

# Breeding biology of the White-winged Nightjar (*Eleothreptus candicans*) in eastern Paraguay

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**ABSTRACT: Breeding biology of the White-winged Nightjar (*Eleothreptus candicans*) in eastern Paraguay.** I present the first detailed description of the breeding biology of the White-winged Nightjar (*Eleothreptus candicans*), based on data collected over three breeding seasons during 1998-2001 at Aguará Ñu, Canindeyú, eastern Paraguay. Male nightjars defended small territories situated on the upper slopes of ridgelines. Each territory contained one or more “display arenas” at which the male performed nuptial display flights. Aggregation indices confirmed that the primary display arenas of males were significantly clustered within the survey area. Within their territories, males apparently selected display arenas on the basis of their structural characteristics: mounds used as arenas were significantly lower and broader than random mounds. Males engaged in display activity from late August to early January. On average, males performed  $0.54 \pm 0.04$  display flights per minute during nocturnal focal watches, but there was considerable intra-male variation in display rate. Following a burst of activity immediately after their arrival at display arenas at dusk, male display rate was best explained by ambient levels of moonlight. Males produced a previously undescribed insect-like “tik tik” call when inactive on their territories. Females made two nesting attempts per season, using a different site ( $360 \pm 31$  m apart) for each attempt. The clutch of two eggs was laid directly on the ground, adjoining a small access “clearing”, in either campo cerrado or wet grassland vegetation. The first egg was laid within two days of a full moon for all seven clutches for which laying date was confirmed. Incubation, brooding and chick provisioning duties were carried out exclusively by the female. The incubation period was 19 days and the nestling period *c.* 19-20 days. Overall, my data are consistent with polygyny – and even an exploded lek or “landmark” mating system – in this population of White-winged Nightjars.

**KEY-WORDS:** Caprimulgidae; *Caprimulgus candicans*; cerrado; male display behaviour; nesting biology

## INTRODUCTION

Owing largely to their cryptic plumage and crepuscular or nocturnal habits, the Caprimulgidae (true nightjars) are comparatively under-studied. Their breeding biology in particular is poorly known, and for many species the only published data are anecdotal or based on single nesting attempts. Studies of the better-known species show them to be generally ground-nesting, with clutches of one or two eggs, and an essentially monogamous breeding system (Cleere 1999, Holyoak 2001). The Caprimulgidae are also one of only a few bird families in which lunar synchrony in reproduction has been documented (Murton & Westwood 1977, Holyoak 2001).

The White-winged Nightjar (*Eleothreptus candicans*) is one of the rarest caprimulgids in the Americas, considered Endangered by BirdLife International (2013). Research in Paraguay since the discovery of a population in 1995 at Aguará Ñu, Mbaracayú Forest Nature Reserve (Lowen *et al.* 1997), has clarified some aspects of its breeding biology, including the nest site, eggs and

chick (Capper *et al.* 2000, Clay *et al.* 2014) and male display behaviour (Clay *et al.* 2000). Male White-winged Nightjars were found to perform ritualised display flights at small arenas – low anthills or termite mounds – located on the upper slopes of ridgelines in areas of open grassland. Although males were present near these arenas throughout the night, display activity was highest under cloudless conditions on moonlit nights. Display flights were accompanied by a dull “tk...grrrrr” sound (recording in Ranft & Cleere 1998), perhaps produced by movement of air through the outer primaries.

Based on the apparent clustering of male display arenas at Aguará Ñu, Clay *et al.* (2000) suggested that this population of White-winged Nightjars might exhibit a lek or “landmark” mating system. Leks can be broadly defined as any aggregation of males visited by females primarily for the purpose of copulation, whereas landmark species are characterised by the use of a specialised habitat as encounter sites for mating (Höglund & Alatalo 1995). Four criteria were proposed by Bradbury (1981) to distinguish “classical” leks from other lek-like mating

systems: (1) lack of male parental care; (2) aggregation of males at an arena to which females come for mating; (3) arenas containing no resources required by females (e.g. nest sites, food) except males themselves; and (4) free mate choice by females visiting an arena. Lekking has been suggested to occur in at least three other species of caprimulgid (see Holyoak 2001). However, no nightjars were included on a list of 97 lek-mating bird species compiled by Höglund & Alatalo (1995).

Here I present the first comprehensive description of the breeding biology of the White-winged Nightjar, on the basis of data collected during a three-year study in Paraguay, including male display behaviour, the distribution of male territories and details of nesting biology based on data from multiple nesting attempts. I use these and other data to assess whether the study population exhibits a polygynous or lekking mating system, and consider the implications for the species's conservation.

## METHODS

Fieldwork was conducted over three breeding seasons (September-January) between October 1998 and January 2001 at Aguará Ñu (24°10'S, 55°17'W), a c. 5500-ha area of open-country habitats within Mbaracayú Forest Nature Reserve, Canindeyú department, eastern Paraguay. Aguará Ñu is a low plateau, 170-270 m above sea level, which forms a natural island of cerrado vegetation, flanked by forest to the south and west, and isolated from Paraguay's main areas of cerrado in the departments of Concepción and Amambay to the north-west (Jiménez & Knapp 1998).

Most fieldwork was focused on an area of c. 400 ha in southern Aguará Ñu, where a series of shallow valleys drain southwards into the Arroyo Guyrá Kehá. The seasonally wet grasslands of the valley bottoms and lower slopes are dominated by grass and sedge species, and woody vegetation is almost entirely absent. The drier soils of the upper slopes and ridge-tops support "campo cerrado" vegetation, consisting primarily of grasses and herbs, but with a scattering of shrubs (e.g. *Cochlospermum regium*, *Caryocar brasiliense*), Yata'i palms (*Butia paraguayensis*), saplings and the occasional fully grown tree. Palm density is lowest at the tips of the ridges in the south, where the campo cerrado is relatively open. Termite mounds, 15-90 cm in height, are present throughout the campo cerrado and wet grassland, and low anthills occur occasionally in the campo cerrado.

