

## Effects of light and prey availability on nocturnal, lunar and seasonal activity of tropical nightjars

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Nightjars and their allies represent the only major group of visually hunting aerial insectivores with a crepuscular and/or nocturnal lifestyle. Our purpose was to examine how both light regime and prey abundance in the tropics, where periods of twilight are extremely short, but nightjar diversity is high, affect activity across different temporal scales. We studied two nightjar species in West African bush savannah, standard-winged nightjars *Macrodipteryx longipennis* Shaw and long-tailed nightjars *Caprimulgus climacurus* Vieillot. We measured biomass of potential prey available using a vehicle mounted trap and found that it was highest at dusk and significantly lower at dawn and during the night. Based on direct observations, both nightjars exhibit the most intense foraging behaviour at dusk, less intense foraging at dawn and least at night, as predicted by both prey abundance and conditions for visual prey detection. Nocturnal foraging was positively correlated with lunar light levels and ceased below about  $0.03 \text{ mW m}^{-2}$ . Over the course of a lunar cycle, nocturnal light availability varied markedly, while prey abundance remained constant at dusk and at night was slightly higher at full moon. Both species increased twilight foraging activity during new moon periods, compensating for the shorter nocturnal foraging window at that time. Seasonally, the pattern of nocturnal light availability was similar throughout the year, while prey availability peaked shortly after onset of the wet season and then slowly decreased over the following four months. The courtship and breeding phenology of both species was timed to coincide with the peak in aerial insect abundance, suggesting that prey availability rather than direct abiotic factors act as constraints, at least at the seasonal level. Our findings illustrate the peculiar constraints on visually orienting aerial nocturnal insectivores in general and tropical nightjars in particular and highlight the resulting nocturnal, lunar and seasonal allocation of activities.

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Natural selection should favour individuals who time their activities in a manner that maximises lifetime reproductive success. Foraging is a prominent activity that is tightly linked to individual fitness and efficient energy intake contributes significantly to individual survival and fitness of offspring (Stephens and Krebs 1986, Lemon 1991). The costs and benefits of foraging are affected by a variety of conditions that can vary over both short and long time scales (Brown 1989, Abrams 1993). From a temporal perspective, four major con-

straints on foraging are discernible. First, physiological limitations (e.g. vision) may impose constraints on visual foraging efficiency and predetermine windows of potential activity (Cheverton et al. 1985, Brigham and Barclay 1995, Rojas et al. 1999). Second, temporal patterns of prey abundance and availability will affect the rate of energy intake (Lack 1954, Poulin et al. 1992). Third, the presence of predators may suppress foraging (Lima and Dill 1990, Endler 1991, Meyer and Valone 1999). Fourth, interspecific (and intraspecific)

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interactions with competitors may limit foraging success (Mitchell et al. 1990, Bouskila 1995).

The intensity and interaction of these constraints are likely to vary markedly over time, both diurnally and seasonally (O'Farrell 1974, Halle 1993). Abiotic factors such as light and temperature exhibit high diurnal variation and are likely to affect directly the activity of both predator and prey as well as interact with physiological constraints. Levels and daily variability in conditions are also likely to vary seasonally, resulting in periods that allow higher net energy intake than others. For birds seasonal variation may determine seasonal distribution and, if the foraging rate affects offspring fitness, timing of breeding (Moreau 1950).

In visually orienting nocturnal animals, trade-offs are likely to be modulated by the availability of light which by itself may determine activity patterns of both predators and prey. Many nocturnal predators such as carnivores, owls and auks concentrate activity around dusk, dawn and during periods of the night with full moon (McNeil et al. 1993, Lizcano and Cavelier 2000) and achieve the greatest hunting success in bright conditions (Kotler et al. 1988, Clarke et al. 1996, Mougeot and Bretagnolle 2000). This is similar for nightjars and allies (Caprimulgiformes), which together with bats comprise the guild of nocturnal aerial insectivores (Cleere 1998, Holyoak 2001). Among birds, nightjars and owls are the only orders predominantly active at night. The advantages of evolving nocturnality such as reduced risk of predation and possibly higher prey abundance are great, but the dependence on vision for prey detection may have prevented repeated evolution of nocturnality in birds (Lythgoe 1979). Nightjars appear to minimize activity during periods with profound darkness (Brigham et al. 1999) and some species (at least under cold conditions) enter torpor during prolonged periods of inactivity (Brigham 1992, Kortner et al. 2000). In the temperate zone, where almost all detailed studies of nightjars have taken place so far, nocturnal activities such as singing and foraging usually peak at times of high azimuth and high moon phase (Jackson 1985, Mills 1986, Brigham and Barclay 1992, Holyoak 2001). Furthermore, temperate nightjars appear to counteract the constraint of nocturnal light availability by elevating activity at dusk and dawn. However, in the tropics the duration of twilight is extremely short – while diversity of nightjars is high. One purpose of this study was to examine in detail the effect of light availability as a constraint on nightjars in a tropical environment and to measure its consequences for daily, lunar and seasonal patterns of activity.

Besides physiological constraints, the temporal pattern of prey availability is likely to be a second major determinant of animal foraging activity (Lack 1954). The major prey for almost all nightjar species are flying insects (Holyoak 2001). Many groups of insects exhibit peak flight activity during twilight, particularly at dusk

when temperatures tend to be higher than at dawn (Racey and Swift 1985). At night, aerial insect numbers are generally lower, and taxa exhibit variable responses to moonlight through the night and across the lunar cycle (Bowden and Church 1973, Fullard and Napoleone 2001). In tropical habitats with distinct dry and wet seasons, insect abundance usually peaks shortly after the onset of the wet season (Janzen 1973, Poulin et al. 1992). In addition to the effect on a daily and monthly scale, the patterns of lunar light and prey abundance are likely to affect the seasonality of nightjar behavior. The adaptive significance of timing of breeding or migration is likely to be under similar constraints as the shorter term patterns of foraging. Temperate birds typically time breeding or fledging of young to coincide with annual peaks in food availability (Lack 1954, Perrins 1970, Martin 1987). This is also true in tropical habitats with sharply defined wet and dry seasons (Poulin et al. 1992) and, to a lesser degree, in relatively aseasonal rainforest habitats (Fogden 1972).

Our purpose was to assess how light and prey availability interact in a tropical environment as determinants of nightjar activity across the temporal scales of a single night, a lunar period and several seasons. We intensively monitored foraging activity by two nightjar species of tropical bush savannah in West Africa and measured moon phase, light availability and prey abundance across several temporal scales. Specifically, we addressed the following: What are the nocturnal, lunar and seasonal patterns of light availability, biomass of nightjar prey and nightjar foraging activity and phenology? And finally, is nightjar foraging and phenology related to both the observed light and prey availability?

## Methods

### Study site and timing

We conducted our study in the southern part of Comoé National Park, Côte d'Ivoire (8.45° N, 3.48° W) which is part of the mesophile Guinea savannah zone. The area has a seasonal climate with a fairly distinct dry season beginning in October/November and continuing until March/April during which there is little or no rainfall, but considerable daily variation in temperature (Fig. 1). Annual rainfall varies between 700 and 1200 mm. Towards the end of the wet season, herbaceous cover can be as high as 2 m and grass stems well over 2 m long (Fig. 1). Annual fires at the onset of the dry season reduce grass cover to a few centimetres in most places. We defined the onset of the wet season as the date of first rain that was followed by an extended period with rain (at least once in each ten-day period). The dates for the onset of the wet season were 30 March in 1998 and 14 March in 1999.

