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Influence of the nycthemeral cycle on the roosting behaviour of the Orange-winged Amazon

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ABSTRACT

Environmental stimuli exert important effects on the expression of the endogenous rhythms. Daily movements of groups of parrots in response to the light/dark cycle have been studied by several researchers. However, the factors modifying the intrinsic rhythmicity of this behaviour remain little known. This study describes how the nycthemeral/circadian periodicity of roost daily movements of the Orange-winged Amazon *Amazona amazonica* is modified by weather factors. Numbers of parrots arriving or leaving the roosting site Ilha dos Papagaios were determined on a minute by minute basis. More parrots have significantly arrived at the roost after sunset than before, while more parrots have significantly left the roost before sunrise than after. The peak exodus of parrots occurred at 23 ± 5.24 minutes before sunrise, when the average light intensity was 1 lux. The peak influx of parrots occurred at 6 ± 6.1 minutes after sunset, when the average light intensity was 50 lux. By altering ambient light intensity, weather conditions have significantly influenced the arrival and departure times, with parrots leaving later and arriving earlier when conditions were overcast at the roost site.

Key words: *Amazona amazonica*, Amazônia, biological rhythms, light/dark cycles, roosting behaviour, weather conditions.

INTRODUCTION

Biological rhythms of activity/rest related to light/dark cycles are referred as nycthemeral cycles, and have been found in organisms ranging from simple unicellular prokaryotic cyanobacteria to mammals. They confer an adaptive advantage on the organism by allowing it to adjust its physiology and behaviour in anticipation of changes in the environment (Forattini et al. 1981, Hall and Rosbash 1993, Menaker et al. 1997, Sheeba et al. 1999, Menna-Barreto 2003, Paranjpe and Sharma 2005).

From a physical point of view, the alternation of light and dark forms is the primary demarcation of daily time. In order to adjust their physiological systems to daily variations in the environment, living organisms need (1) an endogenous clock, that is pre-programmed to correspond with the daily environmental pattern; (2) sense organs, which can detect abnormalities in the environmental rhythm; and (3) neural systems, which can alter the intrinsic rhythm in response to the sensory information (Markus et al. 2003).

Nycthemeral rhythms are fundamental for the temporal organization of the behaviour and physiology of birds. Compared with mammals,

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birds are equipped with rather complex and diverse diurnal pacemaker systems that correspond to the complexity and diversity of the various lifestyles birds have evolved in a variety of different environments (Gwinner and Brandstätter 2001). Perception of the photic environment by birds is achieved by retinal, pineal and deep encephalic photoreceptors (Cassone and Menaker 1984). These three components interact jointly with each other to regulate the behavioural and physiological rhythmicity: the pineal gland, by rhythmically releasing melatonin, a hormone that plays a central role in the circadian organization of birds; the hypothalamic oscillator, possibly acting through neural output signals; and the retina, acting either via periodic melatonin secretion or neural output signals (Cassone and Menaker 1984, Gwinner and Brandstätter 2001, Brandstätter 2003).

Among birds, some parrots had been studied in relation to their daily roosting behaviour (Rocha et al. 1988, Mabb 1997, Harms and Eberhard 2003, Cougill and Marsden 2004, P.C.R. Costa, unpublished data). However, the factors influencing the time of arrival and departure of parrots in roosts are still little known (Sick 1997). The aim of this study was to determine the influence of ambient light conditions on the dynamics of daily movements of the Orange-winged Amazon *Amazona amazonica* at the roosting site Ilha dos Papagaios in Belém, Pará, Brazil.

METHODS

STUDY AREA

Ilha dos Papagaios is a roosting site for a significant Orange-winged Amazon population, a common species in the region. It is located in Guajara Bay, south of Belém, Brazil (01°31'16"S, 48°30'23"W), and has an area of 7.4 ha. The island is low and subject to periodic tidal flooding (Novaes and Lima 1998).