I identified breeding seasons by their principal year, so the season from September 2000 to January 2001 is termed the "2000 season". Adult White-winged Nightjars were captured, sexed and ringed, and lightweight (1.3-2.5 g; <5% of adult body weight) radio-transmitters were

attached to certain individuals, including all adult females captured (see Pople 2003 for details).

### Male territories and display arenas

I use the term "territory" to describe the relatively small area within which a male nightjar conducted all his breeding-season display activity (as per Clay *et al.* 2000). Each territory contained a primary "display arena" at which the male carried out most display activity, but some also contained one or more secondary arenas, which were used more sporadically, for example when the male was disturbed from its primary arena (Clay *et al.* 2000). For simplicity, the location of each territory was defined by its primary display arena. Radio-telemetry showed that c. 95% of nocturnal breeding-season fixes for radio-tagged males fell within 100 m of their display arenas (Pople 2003). In occasional cases when the primary display arena of a territory changed between or, more rarely, within seasons, the display arena used for longer was selected for subsequent analyses.

The study site was surveyed for displaying males each season between August and December. Males were initially located by the "tk...grrrrr" sound produced during display flights, which was often audible from up to c. 200 m. Surveys were mainly conducted on dry, relatively still, moonlit nights, when male display activity was at its highest (Clay *et al.* 2000). Once a displaying male was detected, it was observed for 10-15 minutes to identify its primary display arena, the precise location of which was recorded using a Magellan 2000 XL GPS receiver. It was then captured and fitted with an individually numbered metal tarsus ring, a coloured plastic ring, and a small, uniquely shaped piece of reflective tape, affixed to the dorsal side of one of the non-central tail feathers. This tail mark was unobtrusive when birds were at rest during the day, but conspicuous when illuminated with a torch at night. Territories were repeatedly revisited to study male display behaviour. During these visits, the identity of the male and the location of the display arena(s) were confirmed.

To investigate aggregative tendencies in displaying males, nearest-neighbour analysis (Clark & Evans 1954, Krebs 1989) was used to quantify the spatial distribution of territories (see also Höglund & Stöhr 1997). The distance from each primary arena to its nearest neighbour (i.e. the measure used herein to represent distances between territories) was derived from GPS locations, and the average nearest-neighbour distance (NND) within each season was calculated. Estimates of expected NND were then obtained (Clark & Evans 1954), assuming a random distribution of males within the survey area. The latter was defined by a convex polygon (of c. 400 ha) encompassing the zone surveyed most thoroughly

for territories (see Results). Since the small sample sizes in the current study prevented the use of a boundary strip, estimates of expected NND were corrected using Donnelly's (1978) adjustment for edge-effect bias. An index of aggregation (R) was obtained for each season by dividing the mean observed NND by the mean expected NND. When  $R = 1.0$  the observed spatial distribution does not deviate from random, whereas values of R between 1 and 0 indicate an increasing degree of clustering (Krebs 1989).

The gross topographical characteristics of male territories and an equal number of random points were measured using a digital version of a 1:50000 Paraguayan Instituto Geográfico Militar map, imported as a layer into a geographical information system (GIS) in ArcView 3.2 (ESRI 1999). The following variables were recorded for each site: (i) *gradient*, to nearest 1°; (ii) *altitude*, to nearest 5 m above sea level; (iii) *altitude difference*, from nearest "spot height" (peak local altitude); (iv) *distance to spot height*, to nearest 25 m; (v) *distance to stream*, to nearest 25 m; (vi) *aspect*, allocated to one of four quadrants (north-east, south-east, south-west and north-west).

Qualitative observations suggested that males did not select display arenas at random, even within territories. To determine how mounds used as display arenas differed from available mounds, the structural characteristics of nine display arenas used during the 2000 season were measured and compared to those from a sample of random mounds. The arenas included seven primary arenas and two (regularly used) secondary arenas of seven males. For each mound I measured: (i) *maximum height* (including any "towers"), to nearest 5 cm; (ii) *modal height*, *i.e.* height of the majority of the mound (excluding any "towers"), to nearest 5 cm; (iii) *basal "circumference"*, to nearest 0.1 m; (iv) *maximum basal chord*, across the longest axis of the mound, to nearest 0.1 m; (v) *presence/absence of "towers"*, *i.e.* free-standing vertical structures projecting above the modal level of the mound (see Figure 3a). For each display arena, four random mounds were selected by walking 20 m from the display arena on each of the four cardinal points of the compass, and then identifying the nearest mound. On two occasions it was not possible to locate a mound, hence the total number of random mounds measured was 34.

### Male display behaviour

To collect quantitative and qualitative data on male display behaviour, 30-minute focal watches were conducted on dry, relatively still evenings at the primary display arenas of territory-holding males. Focal males were monitored from *c.* 10-20 m away with the aid of a torch set on diffuse beam. Individuals did not appear to be disturbed by the presence of an observer, and on other occasions continued to display when I was just 5

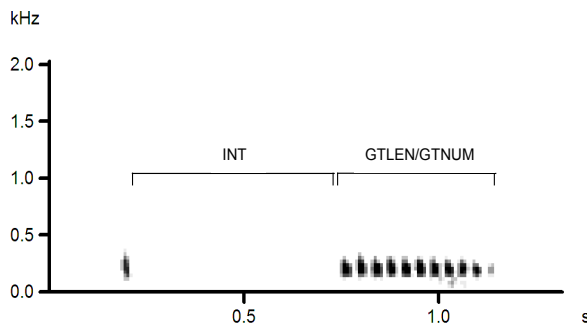
m away. Nautical twilight (the time at which the sun is 12° below the horizon) was used as the point delineating dusk or dawn from true "night" (Brigham & Barclay 1992). Until this point, lunar illumination is exceeded by residual solar light (Austin *et al.* 1976). Seventy-one per cent (64 of 90) of focal watches were begun before the end of nautical twilight, and thus termed "dusk watches". The remaining 26 watches were conducted under truly nocturnal conditions and termed "night watches".

During dusk watches, the observer arrived at the observation point shortly after sunset, and the watch commenced when the focal male arrived at the display arena. The number and time of all displays were then recorded, as well as details of any interactions with other individuals. A "display" was defined as any flight up from the display mound accompanied by both the "tk" and "grrrrr" sounds. Following the completion of the watch, the identity of the focal male was confirmed based on its reflective tail mark and/or colour rings.