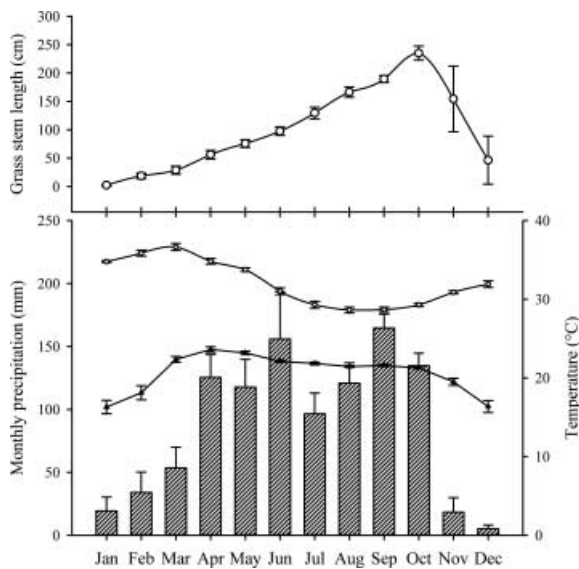


Fig. 1. Weather conditions and vegetation at the study site (7-year average, January 1994 to November 2000). Top: mean grass stem length ( $\pm$  s.e.) in selected savannah plot (selected grass stems on a small study plot in open savannah were measured twice a month). Bottom: Mean ( $\pm$  s.e.) sum of monthly precipitation, daily minimum (triangle) and daily maximum (circles) temperatures. After end of the wet season, in November and December, grass was reduced by bush fires.

The core study plot, consisted of a 1100  $\times$  1100 m area adjacent to gallery forest characterised by a mixture of tree and bush savannah with patchy tree cover and open alluvial plains and laterite pans lacking trees and bushes. The nearby river Comoé (50–100 m wide) is separated from the plains and tree savannah by a 30–200 m wide stretch of dense gallery forest. Preliminary observations were conducted from March–June and September–October 1998 leading to the core field season from December 1998 to September 1999.

### Weather and light conditions

Climatic conditions were recorded at 15-minute intervals using an automated weather station in association with a Campbell CR10X Logger located at the north-western edge of the study site. A Campbell 50Y Temperature and Relative Humidity Probe was mounted 1.5 m above ground. Both temperature and humidity covary strongly with time of the night. Levels of incident light were measured using a Skye Instruments High Output Light Sensor SKL 2640, 3 m above ground. This sensor has a cosine corrected head (all light rays perpendicular to the sensor are fully measured) and measures incoming levels of energy per unit area uniformly for all wavelengths between 400 and 700 nm. Sensor output is affected by ambient temperature (zero drift better than 0.048 mW m<sup>-2</sup> per 1°C according to the manufacturer) and therefore all values were

corrected for temperature using a regression derived from data for dark new moon nights. Seasonal pattern of night (solar azimuth  $< -12^\circ$ ) and twilight (solar azimuth  $< -6^\circ$  and  $> -12^\circ$ ) duration at the study site and selected latitudes were calculated using “AstroWin” (Strickling 1995).

### Prey abundance

We quantified prey abundance by driving along transects with a roof mounted tow-net with a 95  $\times$  95 cm entrance area and 2.5 m length. The lower edge of the net was 168 cm above ground and set 15 cm in front of and 20 cm above the windscreen to avoid insects being drawn in from air turbulence over the car surface. The funnel-like net (mesh size 0.5 mm) led to a sock-like net bag from which insects were transferred into 90% alcohol within 5 seconds of stopping. When the vehicle stopped, air traction caused the net to immediate close and the number of insects which escaped was negligible. We sampled at roughly weekly intervals between 20/12/98 and 1/9/99 on nights with stable, calm and dry weather conditions only. Four samples were taken at different times of the night on a 5000 m stretch of gravel road between 200 and 800 m from the gallery forest along the river Comoé, near and partly overlapping with the study area. The road was between 3 and 3.50 m wide and led through habitat very similar to the study site, semi-open tree savannah and plains. We drove at a constant speed of 38 km/h ( $\pm$  2 km/h) with dipped lights (non-main beam) to minimise the effect on insects reacting to light. The road was hilly and winding and at no time could the lights be seen from more than 200 m distance (and usually well under 100 m) and thus the effect of the lights was likely negligible.

We used solar azimuth to standardise the timing of sampling at twilight. Thus, we started our evening sample at the onset of civil dusk (solar azimuth =  $-6^\circ$ ) and timed the drive for the morning sample so that it would finish at civil dawn (solar azimuth =  $-6^\circ$ ). Night sampling took place in the first (ca 10:00 pm) and second (ca 02:00 am) half of the night.

82,663 arthropods were collected while driving 127 transects. All insects (the samples also included several ballooning arachnids) were subsequently sorted to the level of order, counted and their length recorded in 1 mm categories (i.e. 0–1 mm, 1–2 mm etc.). As the size-distribution of all insects of any given sample was highly skewed, geometric instead of arithmetic means between the two envelope sizes of a category were used to estimate size and, by applying the formula of Rogers et al. (1976), the biomass of each individual arthropod. The study birds of nightjars feed on a variety of aerial insects, predominantly of orders Coleoptera, Lepidoptera, Homoptera and Isoptera (Jackson 2000a). Our own observations, and other studies on afro-tropical

nightjars indicate that prey less than 3 mm long are not normally eaten (Jackson 2000b). Thus, for subsequent analyses all arthropods less than 3 mm in length were excluded.

### Nightjar species

Of the approximately 25 nightjar species recorded for tropical Africa, three regularly breed in the study area and two others are migratory visitors (Salewski 2000). One of the three breeding species, the black-shouldered nightjar (*C. nigriscapularis* Reichenow) was not included in our study. It inhabits densely wooded areas such as the gallery forest, where it hunts above the tree canopy and in gaps. The two focal species of this study commonly nest in the study region. The long-tailed nightjar (*C. climacurus*) is a year-round resident and the standard-winged nightjar (*M. longipennis*) is an intra-African migrant that spends the non-breeding season in the savannahs north of Ivory Coast.

### Nightjar observations

Data about the onset of activity of the two breeding species were collected on 68 evenings from March to June 1998 and January to April 1999. Starting 15 minutes before the onset of civil dusk, we watched for birds in the vicinity of a known roosting site or nest in the study area and recorded the time of first flight activity. Many individuals were individually banded and we estimate that five to seven different individuals each of *C. climacurus* and *M. longipennis* were regularly observed. Individual birds were captured both manually (by hand or with hand-held nets using a torchlight) and with mist-nets.

Direct observations of focal individuals of the two breeding species were used to quantify foraging activity. Different observation schemes were used for the two species. Male and to a lesser extent female *M. longipennis* regularly gather at specific patches with little vegetation ('arenas') where males perform display flights and forage. We visited five of these display arenas in the study area on 24 nights over a 5-week period beginning at the end of January 1999. If no male was present, a new arena was chosen. If at least one male was present focal animal sampling (Martin and Bateson 1993) of 10 minute duration was undertaken to collect data on the frequency of foraging behaviour. Each male was observed only once at each arena visit and, at maximum, twice per night (separated by at least eight hours). Between 16/12/98 and 8/8/99 we searched for both female and male *C. climacurus* in different parts of the study plot and observed their foraging activity for 5 minutes. In both schemes, observations started 5 minutes after arrival and were made from approximately 20

m distance with night vision goggles (Argus PC1MC-IV, 2nd generation) or, at twilight and on moonlit nights, with binoculars. Based on repeated sightings of marked individuals, we estimate that we recorded data for 8–12 *M. longipennis* and 6–10 *C. climacurus*. Both active and inactive birds were usually detected from their eye-shine reflecting torchlight from distances up to 200 m, and we do not believe that there was a bias in selecting active or inactive animals.

Between December 1998 and September 1999, we conducted standardized transect counts of road-perched nightjars on a 16 km stretch of gravel road in the immediate vicinity of the study plot. Weekly counts were undertaken except at new moon at the time of the highest lunar azimuth on cloudless or only lightly (< 30%) clouded nights. The vehicle was driven with its high beam lights on at a constant speed of approximately 20 km/h and nightjars were identified using binoculars. Only in rare cases did nightjars fly off before identification was possible. For 5 km, the transect followed the same transect used for insect trapping. For the remaining 11 km (on the opposite side of the study plot) it passed through areas with vegetation similar to that in the study plot.

