.

Insect responses to moonlight. Studies used light traps (1), suction traps (2), intercept traps (3), food harvesting (4), and nest activity (5).

Table 3.

Taxa	Philic	Phobic	Indiff.	Method of Study	References
Lepidoptera					
Noctuidae					
<u>Heliothis punctiger</u>			+	(1)	Morton et al 1981
<u>Heliothis armiger</u>	+			(1)	Morton et al 1981
<u>Agrotis</u> spp.			+	(1)	Blair 1982
<u>Catocala</u> spp.		+		(4)	R. M. Runtz, pers. comm.
Sphingidae					
various spp.		+		(1)	Stradling et al 1983
<u>Erinnyis ello</u>		+		(1)	De Abreu 1982
Pyralidae		+		(1)	Banerjee and Mondal 1983
Coleoptera					
Scolytidae	+			(4)	Jahn 1982
Diptera					
Ceratopogonidae	+			(3,1)	Barnard and Jones 1980; Song 1983
Culicidae			+	(2,1)	Snow 1979, 1982; Nasci and Edman 1981
Hymenoptera					
Halictidae	+			(4,5)	Kerfoot 1967

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Table 4.

Responses of various vertebrates to moonlight. Studies used observation (1), censuses (2), photographic or automatic recorders (3), nets (4), sand transects (5), telemetry (6), road kills (7), roost observations (8), food harvesting (9), and simulation in experimental chambers (10).

Table 4.

Taxa	Response	Method of Study	References
American Toad (<u>Bufo americanus</u>)	Phobic	(5)	Fitzgerald 1974
Tawny Owl (<u>Strix aluco</u>)	Indifferent	(6)	Nilsson 1978
Kangaroos and Wallabies (Macropodidae)	Philic	(7)	Ooulson 1982
Egyptian Fruit Bat (<u>Rousettus aegyptiacus</u>)	Phobic	(10,8)	Erkert 1976; Herzig-Straschil and Robinson 1978
Phyllostomid Bats	Phobic	(3,4,6,8,9)	Crespo et al 1972; Heithaus et al 1974; Turner 1975; Heithaus and Fleming 1978; Morrison, 1978, 1980
Night Monkey (<u>Actus trivirgatus</u>)	Philic	(10)	Erkert 1976
Red Fox (<u>Vulpes vulpes</u>)	Philic	(9)	Kruuk 1964
Springhare (<u>Pedetes capensis</u>)	Phobic	(2)	Butynski 1984
Kangaroo Rats (<u>Dipodomys</u> spp.)	Phobic	(3,9)	Lockard and Owings 1974; Kottler 1984
Woodland Jumping Mouse (<u>Napaeozapus insignis</u>)	Phobic	(5)	Vickery and Bider 1981
Cribetid Rodents (various genera)	Phobic	(3,5,9,10)	Pearson 1960; Owings and Lockard 1971; Jahoda 1973; Vickery and Bider 1981; Kottler 1984
Desert Mouse (<u>Peromyscus eremicus</u>)	Philic	(10)	Owings and Lockard 1971
Roe Deer (<u>Capreolus capreolus</u>)	Indifferent	(1)	Turner 1980
Galapagos Fur Seal (<u>Arctocephalus galapagoensis</u>)	Philic	(1)	Trillmich and Mohren 1981

Figure 1.

A whip-poor-will outfitted with a 4.9 g radio transmitter.

Figure 2.

The influence of moonlight on whip-poor-will locomotory activity during the twilight-night transition. Percentage movement is the percentage of radio readings taken (numbers above each bar) that were moves. Open circles represent moonlight conditions (>25% MFI) and closed circles represent moonless conditions. There is no lunar influence when the sun is 10° - 13° below the horizon, but the influence of the moon is significant for the 13° - 16° position ($\chi^2=35.5$; d.f.=1; $P<.005$).

Figure 3.

The influence of %MFI (a) and moon height (b) on whip-poor-will movement. Percentage movement is the percentage of radio readings taken (numbers above each bar) that were moves.

Figure 4.

Whip-poor-will movement during twilight. Percentage movement is the percentage of radio readings taken that were moves. Patterns are the same by light conditions ($\chi^2=1.5$; d.f.=4; $.9 > P > .8$) but are different by temporal sequence ($\chi^2=11.4$; d.f.=4; $P < .025$). The 13⁰-16⁰ categories represent only moonless conditions.

Figure 5.