Potential environmental correlates of male display rate were investigated using a multiple regression model, with the following variables: (i) *time*, in minutes, in relation to nautical twilight; (ii) *temperature*, minimum recorded during the watch; (iii) *moon phase*, proportion of the moon face illuminated (MFI); (iv) *moon height*, estimated degrees above the horizon; (v) *moonlight*, estimated lunar illuminance (see below). Ambient temperature was measured every 15 minutes with an electronic logger. Details of astronomical phenomena (*i.e.* MFI, times of sunrise/sunset, moonrise/moonset and twilights) were obtained from astronomical almanacs. Moon phase and height significantly influence overall lunar illuminance (Austin *et al.* 1976), but neither factor shows a simple linear relationship with illuminance (R. Willstrop *in litt.*), so their combined effects were estimated, using information in Austin *et al.* (1976), and treated as a separate measure: "moonlight".

Tape recordings of male display sounds and other "vocalisations" were made at the display arenas of marked males, from distances of *c.* 5-10 m, during the 1999 and 2000 breeding seasons. Recordings were later digitised and spectrograms of male display sounds generated in Avisoft using the following settings: FFT-length = 128; frame size = 100%; window = Blackman; overlap = 75%. These settings provided sufficiently fine temporal resolution (8 ms) to distinguish the separate elements of the "grrrrr" sound. The following temporal measures were obtained using the on-screen cursors (Figure 1): interval between "tk" and "grrrrr" components (INT); length of "grrrrr" component (GTLEN); number of elements constituting "grrrrr" component (GTNUM). Frequency measures were not taken, however, given the relatively poor resolution (31 Hz) and limited frequency range of display sounds.





**FIGURE 1.** Spectrogram of male White-winged Nightjar display sound showing “tk” and “grrrrrt” components and the three temporal variables measured for each recording (see text for definitions).

### Nesting biology

Nest sites were located by monitoring radio-tagged females and checking their daytime “roosts” for eggs every *c.* 2 days during the breeding season. The “initiation date” for a nesting attempt was defined as the date on which the first egg was laid: presence of eggs was the only factor reliably distinguishing nest sites from roost sites. Once a nest was initiated, its precise location was recorded using a GPS receiver. Gross topographical characteristics of nest sites and an equal number of random sites were measured as described above for male territories. To ensure that random sites reflected those available to, but not used by, nesting females, they were selected to fall within 400 m of the nest sites with which they were paired. Two radio-tagged females monitored during the 2000 breeding season ranged up to  $403 \pm 33$  m from the centre of their breeding ranges (pers. obs.).

The following variables were recorded for each site: (i) *gradient*, to nearest 1°; (ii) *altitude*, to nearest 5 m above sea level; (iii) *distance to nearest stream*, to nearest 25 m; (iv) *distance to nearest male display arena*, to nearest 10 m; (v) *aspect*, allocated to one of four quadrants (north-east, south-east, south-west and north-west); (vi) *habitat*, classified as one of two dominant types (campo cerrado and wet grassland). Habitat type was determined from a simplified habitat map of the study site, added as a layer to the GIS (see Pople 2003 for details).

The mass of freshly laid eggs was measured to the nearest 0.5 g. Measures of length and maximum breadth of eggs were taken to the nearest 0.1 mm. Egg volume was estimated following Hoyt (1979), using the equation:  $\text{volume} = 0.51 \times \text{length} \times (\text{maximum breadth})^2$ . During the egg stage, nests were visited every three to five days to confirm the sex of any adults present. These “spot-checks” were carried out at various times of day and night, independent of ongoing radio-telemetry fixes taken to characterise the home range and movements of individuals. Although radio-tracking equipment was sometimes used to confirm an adult’s identity, the bird’s location was not known prior to any spot-check.

Hatching success was calculated as the percentage of eggs laid that hatched successfully. This method can bias values for hatching success upwards, as it takes no account of nests failing before they are found (Beintema & Müskens 1987). However, my method of nest location reduced this risk, and the sample size was insufficient to use the daily exposure method (Mayfield 1961, 1975). Nests were visited every two to four days after hatching, and chicks were weighed (to nearest 0.5 g) to obtain data on their growth and development. Chicks were ringed at *c.* 10 days old, when their tarsus width was similar to adult birds. Younger chicks were individually marked with non-toxic white correction fluid on their feet.

During the nestling period, nocturnal focal watches of 50–255 minutes were conducted at nests to characterise the division of chick brooding and provisioning duties by the parents. Nest sites were monitored from distances of *c.* 10–20 m, using a head-torch with diffuse beam to obtain eye-shine from adults without disturbing them. The duration (to nearest five seconds) of each visit was recorded, along with the sex of the visiting adult. Radio-tracking equipment was occasionally used to confirm the identity of tagged birds, but monitoring was primarily visual. The data collected were used to calculate mean visit rates and average times spent at, or away from, the nest site. A small number of daytime spot-checks were conducted to assess parental allocation of diurnal brooding duties.

### Statistical analysis

All data were tested for normality and homoscedasticity, and then analysed using standard parametric or non-parametric univariate tests, as appropriate. If appropriate, data were subsequently also analysed using multivariate techniques. When the dependent variable was continuous (*e.g.* male display rate), multiple linear regression was used to investigate the effects of potential covariates. Analyses were conducted using a forward stepwise procedure with entry and removal probabilities set at  $P = 0.05$ . At each step, the variable with the most significant score statistic was entered into the model, provided that its inclusion significantly improved model fit: significance was tested using partial F-tests (Hair *et al.* 1995). This process was repeated until no further variables met the criteria for entry or removal, at which point the model was considered final.