The climate is tropical humid and the source of seasonality is precipitation, although there is no

pronounced dry season. There are two seasons: a rainy season and a weak dry season. The rainy season begins in December, with a peak in March, and subsides in May. January, February and March are the wettest months, with average monthly rainfalls exceeding 400 mm. The less rainy season usually corresponds to the period from June to November, and October is the driest month with an average precipitation of 86 mm (annual precipitation = 2800 mm). Temperatures are typically high at every month of the year, resulting in an annual average of 26° C, with a thermal amplitude of approximately 8° C (minimum monthly average of 23° C and maximum of 31° C). Relative air humidity has an annual average of about 80% and reaches 90% in the period from December to June (SECTAM 1994).

The vegetation is mostly ombrophilous dense alluvial forest, with emergent and uniform canopy in areas of lowland floodplain. Flooded forests and sandy alluvial deposits (beaches) covered by scarce vegetation, which are characteristic of Guajara Bay as a whole, are also present (Novaes and Lima 1998).

FIELD METHODS

We observed 63 arrivals at the roost and 50 departures from ($n = 113$ days) between September 2004-September 2005 and between August-December 2006. Parrots were observed from a medium-sized boat positioned in a strategic point (south-east of the island), from where it was possible to clearly observe the parrots' arrival and departure.

When possible, two visits were done every week, one in the afternoon, between 17:00-19:00 h, and the other in the morning of the following day, between 05:00-8:00 h, beginning before sunset and sunrise, respectively. Estimates of arriving or departing parrots were made continuously on a per minute basis throughout the observation period by three teams each in a different part of the boat. Each team consisted of at least one observer and one

auxiliary. The observers announced the number of all arriving or departing parrots as seen with the aid of 7x50 binoculars, being careful not to duplicate individuals already counted by themselves or by another team. The auxiliaries recorded the data, controlled the digital chronometer and registered environmental data.

Weather conditions were represented by codes (C1 = cloudless; C2 = overcast; R1 = without rain; R2 = raining). Data on temperature and humidity were obtained with a thermohygrometer (Oregon Scientific). Wind speed was determined with a digital anemometer (MANUFACTURER, AD-250). Local luminosity was measured minute by minute with a luxmeter (MANUFACTURER, LD-201 Minolsystem).

Data were analyzed with Statistica Software 7.1 (Statsoft Inc. 2005) and were expressed as means \pm sd. Variables were examined for normality using Kolmogorov-Smirnov tests. The Mann-Whitney nonparametric test was used when the distribution of values differed significantly from normality, and in normal distribution Student's t-test for independent samples and Pearson's correlation were used. The tests were considered statistically significant at $P < 0.05$.

RESULTS

ARRIVAL OF PARROTS AT THE ROOSTING SITE AND ABIOTIC FACTORS

In 52 out of 63 birds arriving at a roost, the majority of parrots arrived after sunset. For all observations combined, the percentage of parrots arriving after sunset was significantly greater than the percentage of individuals arriving before sunset (Mann-Whitney Test, after sunset = $75 \pm 29\%$ vs before sunset = $23 \pm 28\%$, $U = 432$, $P < 0.0001$; Fig. 1).

On average, the first parrots arrive at the roosting site 27 ± 18.5 minutes before sunset ($N=63$), the peak of arrival of individuals occurs 6 ± 6.1 minutes after sunset, and the last parrots arrive 20 ± 5.99 minutes after sunset.

We found that when the sky was cloudless (C1, $N=29$), the number of individuals arriving at the roosting site after sunset (AS) was greater than when the sky was overcast (C2, $N=34$) (Student's t-test: $ASC1 = 91 \pm 13\%$ vs $ASC2 = 63 \pm 32\%$, $t_{61} = 4.45$, $P < 0.0001$). On days with rain (R2), more birds arrived before sunset ($ASR1 = 82 \pm 25\%$ vs $ASR2 = 44 \pm 29\%$, $t_{61} = 4.4$, $P < 0.0001$).