Between March and June 1998 and December 1998 and September 1999, all parts of the study plot were visited regularly. Attendance by male *M. longipennis* at display arenas and the presence of singing territorial male *C. climacurus* was recorded. We searched for eggs and young. We visited nests daily and weighed chicks to allow us to back-date to the probable laying date. Brood size was two eggs in all cases and the estimated duration of incubation for *M. longipennis* is 17 days.

### Statistical analyses

Associations between predictor variables, insect biomass and nightjar activities were evaluated using generalized linear models (McCullagh and Nelder 1989) employing maximum quasi-likelihood estimation of the response mean-variance relationship (Wedderburn 1974). Because all response variables were highly right-skewed, we employed a log link function for the models and assumed a Poisson distribution of errors. Humidity and time of the night were dropped from the list of predictors, because of their lack of independence from temperature (which tended to be the better predictor in preliminary analyses). Thus, temperature (Temp), log-transformed light measurements (LogLight) and moon phase (MPhase) were included as environmental predictor variables in the analysis. We began analysis of a given response variable with a full model including all main effects and interactions. Then the most parsimonious model was selected by successively dropping terms from a full model including first-order interactions following the Akaike Information Criterion (AIC,

Sakamoto et al. 1986). The significance of model changes was further checked using F-tests on the change in deviance for each term.

To simplify interpretation of model results, we examined patterns separately for night, dusk and dawn conditions. For the analysis of insect biomass and foraging effort of *C. climacurus*, we included the count of days since onset of the last wet season (Dayswet, 30/3/1998 and 14/3/1999, respectively) as an additional variable. Feeding effort by *M. longipennis* males at display arenas may be influenced by identity of the arena or whether females were present in the arena. To control for these effects these variables were included in the analysis as blocking factors, but their significance not examined any further. The strength of first-order interactions was checked with conditional plots. All statistical analyses were performed using SPlus.

## Results

### Nocturnal and lunar

#### Light conditions

The monthly variation in duration of light availability was strong, and at no time in the five days before and five days after new moon did light levels exceed  $0.03 \text{ mW m}^{-2}$  (measured 1/10/98 to 30/9/99). Maximum nocturnal light levels occurred on cloudless and clear nights at highest moon phase and never exceeded  $1.4 \text{ mW m}^{-2}$ . The frequency distribution of light levels was highly right-skewed with levels under  $0.03 \text{ mW m}^{-2}$  occurring 63% of all time (9247 of 14,704 nocturnal 15-minute intervals).

#### Prey biomass

During both dry and wet season, Coleoptera (beetles), Isoptera (termites), Lepidoptera (moths), Homoptera (mainly cicadas), Neuroptera (lacewings) and Diptera (flies) predominated in terms of biomass (Fig. 2). Isoptera occurred only during the wet season. Different orders showed distinct activity patterns, some groups being active at dusk, but not at night or dawn. The contribution of insects under 3 mm to the overall biomass was negligible for most orders.

Biomass differences within nights were affected by season, and we included the seasonal effect in a two-factorial model with time of night and season (wet or dry) as factors. The interaction of the two terms was not significant (change in deviance by 2.3%,  $F_{1,121} = 2.25$ ,  $p = 0.09$ ) and accordingly we excluded it from the model which then explained 63.9% of the deviance (change in deviance test:  $F_{5,122} = 58.55$ ,  $p < 0.001$ ). Controlling for seasonality, biomass was significantly higher both at dusk and dawn relative to at night (Fig. 2, decrease in deviance by 45.6%,  $F_{2,121} = 62.60$ ,  $p < 0.001$ ). The number of days since the onset of the last

wet season (Dayswet) was a significant alternative predictor to season as a factor (change in deviance by 29.5%,  $F_{1,125} = 38.44$ ,  $p < 0.001$ ). We used this continuous variable in subsequent analyses to incorporate the effect of seasonality.

At dusk, no environmental variables besides seasonality affected prey biomass (Table 1). At night, and only soon after onset of the wet season, prey biomass increased with moon phase and thus brightness. At dawn, high light levels depressed aerial insect biomass. As sampling was done at fixed solar azimuth, this suggests an effect of cloud cover rather than solar height. In contrast to the relationship at night, insect biomass at dawn was lower during bright moon phase. Full moon nights have bright light conditions earlier on. Increasing temperature had a significant positive effect on prey biomass, especially near full moon.

#### Nightjar foraging activity

Both *M. longipennis* and *C. climacurus* left day roosts and became active at approximately civil dusk, the time when the sun is 6 degrees below the horizon (Fig. 3). The first observed flight activity was linearly related to civil dusk with a slope indistinguishable from 1 for both *M. longipennis* ( $F_{1,47} = 41.66$ ,  $p < 0.001$ ,  $n = 48$ ; Onset =  $-0.06 + 1.08 \text{ Civil Dusk}$ ,  $t_{(\text{slope} = 1)} = 0.48$ ,  $p = \text{n.s.}$ ) and *C. climacurus* ( $F_{1,14} = 29.70$ ,  $p < 0.001$ ,  $n = 15$ ; Onset =  $0.11 + 0.86 \text{ Civil Dusk}$ ,  $t_{(\text{slope} = 1)} = -0.90$ ,  $p = \text{n.s.}$ ). *M. longipennis* tended to become active before *C. climacurus* (ANCOVA testing the difference in intercept of the time of dusk- activity onset relationship,  $t = -2.18$ ,  $p < 0.05$ ,  $n = 63$ ).

For *C. climacurus* civil twilight (solar azimuth of  $-6^\circ$  to  $-12^\circ$ ) was marked by high foraging activity (Fig. 4). The species foraged much more intensely at twilight than at night (53.5% change in deviance from model including variable Dayswet to control for seasonal effects.  $F_{1,54} = 63.62$ ,  $p < 0.001$ ). At twilight, there was significantly more foraging activity at higher ambient temperatures (an enhancing effect of low moon phase was marginally non-significant, Table 2). Nocturnal foraging was significantly positively affected by light, especially in the dry season.

The general temporal foraging pattern of *C. climacurus* was repeated in *M. longipennis* males at their display arenas (Fig. 4). Foraging activity was greater at twilight than at night (change in deviance:  $F_{1,194} = 4.78$ ,  $p = 0.03$ ). Foraging at dusk increased during low moon phase (Table 2, negative interaction of MPhase term with Dusk). Foraging was greater at dusk than at dawn and was affected by light levels (LogLight interacting with Dusk). At night, nightjars foraged more actively during the times of the night with light and did so more intensely during low moon phases (negative interaction of LogLight with moon phase).