When the dependent variable could be allocated to one of two discrete categories (*e.g.* male territory or random site, display mound or random mound), binary logistic regression was used to identify which combination of variables best distinguished between the two categories. Analyses were conducted using a forward stepwise procedure as outlined above, but with significance tested using likelihood ratio tests in which

the difference in deviance ( $-2 \times \log_e$  likelihood) between models with and without the variable was treated as  $\chi^2$ , with degrees of freedom (df) equal to the number of parameters being added (Manly *et al.* 1993). When comparing display mounds and random mounds, the inclusion of secondary mounds for two males raised the possibility of pseudoreplication. To address this, parameter estimates produced by the model were jack-knifed following Sokal & Rohlf (1995), taking the male as the sampling unit. Jack-knifed parameter estimates did not differ significantly from those of the original model, suggesting that pseudoreplication was not a major problem.

Categorical data were analysed using the G-test of independence. A form of the G-test for goodness of fit, adjusted using the Williams correction for the two-cell case (Sokal & Rohlf 1995), was used to compare the observed sex ratio of adult captures with that expected on the basis of a 1:1 sex ratio. Statistical significance was set at  $P < 0.05$  unless otherwise specified, and means are given  $\pm$  one standard error (SE). Since the repeated use of a statistical test increases the probability of committing a Type I error, the sequential Bonferroni technique was employed to adjust the initial  $\alpha$  level when making many simultaneous comparisons (Rice 1989).

## RESULTS

Forty-nine White-winged Nightjars (34 adult and 15 young birds; Table 1) were captured and ringed between 1998 and 2001. The sex ratio of captured adults was biased towards males in all three field seasons, and the overall ratio of 3.25:1 male:female differed significantly from parity. The four females captured in 1998 were all caught late in the breeding season, and none of them was confirmed to (re-)nest that season; two individuals captured in late December had already begun post-nuptial moult. Hence, all data on nesting biology were obtained from females caught during the 1999 and 2000 breeding seasons.

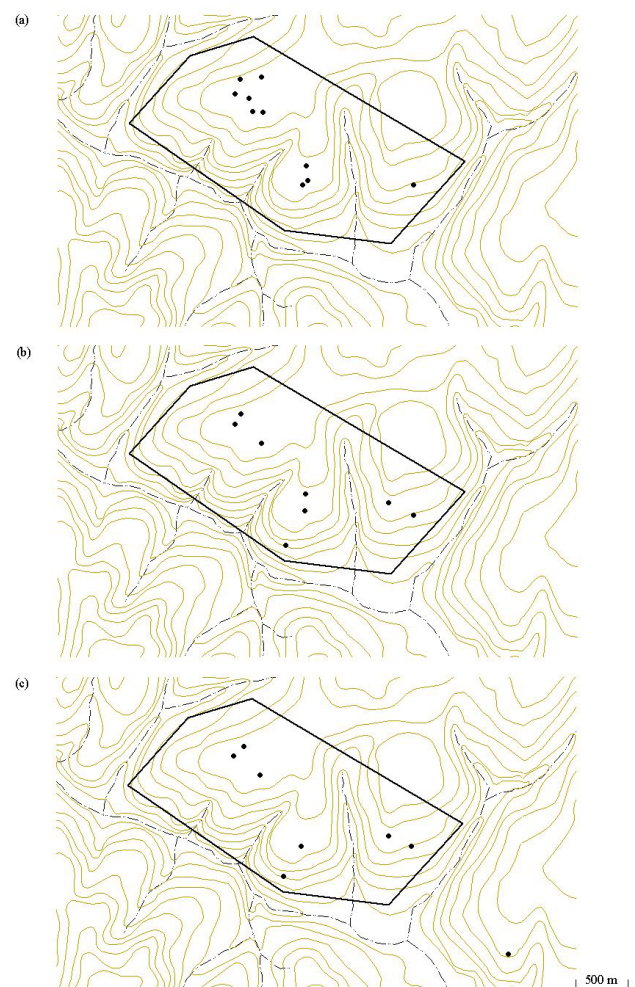
### Male territories

Breeding-season territories were identified for 10 males in 1998 and eight males in each of 1999 and 2000. One territory, discovered late in the 2000 breeding season, was excluded from the nearest-neighbour analysis as it was located outside the normal survey area (Figure 2). The remaining territory-holding males occurred at a mean density of one male per  $50 \pm 5$  ha ( $n = 3$  seasons) within the area surveyed. The closest male display arenas were just 70 m apart (in 1998), but the average nearest-neighbour distance across all three seasons was  $254 \pm 8$  m. Aggregation indices confirmed that primary display

arenas were significantly clustered within the survey area in all three seasons (Table 2).

In total, 13 distinct territories were identified between 1998 and 2000: five of these were occupied in all three breeding seasons, and a further three were occupied in at least two. The ownership of certain territories changed both between and, less frequently, within seasons, probably owing to the death or emigration of the original territory-holding male. In nine of 11 such changes in territory ownership, the original male was never recorded again; in two instances the male moved to a territory vacated by another "missing" male.

Male territories were located almost exclusively on the upper slopes of ridgelines running perpendicular to the main Arroyo Guyrá Kehá valley (running north-west to south-east across the lower half of the maps in Figure 2). Preliminary analysis of gross topographical characteristics using univariate tests suggested that territories differed significantly from random points for only one variable (Table 3). A binary logistic regression model, explaining *c.* 27% of the deviance in site use, also revealed that



**FIGURE 2.** Location of male White-winged Nightjar territories (closed circles) during: (a) 1998; (b) 1999; and (c) 2000 breeding seasons. Pale brown lines are contours, dashed lines are watercourses. The polygon represents the *c.* 400-ha survey area.



“distance to stream” was the only significant predictor (likelihood ratio test:  $\chi^2 = 9.89$ ,  $df = 1$ ,  $P < 0.005$ ): on average, male territories were further from streams than random points. The model correctly reclassified 69% of sites overall, with an equal degree of classification success for territories and random sites. Aspect was not entered into the model, but univariate tests suggested that male territories were more likely to have a westerly than easterly aspect compared to random points (11 of 13 *versus* 5 of 13; G-test:  $G = 5.80$ ,  $df = 1$ ,  $P < 0.05$ ).

