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Influence of Lunar Cycle on Laying Dates of European Nightjars (*Caprimulgus europaeus*)

C. M. PERRINS[1] AND H. Q. P. CRICK[2,3]

[1] *Edward Grey Institute of Field Ornithology, Department of Zoology, South Parks Road, Oxford OX1 3PS, United Kingdom; and*

[2] *British Trust for Ornithology, The National Centre for Ornithology, The Nunnery, Thetford, Norfolk IP24 2PU, United Kingdom*

Mills (1986) suggested that the timing of laying by crepuscular or nocturnal birds, such as caprimulgids, might be related to the amount of ambient light with different phases of the moon. He argued that such birds might be able to collect food more easily at times when the moon was near to full than when it was new. As part of a study of the Whip-poor-will (*Caprimulgus vociferus*), he looked at a combined sample of breeding records of five caprimulgid species, including the European Nightjar (*Caprimulgus europaeus*), and showed that there was indeed a nonrandom distribution of laying dates. More clutches were started in the half-month prior to full moon than in the other half. Furthermore, he found that Whip-poor-wills foraged more (see also Brigham and Barclay 1992), sang more, and fed their nestlings more frequently on moonlit than on dark nights. Mills suggested that the timing of laying was synchronized with the lunar cycle so that the first two weeks of the nestling period would coincide with the greatest amount of moonlight. He also noted that this schedule would result in high levels of moonlight five to six weeks after hatching when the young gain independence from their parents. Similar results have been found for the Fiery-necked Nightjar (*C. pectoralis*), which concentrates egg laying in the week following a full moon (Jackson 1985). However, data for two species of nighthawk—the Common Nighthawk (*Chordeiles minor*) and the Lesser Nighthawk (*C. acutipennis*)—showed no such correlation between laying date and phase of lunar cycle, which Mills (1986) thought was because these species are partially diurnal. The Common Poorwill (*Phalaenoptilus nuttallii*), another nocturnal caprimulgid, nests without relation to the lunar cycle, which Brigham and Barclay (1992) suggest is related to their propensity to attempt two broods within a limited season.

In a brief report by Cresswell (1992), a relatively small sample ($n = 30$) of European Nightjars in southern England were shown to start egg laying around the time of the full moon in the first half of June, but not if the full moon occurred in late May (and so also in late June). He suggested that there might be some advantage for egg laying to occur during a full moon in early June, but that to delay laying until a full moon in late June would limit the chances of successfully rearing a second brood.

The sample sizes in Cresswell's and Mills' papers were not very large (the latter had to combine data from 79 records of five species of *Caprimulgus*, ranging from North America and Europe to South Africa). In this paper we examine the relationship between laying and the lunar cycle for the European Nightjar using a much larger sample of records from Britain ($n = 464$).

Methods.—Our analysis makes use of the Nest Record Card data available from the British Trust for Ornithology. Nest Record Cards are completed by volunteer observers who record details of the nest contents on each visit made to a nest (Mayer-Gross 1970). The information is coded and computerized and, for many records, laying date can be back-calculated on the basis of the nest contents at later stages of nesting. The analysis is based on 464 records with sufficient data for us to estimate the date of clutch initiation to an accuracy of ± 5 days. Most (454, or 98%) of the records come from England, and the rest come from Wales; they were recorded from 1921 to 1991. The English records come mainly from three

[3] Address correspondence to this author.