The effect of light on nocturnal foraging alone substantiates its role as a constraint. Besides the linear

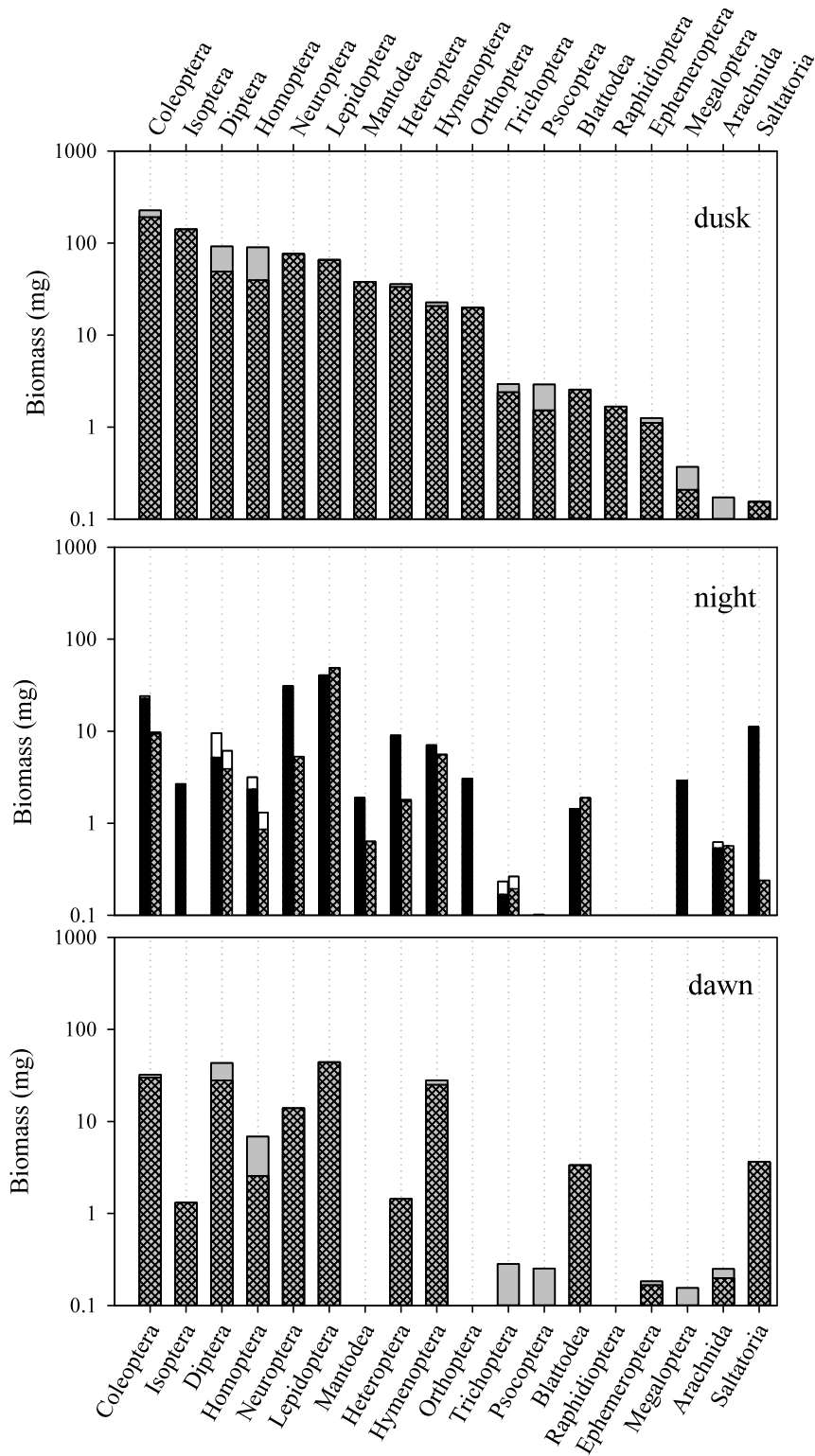


Fig. 2. Biomass (combined dry and wet season) of insect orders as sampled with the car trap at different times of the night, 20/12/98 to 11/3/99. Hatched parts of bars indicate biomass of insects > 3 mm only. Night: left bar first half, right bar second half of the night.

increase noted in the combined model analysis, a distinct drop-off in foraging activity appears to occur below  $0.03 \text{ mW m}^{-2}$  (Fig. 5). In only four of 28 10-minute obser-

vations under such conditions of low light was a foraging attempt observed in *M. longipennis*, and never in nine 5-minute observations of *C. climacurus*.

Table 1. Environmental determinants of biomass of insects above 3 mm at dusk (n = 30 sampling sessions), night (n = 67 sampling sessions) and dawn (n = 30 sampling sessions). Presented are the most parsimonious models selected from full models including all main effects and one-way interactions. Dayswet refers to number of days since onset of the last wet season; MPhase refers to a continuous measure of moon phase between 0 (new moon) and 1 (full moon); Temp refers to temperature. LogLight to log-transformed light levels

Period	Term	d.f.	Proportion deviance (%)	F	p	Coefficient
Dusk	Dayswet	1,28	64.29	47.51	<0.001	-0.01
	Model	1,28	64.29	47.51	<0.001	
Night	MPhase	1,63	7.58	8.32	<0.01	1.33
	Dayswet	1,63	0.01	0.01	0.93	-0.01
	MPhase:Dayswet	1,63	7.66	8.40	0.01	-0.01
	Model	3,63	44.35	12.34	<0.001	
Dawn	Dayswet	1,24	6.88	5.89	0.02	-0.01
	LogLight	1,24	13.07	11.18	<0.01	-1.09
	MPhase	1,24	5.52	4.72	0.04	-12.78
	Temp	1,24	0.70	0.60	0.45	-0.08
	Temp:MPhase	1,24	6.94	5.94	0.02	0.64
	Model	5,24	72.16	12.34	<0.001	

## Seasonality

### Light conditions

The seasonal change in duration of twilight (solar azimuth between  $-6^\circ$  and  $-12^\circ$ ) and night at our study site was minimal (Fig. 6a). While the monthly variation in duration of light availability was significant, the lunar pattern showed little change seasonally. This points to a negligible seasonality in nocturnal cloud cover, which indicates that light conditions per se are unlikely to play an important role regarding the seasonality of nightjars. The broadly similar nocturnal light levels in both seasons are in stark contrast to the daytime conditions, when clouds cover the sky most of the wet season.

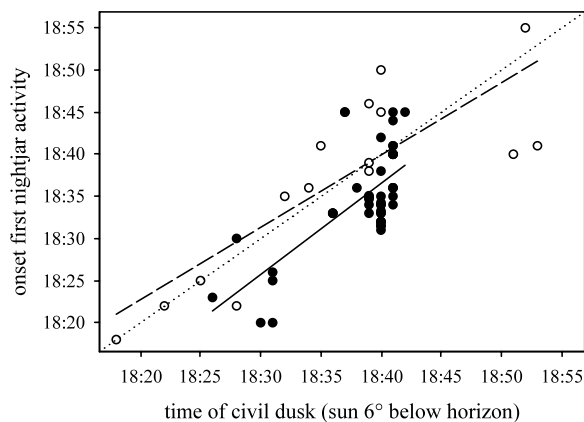


Fig. 3. Relationship between the time of civil dusk (solar azimuth of  $-6^\circ$ ) and the onset of nightjar flight activity from 68 evenings between January and June. Solid circles and solid line: data and regression line for *M. longipennis*. Open circles and dashed line: data and regression line *C. climacurus*. Dotted line: hypothetical 1:1 relationship. For details on regression see results.

### Prey biomass

The results of the two-factorial model which includes time of night (dusk, night, dawn) and season indicate that prey biomass was higher in the wet than in the dry season (change in deviance by 18.2%,  $F_{1,121} = 49.9$ ,  $p < 0.001$ , see Fig. 6b for seasonal pattern). The onset of the rainy season (second week of March) was followed by a peak in insect biomass. The strong seasonal and temporal differences in prey biomass are illustrated by individual models for dusk, night, and dawn, selected from a full model with all one-way interactions (Table 1). Time since onset of the last wet season (Dayswet) was a consistent predictor of prey biomass for all times of the night. At dusk, the seasonal decrease in biomass was solely predicted by Dayswet.

### Nightjar presence and breeding activity

Our transect counts illustrate the different seasonal strategies of nightjars at the study site (Fig. 6c, d). *Caprimulgus climacurus* was present year-round (several individuals were recorded on transect counts in early October preceding the study period) and started breeding shortly after the onset of the wet season. *M. longipennis* arrived approximately three months before the onset of the wet season (no individuals were recorded on transect counts in early October preceding the study period). Lek display started shortly after arrival and continued well into the breeding season by which time most males had lost their elongated standards. Individuals left the study site in late June. Breeding was synchronised among females at any given time for all six breeding records in 1999 and five in 1998. The 1999 dates indicate hatching shortly before new moon. In 1998, estimated hatching dates varied between 26 February and 3 March which is shortly after new moon.