At a finer scale, preliminary analysis of the structural characteristics of mounds used as display arenas in 2000 suggested that they differed significantly from random mounds for a number of variables (Table 4). However, a binary logistic regression model, explaining 25% of the

deviance in mound use, showed “modal height” to be the only significant predictor (likelihood ratio test:  $\chi^2 = 11.01$ ,  $df = 1$ ,  $P < 0.001$ ): on average, display mounds were lower than random mounds. The model correctly reclassified 91% of random mounds, but only 22% of mounds used as display arenas, resulting in an overall correct reclassification rate of 77%.

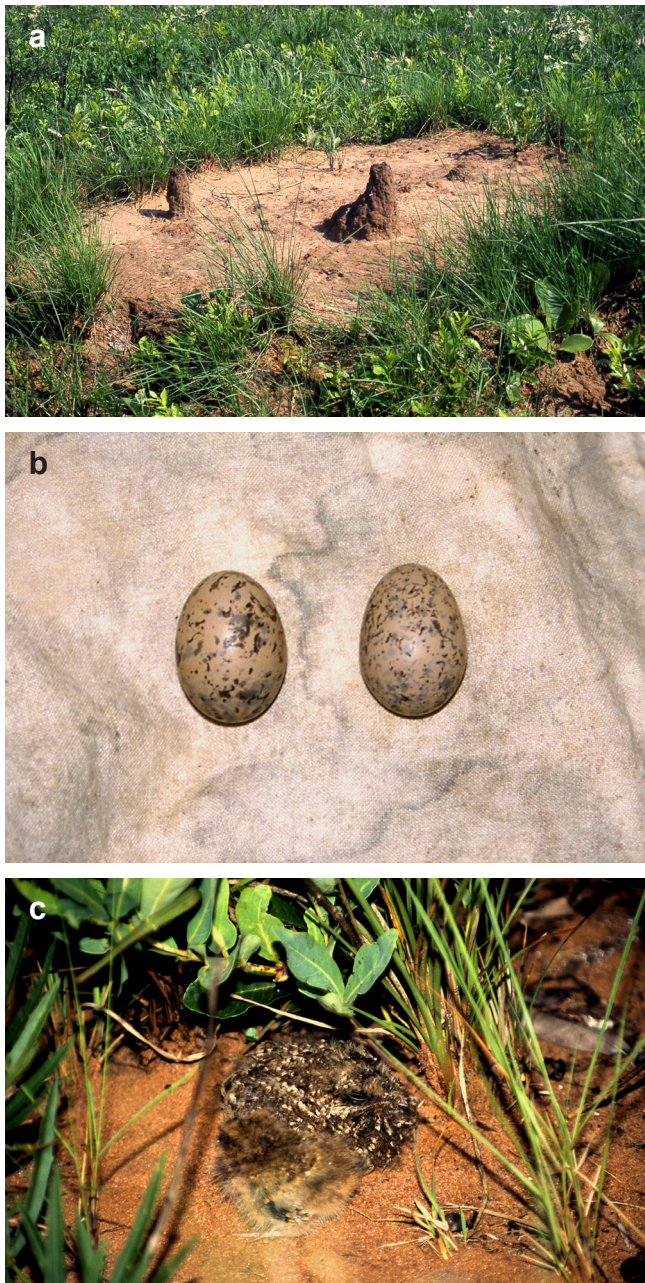
### Male display behaviour

In both 1999 and 2000, sporadic display activity was noted on certain nights leading up to the August full moon, but male display activity did not commence in earnest until September. Activity levels remained high through to December, but subsided soon after: the latest date on which display activity was noted was 6 January.

Although an attenuated version of the mechanical “grrrrr” sound was occasionally heard at the start of foraging sallies, the full “tk... grrrrr” display sound was only ever noted during male display flights at arenas. Of 132 display flights by five males in 2000, the majority (63%) were initiated from a nearby perch, but 23% immediately followed the return of the male from a foraging sally, and the remaining 14% involved males already sitting on their display arena. In these latter cases, the male was observed to jump up and down on the display arena to produce the “tk” (probably by contact with the mound), before flying up with the “grrrrr” sound as per usual. Display activity was not solely restricted to males in “definitive” plumage. A young male moulting into definitive plumage, but still retaining five or six (brown) juvenile outer primaries, was observed to display on two nights in early November 1998 (see below).

Recordings of 8-19 display sounds were obtained for eight marked males during the 1999 and 2000 breeding seasons. Spectrograms showed that display sounds had a relatively fixed structure, with the “tk” and “grrrrr” components separated by 500 to 700 ms, but with broadly similar frequency ranges (*c.* 100-400 Hz; Figure 1). The display sounds produced by the pre-definitive male in 1998 were of a noticeably higher frequency, but a recording of its display was not obtained for direct comparison. Two of the three temporal measures (GTLEN and GTNUM) were highly correlated (Spearman rank correlation:  $r_s = 0.96$ ;  $n = 103$ ;  $P < 0.001$ ). Only GTNUM was considered further, as it was judged to be less susceptible to measurement error. Males showed significantly more inter- than intra-individual variation for both INT (Kruskal-Wallis test:  $H = 57.82$ ,  $df = 7$ ,  $P < 0.001$ ) and GTNUM ( $H = 60.40$ ,  $df = 7$ ,  $P < 0.001$ ), suggesting consistent inter-individual differences in these temporal measures.

A total of 90 focal watches was conducted at male display arenas over the course of three breeding seasons (1998:  $n = 10$ ; 1999:  $n = 20$ ; 2000:  $n = 60$ ). No significant



**FIGURE 3.** Typical male display arena with “towers” (a), eggs (b) and chicks aged 14 days old (c) of White-winged Nightjar at Aguara N’u.

**TABLE 1.** Sex and age composition of White-winged Nightjars captured.

Season	Males	Females	Young birds	Total	Sex ratio (males/female)	G	P
1998	20	4	3	27	5.00	11.41	< 0.001
1999	14	3	5	22	4.67	7.50	< 0.01
2000	9	3	9	21	3.00	3.01	ns
Overall <sup>a</sup>	26	8	15	49	3.25	9.89	< 0.005

(a) Column totals do not equal "Overall" total due to recapture of certain individuals between seasons.

**TABLE 2.** Mean  $\pm$  SE nearest-neighbour distances (NND) and degree of aggregation for breeding-season territories of male White-winged Nightjars.