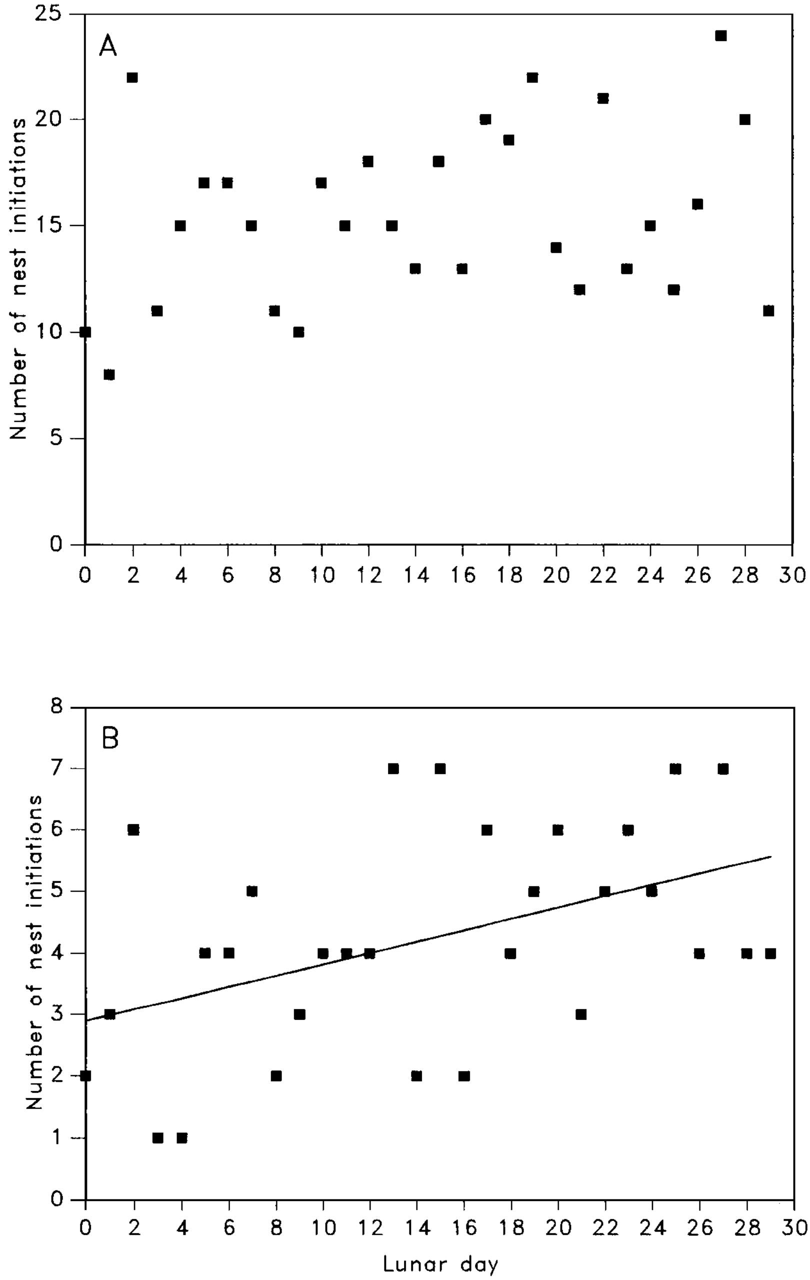

Fig. 1. Numbers of European Nightjar nests initiated on each day of the lunar month based on data from (A) 464 nest records from all calendar months, and (B) 127 records for which laying began between 5 and 18 June. Linear regression for the latter is: $Y = 2.9 + 0.0919X$, where Y is the number of initiations and X is the lunar day ($F = 7.34$, df = 1 and 28, $P = 0.011$).

counties (Surrey, 119; Nottinghamshire, 102; and Hampshire, 79). This represents a relatively restricted geographic area stretching ca. 200 km north-south over which environmental factors (such as length of twilight) vary relatively little.

For each clutch, the date of the full moon prior to when the clutch was started was calculated. This was done by selecting the date and time of a full moon and repeatedly subtracting the mean lunar month from this so as to obtain the dates of the full moons throughout the period under study (Tennent 1990). The difference between the date of the full moon prior to the start of each clutch and the actual start of each clutch provided the number of "lunar days" delay between full moon and the start of each clutch. Quadratic and linear regressions were used to investigate the relationship between the number of nests initiated and lunar date. Quadratic regression was favored if it provided a significant improvement over linear regression. In addition, the median frequency of nests recorded on each lunar date was compared for the first (lunar days 0–14) and second (lunar days 15–29) halves of the lunar month using Wilcoxon two-sample tests. Analyses were undertaken using SAS programs (SAS Institute 1990).

Results.—There was no significant linear or quadratic relationship between nest initiation and lunar date (Fig. 1A; $P > 0.10$), and there also was no significant difference between median frequencies of nest initiations for the first and second halves of a lunar month ($z = 1.45$, $P = 0.15$). Birds losing their first clutches probably cannot delay relaying until the "right" time in relation to the next full moon, as too much potential breeding time might be lost. Therefore, it may be more likely that only first clutches would show any relationship with moon phase. For clutches initiated in May, our results were similar to those for the whole data set (Fig. 1A), and there was no sign of any relationship between laying date and phase of moon.

Finally, we tested to determine if Cresswell's (1992) suggestion that synchronization between the moon and egg laying only occurred when the full moon fell in mid-June (5–18 June). We found a significant linear relationship (Fig. 1B) of increasing frequencies of nest initiations during the lunar month. Consequently, there were more nest initiations per day in the second half of a lunar month than in the first ($z = 2.37$, $P = 0.018$). Thus, in mid-June, fewer birds than expected start clutches during a waning moon, and more than expected during a waxing moon.

Discussion.—The European Nightjar is a species that is thought to capture most of its prey by silhouetting them against the light of the sky at night (Cramp 1985). Thus, one might expect that the ease with which they can catch their food (mainly flying insects) would be enhanced by lunar light. This is not because of increased prey availability, because most insects are lunarphobic, especially moths (Mills 1986). Radio-tagged European Nightjars make flycatching sallies from perches during moonlit conditions, but when the night is dark they forage during continuous flight, an energetically more demanding behavior (Cresswell and Alexander 1992). Our analyses support Mills' (1986) conclusions that variation in the phase of the moon affects the date on which nocturnal caprimulgids lay their clutch. However, for the European Nightjar, this only appears to hold for birds laying in mid-June, which supports Cresswell's (1992) exploratory analysis and is the main period of laying of first clutches in England (Nest Record Card data).