There was a moderate positive correlation between the temperature and the percentage

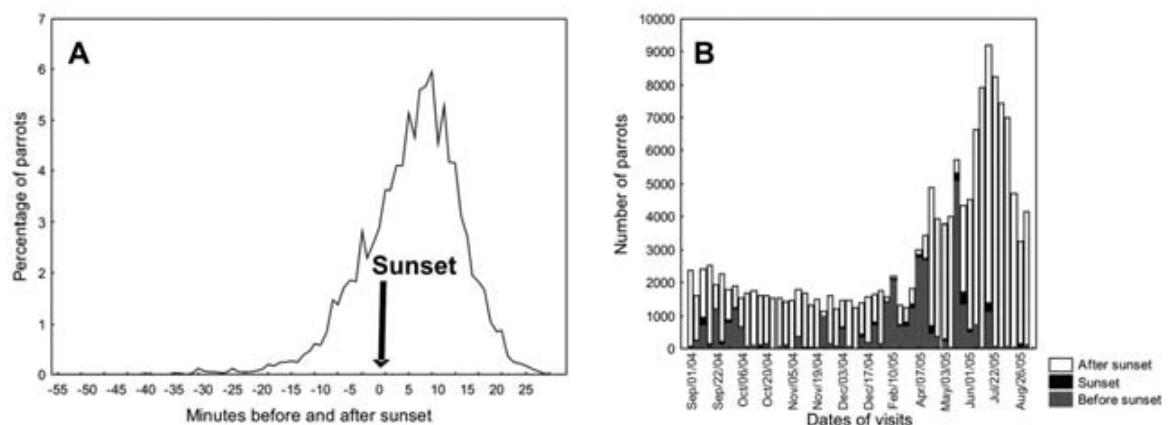


Fig. 1. **A** Results for a typical observation period showing the percentage of parrots arriving at the roosting site minute by minute before and after sunset. **B** Results for all observation periods showing the number of parrots arriving before, during and after sunset.

of individuals arriving after sunset (Pearson's correlation: $r_{56} = 0.544$, $P < 0.0001$). There was a moderate negative correlation between humidity and the number of individuals arriving after sunset ($r_{56} = -0.519$, $P < 0.0001$). There was no statistical correlation between the wind speed and the arrival time of parrots ($r_9 = 0.48$, $P = 0.186$).

Considering the amount of local luminosity (lux) at the moment of sunset (280 ± 150.8 lux), we verified that on average $94 \pm 5.4\%$ of individuals arrived at light intensities between 300-2 lux, with most parrots arriving at 50 lux (Fig. 2). There was a strong negative correlation between the luminosity and the arrival time of parrots. When luminosity at sunset reduces, more individuals arrives at the roost ($r_{43} = -0.75$, $P < 0.0001$).

On cloudy or rainy days the light intensity at sunset is lower than in sunny or cloudless days (cloudless days = 421 ± 161 lux vs cloudy days = 210 ± 90 lux; without rain = 345 ± 145 lux vs rainy days = 150 ± 18 lux).

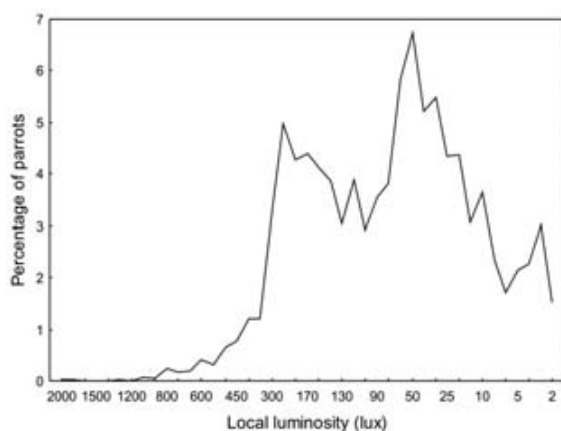


Fig. 2. Average percentile rank for individuals arriving at the roosting site, considering the gradient of luminosity.

DEPARTURE OF PARROTS FROM THE ROOSTING SITE AND ABIOTIC FACTORS

For 49 out of 50 observation periods, the majority of parrots left the roost site before sunrise (before sunrise = $76 \pm 15\%$ vs after sunrise = $24 \pm 15\%$, $U = 87.5$, $P < 0.0001$; Fig. 3).