Season	No. male territories	Observed NND (m)	Expected NND (m) <sup>a</sup>	Aggregation index (R)	Significance <sup>b</sup>
1998	10	253 $\pm$ 97	372 $\pm$ 69	0.68	$z = -1.71$ , $P = 0.044$
1999	8	241 $\pm$ 35	425 $\pm$ 89	0.57	$z = -2.07$ , $P = 0.019$
2000	7	268 $\pm$ 34	460 $\pm$ 103	0.58	$z = -1.87$ , $P = 0.031$

(a) Assuming random distribution of males within 406 ha survey area (see Methods).

(b) P-values from one-tailed z-tests (Campbell 1996).

**TABLE 3.** Mean  $\pm$  SE values of topographical variables for male White-winged Nightjar breeding-season territories and an equal number of random points.

Variable	Male territories (n = 13)	Random points (n = 13)	Significance <sup>a</sup>
Gradient ( $^{\circ}$ )	2.2 $\pm$ 0.6	4.5 $\pm$ 0.7	$W = 220$ , $P = 0.023$
Altitude (m)	232 $\pm$ 4	214 $\pm$ 6	$t_{24} = -2.51$ , $P = 0.019$
Altitude difference (m)	11 $\pm$ 3	29 $\pm$ 7	$W = 220$ , $P = 0.023$
Distance to spot height (m)	406 $\pm$ 77	683 $\pm$ 110	$t_{24} = 2.06$ , $P = 0.050$
Distance to stream (m)	567 $\pm$ 74	310 $\pm$ 46	$W = 122$ , $P = \underline{0.007}$
Aspect – number of sites facing:			
NE (0-90 $^{\circ}$ )	0 (0%)	0 (0%)	
SE (90-180 $^{\circ}$ )	2 (15%)	8 (62%)	
SW (180-270 $^{\circ}$ )	6 (46%)	2 (15%)	
NW (270-360 $^{\circ}$ )	5 (38%)	3 (23%)	

(a) From unpaired t-tests or Mann-Whitney U-tests. Values underlined indicate table-wide significance at an adjusted initial a level of 0.01 (Rice 1989).**TABLE 4.** Mean  $\pm$  SE values of the structural characteristics of male White-winged Nightjar display arenas used during 2000 breeding season compared to a sample of random mounds.

Variable	Display arenas (n = 9)	Random mounds (n = 34)	Significance <sup>a</sup>
Maximum height (m)	0.42 $\pm$ 0.10	0.61 $\pm$ 0.04	$W = 831$ , $P = 0.014$
Modal height (m)	0.24 $\pm$ 0.03	0.51 $\pm$ 0.05	$W = 842$ , $P = \underline{0.006}$
Basal "circumference" (m)	6.0 $\pm$ 0.8	3.7 $\pm$ 0.5	$W = 665$ , $P = \underline{0.013}$
Maximum basal chord (m)	2.1 $\pm$ 0.3	1.1 $\pm$ 0.1	$W = 654$ , $P = \underline{0.005}$
"Tower(s)":			
present	3 (33%)	8 (24%)	$G = 0.32$ , ns
absent	6 (67%)	26 (76%)	

(a) From Mann-Whitney U-tests or G-test. Values underlined indicate table-wide significance at an adjusted initial a level of 0.01 (Rice 1989).

differences in display rate were apparent between seasons (Kruskal-Wallis test:  $H = 1.18$ ,  $df = 2$ ,  $P > 0.05$ ), so data were pooled for subsequent analyses. On average, males performed  $0.54 \pm 0.04$  displays per minute during focal watches, although considerable variation in display rate was apparent (range: 0.00-1.37 displays/min;  $n = 90$ ). However, when comparing the six males for which five or more focal watches were conducted, no evidence was found for consistent inter-male differences in display rate ( $H = 5.95$ ,  $df = 5$ ,  $P > 0.05$ ).

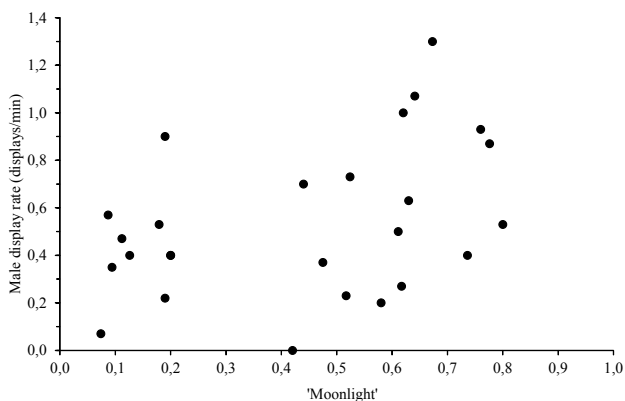
On average, males arrived at their display arenas  $26.6 \pm 0.6$  minutes after sunset and  $27.9 \pm 0.7$  minutes before the end of nautical twilight. On arrival, males showed a burst of high display activity. The mean display rate in the first half of dusk watches was more than twice that in the second half ( $0.75 \pm 0.06$  versus  $0.35 \pm 0.04$  displays/min; Wilcoxon signed ranks test:  $T = 1742$ ,  $n = 64$ ,  $P < 0.001$ ), whereas there was no significant difference between the two halves of night watches ( $0.50 \pm 0.07$  versus  $0.54 \pm 0.06$  displays/min; paired t-test:  $t_{25} = -1.01$ ,  $P > 0.05$ ). When considering night watches alone, "moonlight" was the only environmental variable that explained a significant amount of the variation in display rate (overall fit of model:  $R^2 = 0.166$ ,  $F_{1,24} = 4.77$ ,  $P < 0.05$ ). Display rate was positively related with this estimate of overall lunar illuminance, reflecting a tendency for males to display more when the moon was fuller and higher in the sky (Figure 4). However, even when conditions were not suitable for display activity, males were generally still present – either sallying or resting – on their territories. There was no significant relationship between display rate and sallying rate during focal watches in which the latter was measured (Spearman rank correlation:  $r_s = -0.26$ ;  $n = 36$ ;  $P > 0.05$ ).