A number of complicating factors might obscure such a result at other times of the year. In a country such as England where there often is cloud cover during the early part of the laying season of European Nightjars, this might be more important than the phase of the moon in affecting timing of laying. Although we were not able to analyze this factor, Mills (1986) found that cloud cover was not a significant factor affecting activity levels of Whip-poor-wills. Similarly, other weather variables, such as rain, temperature, and wind speed, all of which are likely to affect prey activity or visibility, might have effects on feeding that could obscure any general relationship between laying date and moon phase throughout the season. Cresswell and Alexander (1992) showed that the proportion of time that European Nightjars were active in the middle of the night was inversely correlated with the nightly minimum temperature. In addition, the temperature in the period prior to egg laying might be important. Warm, cloudy weather might allow more insects to emerge, whereas bright moonlit nights that are cool might have the opposite effect, especially in an already coolish climate. Mills (1986) also noted that the duration of twilight after sunset increases with latitude; on the equator it lasts for 39 min, while at 44° N it lasts for 84 min. In England, which is at higher latitudes (ca. 51° N), the twilight period will be longer still, and the length of the night in June is relatively short (i.e. 6–7 h). This might explain the lack of a relationship between nest initiation and phase of the moon for clutches started in May because nestling demands at those nests would be highest in June when twilight and potential foraging time are longest. Brigham and Barclay (1992) showed that the foraging activity of Common Poorwills increased with an increase in lunar light, but the nesting cycle was not synchronized with the lunar cycle. They suggested this was related to the relatively high latitude of their study area (and, therefore, high availability of feeding time), in addition to their birds typically producing two broods.

Further evidence that, for early clutches, European Nightjars may not be dependent on the stage of the lunar cycle comes from the work of Berry and Bibby (1981), who found that laying dates were correlated with arrival dates. This suggests that some European Nightjars arrive on their breeding grounds with adequate food reserves to lay their first clutches without regard to local food availability (as do some arctic-breeding geese; Newton 1977). Because there was no evidence for synchrony in arrival dates, arrival occurring over a period of 20 days for males and 36 days for females, this might also explain why there was no synchronization between laying dates and phases of the moon early in the season.

Given the cyclic nature of lunar phases, a curvilinear relationship might have been expected in Figure

1B, with the number of nest initiations rising from the middle of the lunar month and falling as the moon wanes. However, curvilinear regression did not provide a significant improvement over linear regression. The statistical relationship may reflect an actual drop in nest initiations soon after the full moon, suggesting a reasonably strong selection pressure to lay during the waxing moon in mid-June. Jackson (1985) found a "saw-tooth" pattern in the distribution of laying dates relative to the lunar cycle for the Fierynecked Nightjar.

European Nightjars laying in June will be feeding young in July and also may initiate a second clutch in July. For these birds, which form a substantial proportion (ca. 50% from Nest Record Card data) of those laying their first clutch in a season, the energetic advantage of laying during a waxing moon could facilitate the production of a second clutch under similar lunar conditions. Typically, they seem to lay their second clutch when the first brood is two weeks old (chicks do not fledge until they are 16 to 17 days old and are dependent on their parents for a further 16 days or so according to Lack [1957]). Cresswell and Alexander (1990) have shown that a female may switch between mates, leaving her first male with the first brood while taking a second male to assist with the second attempt. Laying at that stage in the previous nesting cycle results in consecutive clutches being laid some 30 days apart, very close to the lunar cycle of 29.5 days. Indeed, the mean separation between first and second clutches recorded from 14 pairs on Nest Record Cards was 29 days (range 24-41 days). The nesting cycle is the same as the lunar cycle.

It is tempting to suggest that the nesting cycle of the European Nightjar has evolved to take advantage of the lunar cycle, because nightjars potentially benefit from full moons at three points in the nesting cycle: (1) at laying as discussed above; (2) when the young are one to two weeks old (during the next waxing moon); and (3) when the young are newly independent at six weeks old (during the third waxing moon). Of these three potential advantages of laying at full moon, the first seems the least likely if only because many pairs successfully lay at other stages of the lunar cycle. We have no information enabling us to distinguish between the other two possibilities but, of course, all three may act to promote synchronization with the lunar cycle. In conclusion, European Nightjars that arrive relatively early on the breeding grounds (i.e. in May) appear to start nesting as soon as possible. The rest, which initiate nesting between early and mid-June, tend to synchronize their nesting with the lunar cycle.

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