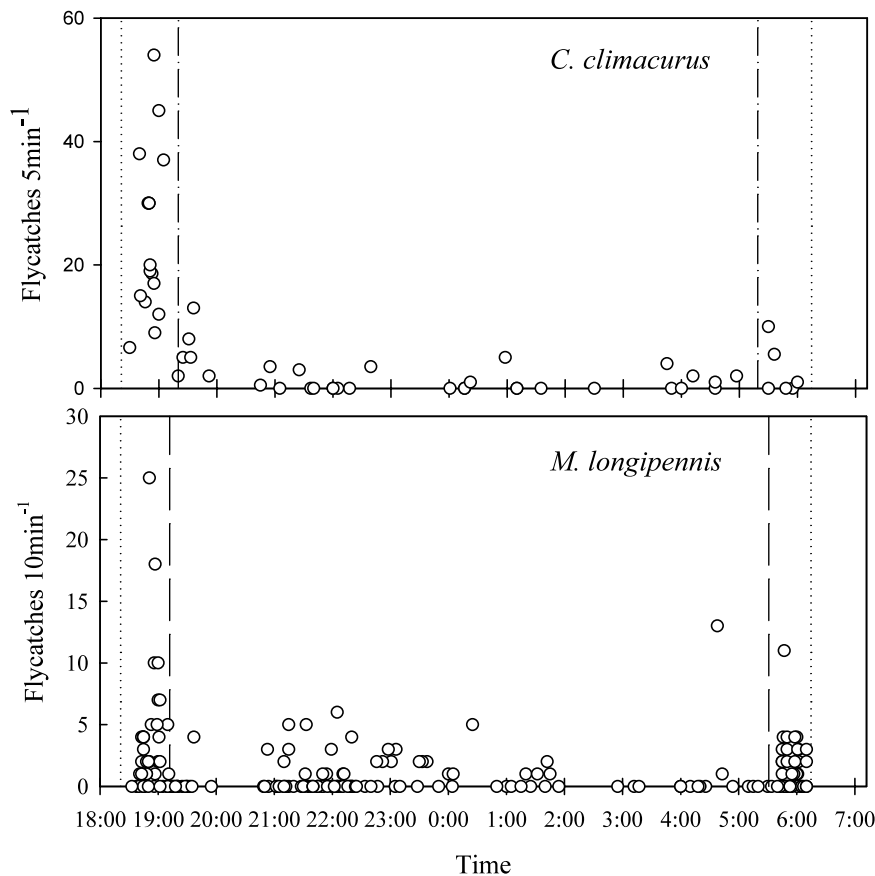


Fig. 4. Temporal foraging pattern of *C. climacurus* males and females and *M. longipennis* males at arenas. Each data point refers to one 5 or 10 minute standardized focal animal observation with night vision goggles. Dotted vertical lines refer to the extreme times of onset and end of civil twilight (solar azimuth between  $-6^\circ$  and  $-12^\circ$ ) during the study period.

## Discussion

### Aerial insect biomass

To our knowledge, this study presents the first seasonal investigation of aerial insect biomass in a tropical habitat derived from a non-attractant trap. We believe that our method achieved a fairly unbiased estimate of relative aerial insect abundances. We caught fast flying Scarabid beetles and cicadas and on two occasions small *Pipistrelle* bats. The most important groups in terms of biomass (Coleoptera, Homoptera, Lepidoptera, Isoptera) also represent the major prey of nightjars and therefore we argue that our measures of temporal patterns of biomass abundance reflect the prey available to nightjars.

We found that aerial insect biomass is significantly higher at dusk than at any other time of the night, as reported previously (Lewis and Taylor 1965, Rautenbach et al. 1988, Caveney et al. 1995). During the wet, but not the dry season, there is a smaller peak in abundance at dawn similar to temperate regions (Racey and Swift 1985, Rydell et al. 1996). The lower morning temperatures and generally smaller number of insects in the dry season may explain this difference (Gupta et al. 1990).

We found that moon phase (which correlates both with light availability and duration of bright night conditions) in the wet, but not the dry season appears to promote flight activity at least of larger insects. Insect biomass shows a strong seasonal pattern, with a two- to five-fold increase approximately six weeks after onset of the wet season. This is due to increases in almost all orders, but also due the emergence of new groups, notably flying sexual termites, that do not undertake mating flights during the dry season. The marked decrease in arthropod abundance through the dry season is characteristic of tropical habitats with seasonal rainfall (Janzen and Schoener 1968, Janzen 1973, Wolda 1978, Tigar and Osborne 1997).

### Daily cycle

Nightjars typically become active shortly after sunset (Wynne-Edwards 1930) and roost before sunrise. Their foraging activity is presumably dependent on and constrained by vision (Brigham and Barclay 1995). Some species such as the common nighthawk (*Chordeiles minor* Forster) appear to forage only at dusk and dawn (Aldridge and Brigham 1991, Brigham and Fenton 1991). However, most species are also active during the



Table 2. Determinants of *C. climacurus* (females and males) and *M. longipennis* (males at arenas) foraging activity at twilight and night. Presented are the most parsimonious models selected from full models including all main effects and one-way interactions.

Period	Term	d.f.	Percentage deviance	F	p	Coefficient	t	
<i>C. climacurus</i>								
Twilight	Temp	1,18	45.91	19.46	<0.001	0.21	3.56	
	MPhase	1,18	9.69	4.11	0.06	-1.33	-1.95	
	Model	2,18	52.73	11.17	<0.001			
Night	LogLight	1,31	18.59	12.94	<0.01	137.50	2.43	
	Dayswet	1,31	22.47	15.64	<0.001	0.03	2.32	
	LogLight:Dayswet	1,31	14.34	9.98	<0.01	-0.40	-2.24	
	Model	3,33	51.14	11.87	<0.001			
<i>M. longipennis</i>								
Twilight	Arena	4,61	10.3	3.34	0.02			
	Temp	1,61	3.0	3.93	0.05	-0.16	-1.90	
	LogLight	1,61	2.5	3.31	0.07	-3.48	-1.64	
	Temp:LogLight	1,61	2.7	3.56	0.06	0.19	1.75	
	MoonPhase	1,61	0.9	1.19	0.28	1.25	1.09	
	Dusk	1,61	10.7	13.97	<0.001	3.58	3.14	
	LogLight:Dusk	1,61	7.9	10.28	<0.01	-3.19	-3.36	
	Mphase:Dusk	1,61	4.7	6.08	0.02	-3.17	-2.51	
	Female	1,61	6.5	8.41	0.01	-4.93	-2.66	
	Female:Temp	1,61	8.5	11.03	<0.01	0.23	3.04	
	Model	13,61	53.8	5.38	<0.001			
	Night	Arena	4,114	7.6	1.96	0.11		
		Female	1,114	3.7	3.75	0.06	1.49	1.92
LogLight		1,114	8.0	8.23	<0.01	58.80	2.71	
Mphase		1,114	0.2	0.21	0.64	0.87	0.46	
Female:LogLight		1,114	8.7	8.95	<0.01	-29.03	-2.71	
LogLight:Mphase		1,114	5.8	5.97	0.02	-52.60	-2.30	
Model		9,114	24.8	2.82	0.01			

middle of the night (Holyoak 2001). Nightjar eyes contain tapeta lucida, an adaptation to enhance vision under poor light conditions (Nicol and Arnott 1974). Despite this adaptation, hunting still appears to be constrained by light levels (Mills 1986, Brigham and Barclay 1992).