During one display watch in November 1998, the focal male produced a previously undocumented, insect-like "tik tik" call whilst perched in the vicinity of its display arena. This vocalisation (or a single "tik" equivalent)

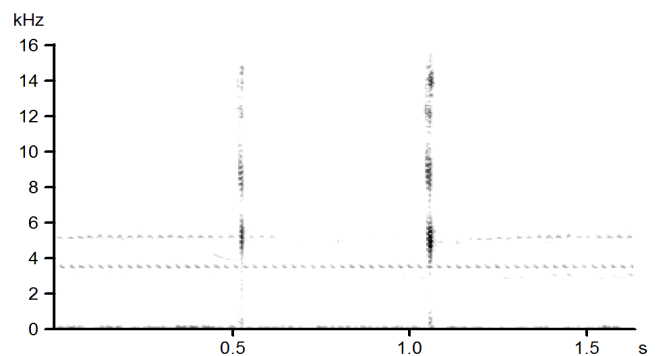
was subsequently recorded on several occasions during display watches (see Figure 5 for spectrogram), and was only observed from males perched in or near their display arena. The thin, high-pitched nature of the call made it difficult to detect under certain conditions, but it was apparently produced at rates of  $1.24 \pm 0.20$  "tik tiks" per minute (range: 0.00-3.33 calls/min; data from 26 display watches). There was no significant correlation between the rate of "tik tik" production and male display rate during display watches (Pearson correlation:  $r = 0.31$ ,  $n = 26$ ,  $P > 0.05$ ).

Aggressive interactions between males were observed during 14 focal watches (30% of watches for which details were noted) and on various occasions during *ad hoc* observations at display arenas. Interactions typically comprised rapid chases, sometimes involving up to three males, and occasionally also physical contact. A soft, liquid "gurgling" call produced during chases was noted on a number of occasions. Aggressive interactions were observed most frequently at one particular display arena (11 of 14 watches), and this bias was significant when allowing for the distribution of watches among display arenas (G-test:  $G = 7.64$ ,  $df = 1$ ,  $P < 0.01$ ). There was a non-significant trend for higher rates of display activity during watches that included male-male chases compared to during those that did not ( $0.74 \pm 0.10$  versus  $0.53 \pm 0.06$  displays/min; unpaired t-test:  $t_{44} = -1.76$ ,  $P = 0.085$ ).

It was not possible to record female visits to male display arenas reliably, owing to difficulties in distinguishing unmarked females from juveniles or from females of other similar-sized species (e.g. Little Nightjar *Setopagis parvulus*). However, during one dusk watch in October 1998, five nights prior to full moon, a female visit and presumed copulation were documented. Over the course of *c.* 20 minutes, the female landed on the display arena at least twice, and three presumed copulation attempts by the focal male were witnessed. Prior to one



**FIGURE 4.** Male White-winged Nightjar display rate in relation to "moonlight", an estimate of lunar illuminance. Data from "night" watches only (Pearson correlation:  $r = 0.41$ ,  $n = 26$ ,  $P < 0.05$ ).



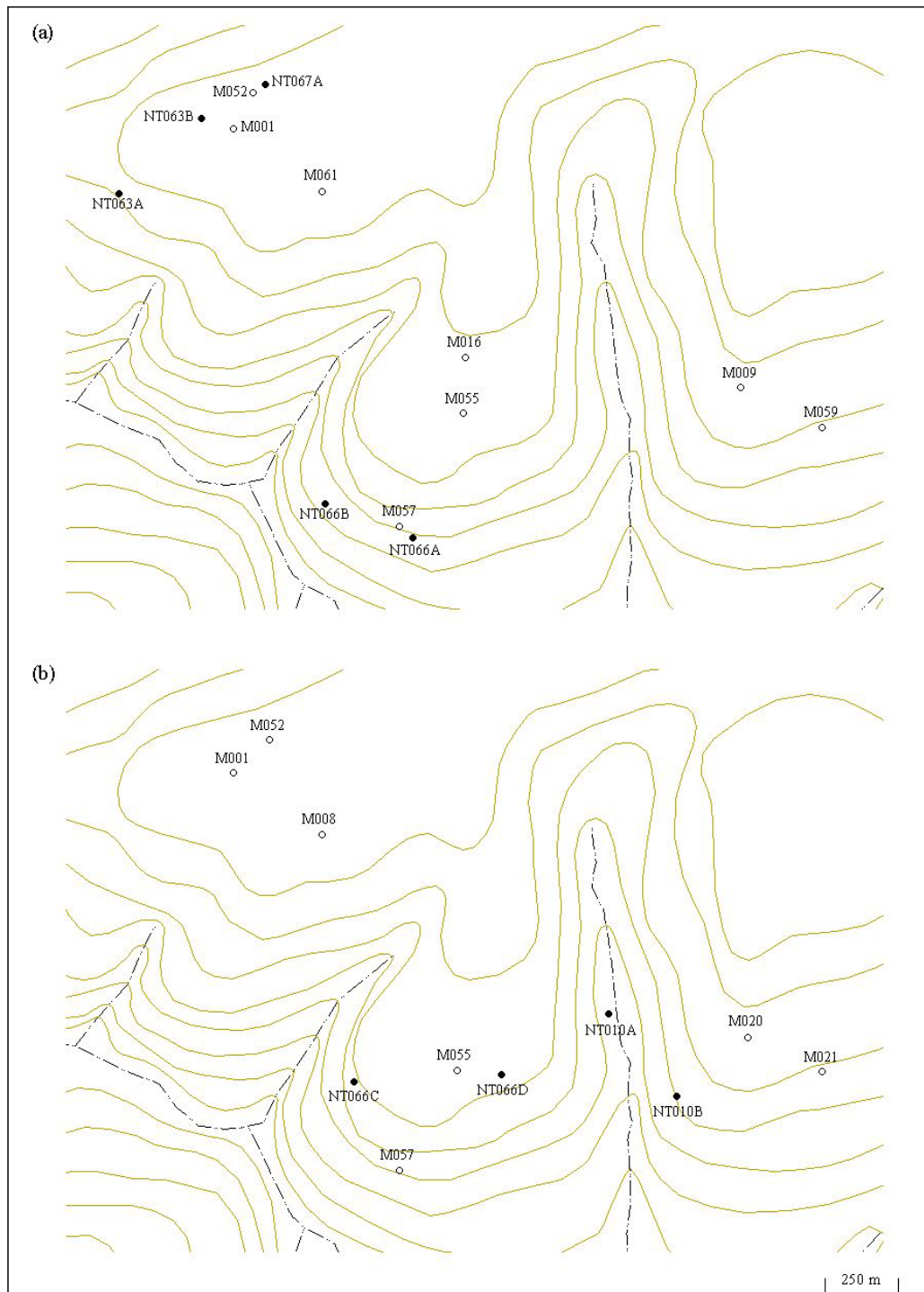
**FIGURE 5.** Spectrogram of previously undescribed, insect-like "tik tik" call given by male White-winged Nightjars when inactive in vicinity of display arenas. Note background insect noise at *c.* 3.5 and 5.0 kHz. Recordings made by M. C. Velázquez at Aguará Ñu in December 2000.