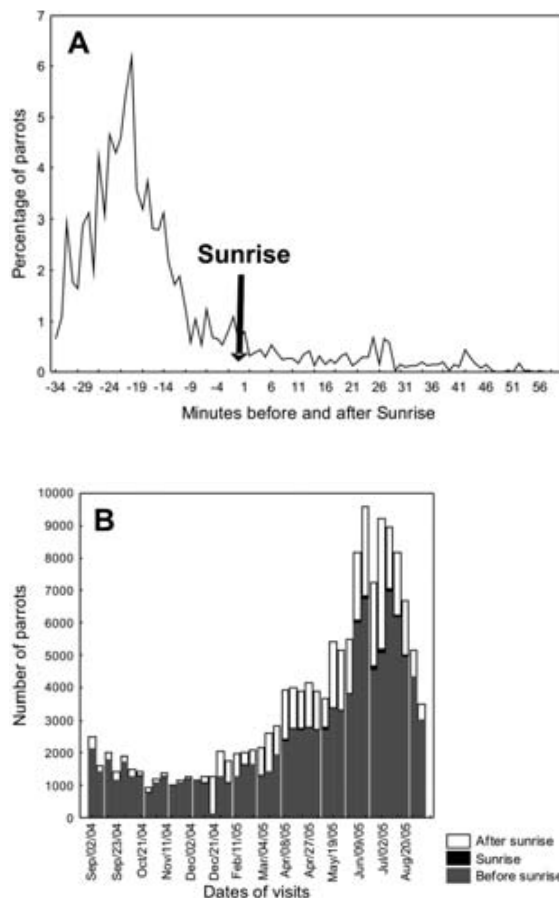


Fig. 3. **A** Representative observation period showing the percentage of parrots leaving the roosting site minute by minute before and after sunrise. **B** Number of parrots leaving the roost site before or after sunset for all observation periods.

On average, the first parrots left the roost site at 29 ± 4.95 minutes before sunrise, and the peak of departure occurred at 23 ± 5.24 minutes before sunrise.

On cloudless days (C1), the number of individuals leaving the roosting site before sunrise (BS) was greater than when the sky was overcast (C2) ($BSC1 = 79 \pm 10\%$ vs $BSC2 = 63 \pm 21\%$, $t_{48} = 3.59$, $P = 0.0009$). It was not possible to test if rain influenced in the departure of parrots because it rained during only four morning observation periods.

There were no statistically significant correlations between temperature, humidity or

wind speed with the time of departure of parrots ($r_{44} = -0.235$, $P = 0.124$; $r_{44} = 0.0019$, $P = 0.99$; $r_8 = 0.335$, $P = 0.462$, respectively).

Average luminosity at sunrise was 299 ± 88 lux, and $83 \pm 5.42\%$ of parrots left the roost site at luminosities between 1-300 lux, with a peak of departure at 1 lux (the minimum measurable luminosity; Fig. 4). There was a weak negative correlation between the luminosity and the time of departure of parrots. When the luminosity reduces, more individuals leave the roost ($r_{59} = -0.30$, $P = 0.02$).

On cloudy or rainy days, the light intensity at sunrise is lower than in cloudless days (cloudless days = 339 ± 40 lux vs cloudy days = 181 ± 93 lux).

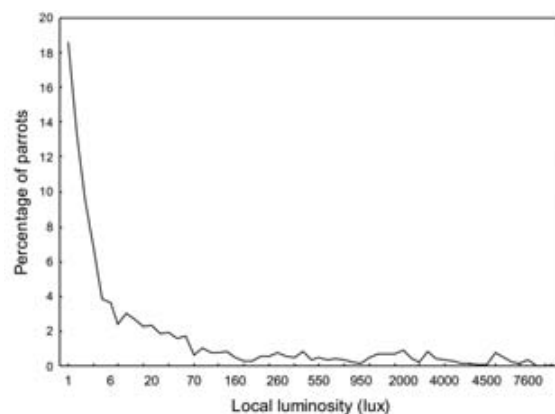


Fig. 4. Dependence of the percentage of parrots leaving on luminosity.