In our study, both species exhibit distinct temporal patterns in foraging activity, highest at dusk, medium at dawn and low, but variable during the night. These differences are broadly correlated with changes in prey biomass, but also likely reflect foraging efficiency, since prey are more visible in brighter conditions. In essence, high levels of foraging activity at dusk and dawn are likely due to both high prey availability and visibility. The generally lower levels of foraging at night may simply be a consequence of both lower light and prey availability, but the complete inactivity at very low light levels suggests light is a threshold constraint. The consistently strong negative relationship between foraging and brightness within nights confirms the role of nocturnal light as constraint more important than prey abundance. Within the three time periods no clear relationship between the abiotic correlates of foraging behaviour and of those of prey biomass were discernible.

### Lunar cycle

Considering the overall scarcity of bright conditions at night, the limitation of foraging to periods with high light levels imposes considerable constraints on the overall time available for daily foraging. These constraints vary cyclically with lunar phase, leaving dusk and dawn as only time for foraging in the days around new moon. In the tropics, twilight conditions are short year-round. Accordingly, we predicted that foraging constraints imposed by lunar periodicity should be reflected in the activity patterns of nightjars. Assuming that foraging at twilight (which is also the peak activity period for many mammalian predators) imposes a high risk of predation, nightjars should exhibit the greatest crepuscular foraging activity around new moon, when nocturnal foraging is not possible. This prediction was supported by the data – twilight foraging activity by both species was negatively associated with moon phase.

The periodic changes in moon light and the resulting periodicity in risk of predation and prey availability affect behavioural patterns in a variety of animals (Neumann 1981, Martin and Busby 1990, Daly et al. 1992, Fischer and Linsenmair 2001). Lapwings (*Vanel-*

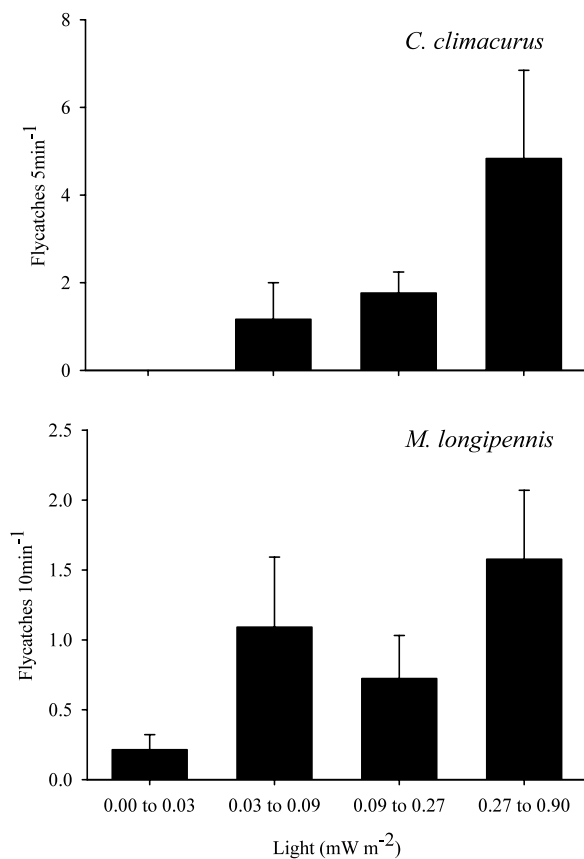


Fig. 5. Effect of moonlight levels on nocturnal foraging activity of *C. climacurus* (n = 35) and *M. longipennis* (n = 124) as measured in standardized focal animal observations using night vision goggles (see Fig. 4).

*lus vanellus* Linnaeus), diurnal birds that outside the breeding season opportunistically forage at full moon nights, reduce day-foraging at full moon (Milsom et al. 1990) and Moluccan Megapodes (*Megapodius wallacei* Gray) synchronize their nocturnal egg-laying with the lunar cycle, probably due to temporal variation in predation risk (Baker and Dekker 2000). Lunar synchronisation of breeding has been hypothesised repeatedly for nightjars (Wynne-Edwards 1930, Mills 1986, Perrins and Crick 1996), but strong support for this assertion has only been reported for fiery-necked nightjars (*Caprimulgus pectoralis* Cuvier) in Zimbabwe (Jackson 1985). Egg-laying in this species coincides with full moon, which allows more effective foraging at a time when young of age 10–20 days need to be fed a month later. Alternatively and additionally, full moon may facilitate the energy expenditure of egg formation (Perrins and Crick 1996).

With our limited data-set for *M. longipennis*, we found strong synchronisation of breeding among females which could be attributable to both social interactions (some females nest close to each other in 50–100 m distance, Jensen and Kirkeby 1980, W. Jetz pers. obs.)

or identical environmental triggers. The timing of what probably are replacement clutches one month later and data from the preceding year support lunar effects. Assuming an incubation period of about 17 days, egg-laying in *M. longipennis* coincides with late waxing to full moon. The resulting hatching dates were around new moon. This could point to an attempt to reduce predation risk from visual predators on new-born young which should be low in dark conditions or maximisation of energy availability for female egg formation or (one month later) for offspring two weeks after hatching, when full moon allows longer time for foraging (Jackson 1985).

### Seasonality

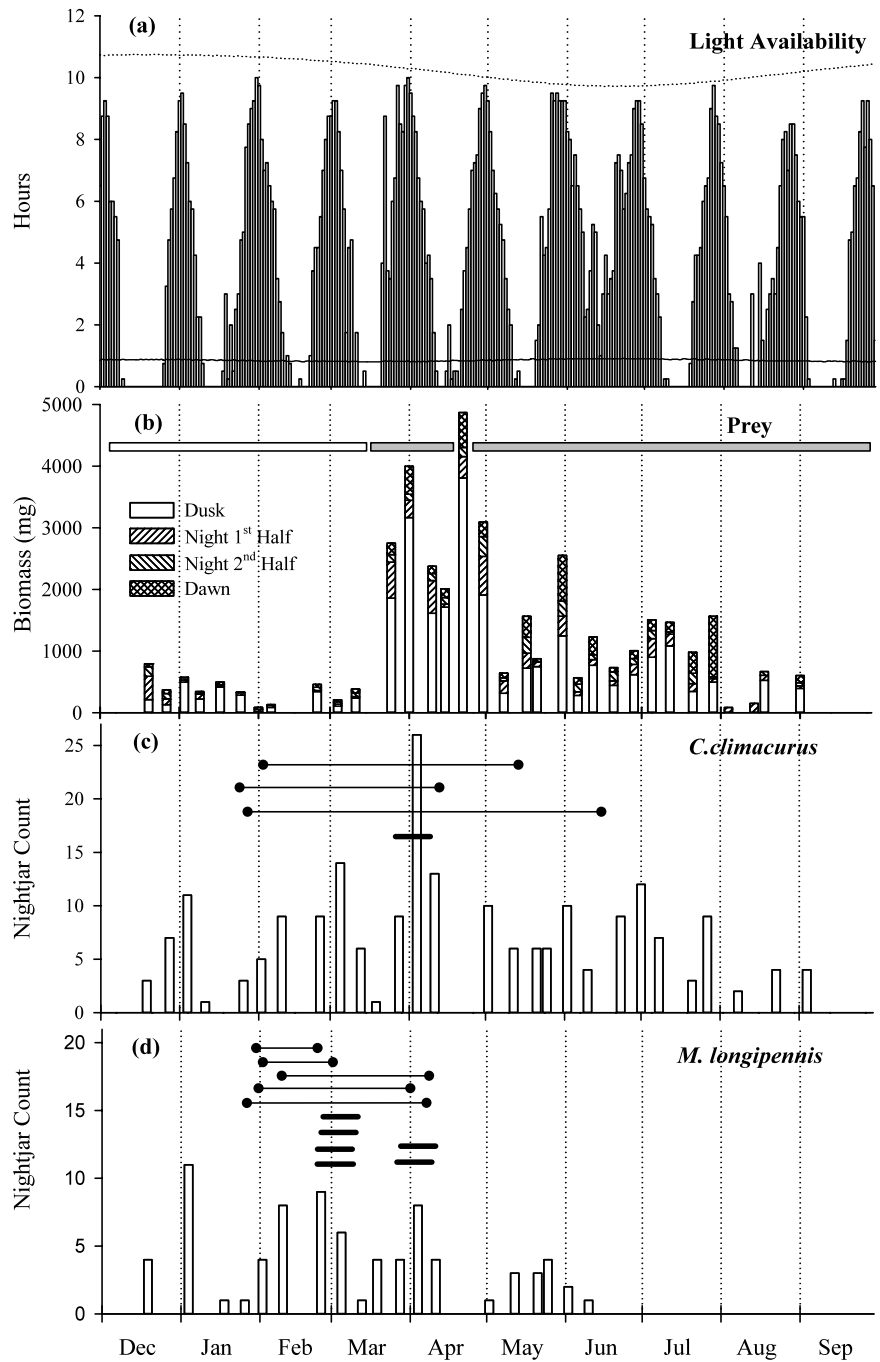
Courtship displays by *M. longipennis* begin about six weeks before the major peak in aerial insect biomass. Egg-laying followed three to four weeks later, a week before the first small rains gave signs of the forthcoming wet season, and still two weeks ahead of the peak in insect abundance. This supports the idea that the timing of breeding is selected so that maximum food supply is available for offspring. Levels of prey biomass at dusk were exceptionally high for a six-week period beginning at the end of March. If nightjars are constrained in the short-term timing of egg-laying by lunar phase, the observed timing would have given them maximum food supply for the first days of both first and replacement brood. The end of male display activity (and female presence) in arenas around early/mid April corroborates evidence from nest records of an end of the breeding season around this time. This coincides with the end of peak insect biomass at dusk and night shortly thereafter.