Comparison of whip-poor-will movement during dusk, dawn, bright moonlight by %MFI (>75% MFI) (%), bright moonlight by moon height (>200 min above horizon) (HT), and darkness (closed circle). Percentage movement is the percentage of radio readings taken (numbers above each bar) that were moves. Line above histogram indicates, by breaks, where statistical differences exist (Bonferonni χ^2 -test; $P < .05$)

Figure 6.

The influence of %MFI (a) and moon height (b) on amount of whip-poor-will song. Percentage theoretical maximum is the amount of song as determined by the scoring system. Number above each histogram bar indicates the number of 10-min periods.

Figure 7.

Amount of whip-poor-will song during twilight. Percentage theoretical maximum is the amount of song as determined by the scoring system. Patterns are different by light conditions ($\chi^2=27.4$; d.f.=9; $P<.0005$) but are the same by temporal sequence ($\chi^2=15.3$; d.f.=9; $.10>P>.05$).

Figure 8.

Comparison of amounts of whip-poor-will song during dusk, dawn, bright moonlight by %MFI (>75% MFI) (%), bright moonlight by height (>200 min above horizon) (HT), and darkness (closed circle). Percentage theoretical maximum is the amount of song as determined by the scoring system. Number above each histogram bar indicates the number of 10-min census periods. Line above the histogram indicates, by breaks, where statistical differences exist (Bonferonni χ^2 -test; $P < .05$).

Figure 9.

Measures of vocal response (a) and visitation response (b) 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. Number above each histogram bar indicates the number of presentations for each of dusk, dawn, moonlight (>50% MFI) (open circles), and darkness (closed circles). Vocal response is a non-random pattern (AOV $F_3=4.79$; d.f.=3,11; $P<.05$) though visitation response is not (AOV $F_3=2.73$; d.f.=3,11; $.10>P>.05$). Line above the histogram in (a) indicates, by breaks, where statistical differences exist (SNK test).

Figure 10.

Song tempos (number of song units per minute of unbroken song) of an unmated male whip-poor-will as dawn approached on 2 July, 1984.

Figure 11.

The influence of %MFI (a) and moon height (b) on the numbers of times incubating whip-poor-wills left nests. Number above each histogram bar indicates the number of minutes of nest monitoring. Only 21 nest departures were witnessed during the night for the five nests, and gross scores are indicated in the tops of the histogram bars.

Figure 12.

The influence of %MFI (a) and moon height (b) on numbers of times parent whip-poor-wills fed nestlings. Number above each histogram bar indicates the number of minutes of nest monitoring. Ninety-three feedings were witnessed during the night for the five nests, and gross scores are indicated in the tops of the histogram bars.

Figure 13.

Comparison of numbers of times incubating whip-poor-wills left the nest during dusk, dawn, bright moonlight by %MFI (>75% MFI) (%), bright moonlight by height (>200 min above horizon) (HT), and darkness (closed circle). Number above each histogram bar indicates the number of minutes of nest monitoring. Line above the histogram indicates, by breaks, where statistical differences exist (Bonferonni χ^2 -test; $P < .05$).

Figure 14.

Comparison of numbers of times parent whip-poor-wills fed the nestlings during dusk, dawn, bright moonlight by %MFI (>75% MFI) (%), bright moonlight by height (>200 min above horizon) (HT), and darkness (closed circle). Number above each histogram bar indicates the number of minutes of nest monitoring. Line above the histogram indicates, by breaks, where statistical differences exist (Bonferonni χ^2 -test; $P < .05$).

NEST
FEEDINGS
PER
1000 MIN

CONTEXT

Figure 15.

Relationships between lunar phase and hatching date (N clutches) for Caprimulgus, Chordeiles, a non-insectivorous nocturnal bird (American woodcock), a diurnal bird (vesper sparrow), and a data set generated from random numbers. Percentage number of clutches indicates what proportion of clutches hatches in each of the six 5-day periods of the lunar cycle. Closed circles and open circles respectively show where new and full moons occur. χ^2 -tests reveal that only Caprimulgus exhibits a non-random relationship (d.f.=5; $P<.005$).

Figure 16.

Relationships between lunar phase and whip-poor-will arrival dates in eastern Ontario (44 years). The lunar cycle is divided ~~into~~ six 5-day periods. Closed circles and open circles respectively show where new and full moons occur. Though more arrival dates are during new moons, the overall pattern is not significantly different from random ($\chi^2=12.8$; d.f.=5; $.3 > P > .2$).

Figure 17.

Idealized picture of a Caprimulgus breeding season as it relates to lunar cycling. Consecutive clutches are one lunar month apart, and broods take about one lunar month to become independent.

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