DISCUSSION

The ability to perceive and respond to changes in luminosity is a feature of the biological clock in all organisms, and luminosity is frequently the main modifier of intrinsic circadian rhythms (Randall et al. 2000). Here we describe the effects of the light/dark cycle on the synchronization of the arrival and departure of the parrot *A. amazonica* at its roost.

Although the Orange-winged Amazon is a diurnal bird, it travels from and to its roosts during periods of low luminosity. These data corroborate many other studies detailing the importance of the crepuscular periods in the behaviour of parrots (Sick 1997).

Observations of some parrot species have suggested that their arrival at the roost site is largely complete by sunset (Rocha et al. 1988, Harms and Eberhard 2003, P.C.R. Costa, unpublished data). For instance, according to P.C.R. Costa (unpublished data), the majority of White-winged Parakeets *Brotogeris versicolurus* arrives at their roost site before sunset, taking advantage of the last daylight for feeding before perching in the Kapok trees *Ceiba petandra*, where they habitually roost. However, in this work we show that 75% of the population of *A. amazonica* studied arrives after sunset.

Our finding that the majority of parrots leave the roost site before sunrise is in agreement with the results of Rocha et al. (1988) for a mixed roost of five parrot species leaving to spend the daylight hours in Terra firme forest. However, our data contrast with those of Harms and Eberhard (2003), who found that *Aratinga pertinax* individuals left the roost site after sunrise.

Daily movements of parrots were described by Forshaw (1966), and the use of roost sites could be to provide a more protected night shelter from predators than those available in Terra firme forests (Lazarus 1972, Snyder et al. 1987). However, we have no data of relevance to this hypothesis. The return from the roost site to Terra firme forest is presumably related to inadequate food supplies for the high number of parrots at the roost (Rocha et al. 1988).

Weather conditions exert important influences on the expression of endogenous rhythms by promoting adjustments through specific biological mechanisms, with each species having defined limits in their responsiveness (Rotenberg et al. 2003). On overcast and rainy afternoons it gets dark earlier, and temperature is lower and humidity higher than on cloud-free afternoons. The parrots respond to change in luminosity by arriving earlier at the roost site. Similarly, the reduction of luminosity on overcast mornings leads to a delayed departure from the roost site. These effects were confirmed here for *Amazona*

brasiliensis, with individuals arriving at the roost site more than three hours before sunset on overcast days (Cougill and Marsden 2004).

In conclusion, adverse weather conditions such as cloudiness and rain can act as masking agents, modifying the biological rhythm of species, in this case the times of arrival and departure of *A. amazonica* at its roost site. The ability to quickly modify nycthemeral rhythms in response to changes in ambient conditions adds an important level of adaptive plasticity to the animal's temporal response to its environment (Marques et al. 2003).

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RESUMO

Estímulos ambientais exercem efeitos importantes na expressão de ritmos endógenos. Deslocamentos diários de grupos de psitacídeos em resposta ao ciclo claro/escuro têm sido estudados por alguns autores. Todavia, os fatores que influenciam a ritmicidade intrínseca deste comportamento não são bem conhecidos. Este estudo descreve como a periodicidade nictemeral/circadiana dos deslocamentos diários de dormitórios do Papagaio-do-mangue *Amazona amazonica* é modificada por fatores climatológicos. Os números de papagaios chegando ou deixando o dormitório Ilha dos Papagaios foram determinados de minuto a minuto. Um número significativamente maior de papagaios chegou ao dormitório após o ocaso, enquanto que um número significativamente maior de papagaios deixou o dormitório antes da aurora. O pico de saída

dos papagaios ocorreu $23 \pm 5,24$ minutos antes da aurora, quando a média de intensidade de luz era de 1 lux. O pico de chegada de papagaios ocorreu $6 \pm 6,1$ minutos após o ocaso, quando a média de intensidade de luz era de 50 lux. Ao alterar a intensidade de luz do ambiente, as condições climatológicas influenciaram significativamente os horários de chegada e saída, com papagaios deixando o dormitório mais tarde ou chegando mais cedo em condições de nebulosidade alta.

Palavras-chave: *Amazona amazonica*, Amazônia, ritmos biológicos, ciclos claro/escuro, comportamento de pernoitar em dormitórios, condições climatológicas.

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