Timing of breeding may also be affected by abiotic constraints (Skutch 1950, Foster 1974). We found no evidence for constraints on timing of breeding due to climate (Foster 1974, Young 1994) or light availability. We found that the periodicity of light conditions that allowed foraging showed only limited intra-annual variation. This contrasts with temperate zones where there are strong seasonal differences in duration of night, twilight and cloud cover. One untested limitation may come from the height of vegetation (Fig. 1), which may affect the performance of sallying flights from the ground. Not long into the wet season *M. longipennis*, which uses more open habitats than *C. climacurus* (Holyoak 2001), leaves the increasingly densely vegetated study area and migrates north to spend the wet season in drier and more open Sahelian bush-woodland savannahs.

### Conclusions

We assessed the constraints nightjars face as nocturnal visual hunters in a tropical habitat where the periods of

Fig. 6. Seasonal patterns of light and prey availability, and nightjar presence, courtship and breeding behaviour, from 1/12/98 to 30/9/99. (a) Daily duration of twilight ( $-6^\circ$  to  $-12^\circ$  solar azimuth, thick line, bottom), daily duration of night ( $< -12^\circ$  solar azimuth, dotted line, top) and nocturnal light conditions  $\geq 0.03 \text{ mW m}^{-2}$  (bars) at the study site; (b) biomass of aerial insects above 3 mm at different times of the night (vertical bars) as sampled with car trap and duration of dry (open, horizontal bar) and wet (grey, horizontal bar) season; (c) and (d) presence, display and breeding activity of nightjars. Vertical bars refer to sums from 16 km transect counts. Thick horizontal bars indicate presence of clutches, thin horizontal bars duration of display activity in arenas in case of *M. longipennis* and duration of territorial song activity in case of *C. climacurus* (each bar refers to one clutch or known individual).



twilight year-round are short. We demonstrated the distinct nocturnal, lunar and seasonal pattern of both light availability and aerial insect biomass and highlighted the significance of moonlight above and beyond prey availability. The lunar cycle appears to affect short-term timing of foraging activity and breeding, while prey biomass, modulated by the patterns of rainfall, governs presence and seasonality of breeding.

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## References

Abrams, P. A. 1993. Optimal traits when there are several costs – the interaction of mortality and energy costs in determining foraging behavior. – *Behav. Ecol.* 4: 246–253.

Aldridge, H. D. J. N. and Brigham, R. M. 1991. Factors influencing foraging time in two aerial insectivores: the bird *Chordeiles minor* and the bat *Eptesicus fuscus*. – *Can. J. Zool.* 69: 62–69.

Baker, G. C. and Dekker, R. 2000. Lunar synchrony in the reproduction of the Moluccan Megapode *Megapodius wallacei*. – *Ibis* 142: 382–388.

Bouskila, A. 1995. Interactions between predation risk and competition: a field study of kangaroo rats and snakes. – *Ecology* 76: 165–178.

Bowden, J. and Church, B. M. 1973. The influence of moonlight on catches of insects in light-traps in Africa Part II. The effect of moon phase on light trap catches. – *Bull. Entomol. Res.* 63: 129–142.

Brigham, R. M. 1992. Daily torpor in a free-ranging goat-sucker, the common poorwill (*Phalaenoptilus nuttallii*). – *Physiol. Zool.* 65: 457–472.

Brigham, R. M. and Barclay, R. M. R. 1992. Lunar influence on foraging and nesting activity of common poorwills (*Phalaenoptilus nuttallii*). – *Auk* 109: 315–320.

Brigham, R. M. and Barclay, R. M. R. 1995. Prey detection by common nighthawks – does vision impose a constraint? – *Ecoscience* 2: 276–279.

Brigham, R. M. and Fenton, M. B. 1991. Convergence in foraging strategies by 2 morphologically and phylogenetically distinct nocturnal aerial insectivores. – *J. Zool.* 223: 475–489.

Brigham, R. M., Gutsell, R. C. A., Wiacek, R. S. et al. 1999. Foraging behaviour in relation to the lunar cycle by Australian owl-nightjars *Aegotheles cristatus*. – *Emu* 99: 253–261.

Brown, J. S. 1989. Desert rodent community structure – a test of 4 mechanisms of coexistence. – *Ecol. Monogr.* 59: 1–20.

Caveney, S., Scholtz, C. H. and McIntyre, P. 1995. Patterns of daily flight activity in onitine dung beetles (Scarabaeinae: Onitini). – *Oecologia* 103: 444–452.

Cheverton, J., Kacelnik, A. and Krebs, J. R. 1985. Optimal foraging: constraints and currencies. – In: Holldobler, B. and Lindauer, M. (eds), *Experimental behavioural ecology and sociobiology*. Sinauer Associates.

Clarke, J. A., Chopko, J. T. and Mackessy, S. P. 1996. The effect of moonlight on activity patterns of adult and juvenile prairie rattlesnakes (*Crotalus viridis viridis*). – *J. Herpetol.* 30: 192–197.

Cleere, N. 1998. Nightjars: a guide to nightjars and related nightbirds. – Pica Press.

Daly, M., Behrends, P. R., Wilson, M. I. et al. 1992. Behavioral modulation of predation risk – moonlight avoidance and crepuscular compensation in a nocturnal desert rodent, *Dipodomys merriami*. – *Anim. Behav.* 44: 1–9.

Ender, J. A. 1991. Interactions between predator and prey. – In: Krebs, J. R. and Davies, N. B. (eds), *Behavioural ecology: and evolutionary approach*. Blackwell Scientific Publications, pp. 169–196.

Fischer, F. and Linsenmair, K. E. 2001. Spatial and temporal habitat use of kob antelopes in the Comoé National Park, Ivory Coast as revealed by radio tracking. – *Afr. J. Ecol.* 39: 249–256.

Fogden, M. P. L. 1972. The seasonality and population dynamics of equatorial forest birds in Sarawak. – *Ibis* 114: 307–343.

Foster, M. 1974. Rain, feeding behaviour and clutch size in tropical birds. – *Auk* 91: 722–726.

Fullard, J. H. and Napoleone, N. 2001. Diel flight periodicity and the evolution of auditory defences in the Macrolepidoptera. – *Anim. Behav.* 62: 349–368.

Gupta, R. C., Kundu, H. L. and Thukral, A. K. 1990. Flight activity of some photopositive coleopterans in relation to temperature. – *J. Environ. Biol.* 11: 405–412.

Halle, S. 1993. Diel pattern of predation risk in microtine rodents. – *Oikos* 68: 510–518.

Holyoak, D. T. 2001. Nightjars and their allies: the Caprimulgiformes. – Oxford Univ. Press.

Jackson, H. D. 1985. Aspects of the breeding biology of the fiery-necked nightjar. – *Ostrich* 56: 263–276.

Jackson, H. D. 2000a. The food of the Afrotropical nightjars. – *Ostrich* 71: 408–415.

Jackson, H. D. 2000b. Prey size in relation to mouth size of nightjars in Zimbabwe. – *Ostrich* 71: 436–437.

Janzen, D. 1973. Sweep samples of tropical foliage insects: effects of seasons, vegetation types, elevation, time of day, and insularity. – *Ecology* 54: 687–708.

Janzen, D. H. and Schoener, T. W. 1968. Differences in insect abundance and diversity between wetter and drier sites during a tropical dry season. – *Ecology* 49: 96–110.

Jensen, J. V. and Kirkeby, J. 1980. The birds of the Gambia. An annotated check-list and guide to localities in the Gambia. – Aros Nature Guides.

Kortner, G., Brigham, R. M. and Geiser, F. 2000. Winter torpor in a large bird. – *Nature* 407: 318–318.

Kotler, B. P., Brown, J. S., Smith, R. J. et al. 1988. The effects of morphology and body size on rates of owl predation on desert rodents. – *Oikos* 53: 145–152.

Lack, D. 1954. The natural regulation of animal numbers. – Clarendon.

Lemon, W. C. 1991. Fitness consequences of foraging behavior in the zebra finch. – *Nature* 352: 153–155.

Lewis, T. and Taylor, L. R. 1965. Diurnal periodicity of flight by insects. – *Trans. R. Entomol. Soc. Lond.* 116: 393–479.

Lima, S. L. and Dill, L. M. 1990. Behavioral decisions made under the risk of predation – a review and prospectus. – *Can. J. Zool.-Revue Can. Zool.* 68: 619–640.

Lizcano, D. J. and Cavelier, J. 2000. Daily and seasonal activity of the mountain tapir (*Tapirus pinchaque*) in the Central Andes of Colombia. – *J. Zool.* 252: 429–435.

Lythgoe, J. N. 1979. The ecology of vision. – Clarendon Press.

Martin, G. and Busby, J. 1990. Birds by night. – Poyser.

Martin, P. R. and Bateson, P. P. G. 1993. Measuring behaviour: an introductory guide. – Cambridge Univ. Press.

Martin, T. E. 1987. Food as a limit on breeding birds – a life-history perspective. – *Annu. Rev. Ecol. Syst.* 18: 453–487.

McCullagh, P. and Nelder, J. A. 1989. Generalized linear models. – Chapman and Hall.

McNeil, R., Drapeau, P. and Pierrotti, R. 1993. Nocturnality in colonial waterbirds: occurrence, special adaptations and suspected benefits. – In: Power, D. M. (ed.), *Current ornithology*. Vol. 10. Plenum Press, pp. 187–246.

- Meyer, M. D. and Valone, T. J. 1999. Foraging under multiple costs: the importance of predation, energetic, and assessment error costs to a desert forager. – *Oikos* 87: 571–579.
- Mills, A. M. 1986. The influence of moonlight on the behavior of goatsuckers (Caprimulgidae). – *Auk* 103: 370–378.
- Milsom, T. P., Rochard, J. B. A. and Poole, S. J. 1990. Activity patterns of lapwings *Vanellus vanellus* in relation to the lunar cycle. – *Ornis Scandinavica* 21: 147–156.
- Mitchell, W. A., Abramsky, Z., Kotler, B. P. et al. 1990. The effect of competition on foraging activity in desert rodents – theory and experiments. – *Ecology* 71: 844–854.
- Moreau, R. E. 1950. The breeding seasons of African birds. 1. Land birds. – *Ibis* 92: 223–267.
- Mougeot, F. and Bretagnolle, V. 2000. Predation risk and moonlight avoidance in nocturnal seabirds. – *J. Avian Biol.* 31: 376–386.
- Neumann, D. 1981. Tidal and lunar rhythms. – In: Aschoff, F. (ed.), *Handbook of behavioural neurobiology*. Plenum Press.
- Nicol, J. A. C. and Arnott, H. J. 1974. Tapeta lucida in the eyes of goatsuckers (Caprimulgidae). – *Proc. R. Soc. Lond. B* 187: 349–352.
- O'Farrell, M. J. 1974. Seasonal activity patterns of rodents in a sagebrush community. – *J. Mammal.* 55: 809–823.
- Perrins, C. M. 1970. The timing of birds' breeding seasons. – *Ibis* 112: 242–255.
- Perrins, C. M. and Crick, H. Q. P. 1996. Influence of lunar cycle on laying dates of European nightjars (*Caprimulgus europaeus*). – *Auk* 113: 705–708.
- Poulin, B., Lefebvre, G. and McNeil, R. 1992. Tropical avian phenology in relation to abundance and exploitation of food resources. – *Ecology* 73: 2295–2309.
- Racey, P. A. and Swift, S. M. 1985. Feeding ecology of Pipistrellus–Pipistrellus (Chiroptera, Vespertilionidae) during pregnancy and lactation. 1. Foraging behavior. – *J. Anim. Ecol.* 54: 205–215.
- Rautenbach, I. L., Kemp, A. C. and Scholtz, C. H. 1988. Fluctuations in availability of arthropods correlated with microchiropteran and avian predator activities. – *Kodoe* 31: 77–90.
- Rogers, L. E., Hinds, W. T. and Buschbohm, R. L. 1976. A general weight vs length relationship for insects. – *Ann. Entomol. Soc. Am.* 69.
- Rojas, L. M., McNeil, R., Cabana, T. et al. 1999. Diurnal and nocturnal visual capabilities in shorebirds as a function of their feeding strategies. – *Brain Behav. Evol.* 53: 29–43.
- Rydell, J., Entwistle, A. and Racey, P. A. 1996. Timing of foraging flights of three species of bats in relation to insect activity and predation risk. – *Oikos* 76: 243–252.
- Sakamoto, Y., Ishiguro, M. and Kitagawa, G. 1986. Akaike information criterion statistics. – D. Reidel Publishing Company.
- Salewski, V. 2000. The birds of Comoé National Park, Ivory Coast. – *Malimbus* 22: 55–76.
- Skutch, A. S. 1950. The nesting seasons of Central American birds in relation to climate and food supply. – *Ibis* 92: 185–222.
- Stephens, D. W. and Krebs, J. R. 1986. *Foraging theory*. – Princeton Univ. Press.
- Strickling, W. 1995. *Astro*. – Freeware.
- Tigar, B. J. and Osborne, P. E. 1997. Patterns of arthropod abundance and diversity in an Arabian desert. – *Ecography* 20: 550–558.
- Wedderburn, R. W. M. 1974. Quasi-likelihood functions, generalized linear models, and the Gauss–Newton method. – *Biometrika* 61: 439–447.
- Wolda, H. 1978. Seasonal fluctuations in rainfall, food and abundance of tropical insects. – *J. Anim. Ecol.* 47: 369–381.
- Wynne-Edwards, V. C. 1930. On the waking-time of the nightjar (*Caprimulgus e. europaeus*). – *J. Exp. Biol.* 7: 241–247.
- Young, B. E. 1994. The effects of food, nest predation and weather on the timing of breeding in tropical house wrens. – *Condor* 96: 341–353.