attempt, the male appeared to display to the female whilst they were both perched on the arena, by spreading its wings and cocking and splaying its tail. When the female left the display arena after copulation, the male followed and flew parallel to her, with wings raised, in a slow buoyant flight, conspicuously different to the rapid flight typical of male–male encounters. On another occasion, in December 2000, a male was observed to conduct a similar “escort” flight, with raised wings, for a presumed female flying through his territory.

### Nesting biology

I documented nine breeding attempts by four different females : five in 1999 and four in 2000 (Table 5). A fifth female captured in early December 2000 was heavily gravid, but not subsequently relocated. Eggs were laid directly on the ground, in campo cerrado (six nests) or wet grassland (three nests) vegetation, within a small “tunnel” between tussocks of grass or herbaceous plants and facing onto a small area of bare earth (c. 25-50 cm in diameter),



**FIGURE 6.** Distribution of White-winged Nightjar nest sites in relation to male display arenas during: a) 1999 and b) 2000 breeding seasons. Nest sites displayed as filled circles; multiple nesting attempts distinguished by “A”, “B”, etc. Display arenas displayed as open circles; labels refer to the territory-holding male. Note the territorial fidelity in successive seasons shown by males M001, M052, M055, and M057.

the latter apparently serving as a “runway” for the adult bird (as at roost sites; pers. obs.). There was no evidence to suggest that the gross topographical characteristics of nest sites differed significantly from those of random sites available to nesting females (Table 6).

Initiation date was confirmed for seven clutches, and consistently fell within two days of a full moon ( $1.3 \pm 0.3$  days; range: 0-2). The earliest initiation date observed was 25 September (in 1999), although two chicks discovered on 13 October 2000 were estimated to be approximately 10 days old, and had probably hatched from eggs laid around the full moon of 14 September. Females made two nesting attempts per season, using a different site for each attempt (mean distance between nest sites:  $360 \pm 31$  m, range: 296-461 m,  $n = 4$ ; Figure 6). The female (F067) captured in late November 1998, whilst brooding a single chick, was probably making a second breeding attempt (Table 5).

Clutch size was two for all seven clutches discovered at the egg stage. It was not possible to check each nest daily, but the second egg was generally laid within 24 hours of the first, although in one case there was a delay of at least 30 hours. Eggs were pale cream-beige, with variable dark brown and mauve-grey speckling and blotching (Figure 3b). Differences in egg patterning were observed within most clutches, with one egg being more densely and uniformly covered in fine markings, and the other showing fewer, larger markings, often with a subapical ring of grey blotches at the obtuse pole. Egg morphometrics are summarised in Table 7. Both eggs of a clutch weighed on day 1 and day 18 of incubation decreased in mass by 0.7 g (11% and 12%) during the intervening period.

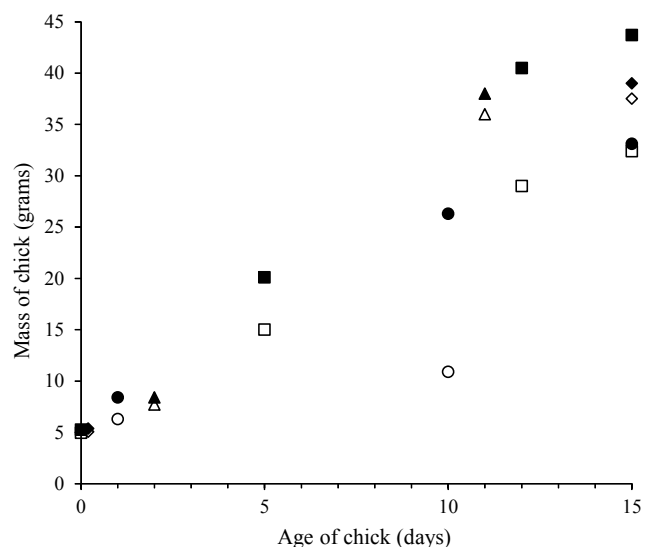
Incubation began with the laying of the first egg, and was carried out exclusively by the female: no male was ever found at the nest site. Thirty-four spot-checks carried out at seven nests during the incubation period found the female in attendance during 100% (20 of 20) of daytime and 57% (8 of 14) of nocturnal checks. During nine daytime checks, the female was present but sitting slightly behind one ( $n = 3$ ) or both ( $n = 6$ ) of the eggs. There was no significant difference in ambient air temperature on these occasions compared to 11 occasions when the female was incubating both eggs (unpaired  $t$ -test:  $23.4 \pm 1.8^\circ\text{C}$  versus  $23.7 \pm 1.3^\circ\text{C}$ ;  $t_{18} = -0.13$ ;  $P > 0.05$ ). Although I could not confirm the hatching date for every clutch, the modal incubation period was 19 days, and chicks probably hatched within 24 hours of each other.

Hatching success was 86% (12 of 14 eggs) for the seven nests for which initial clutch size was known. At hatching, chicks had open eyes and were covered in a pale buff-coloured down, with greyish legs and pale-tipped greyish bill. The average mass of four chicks (from two clutches) on day of hatching was  $5.2 \pm 0.1$  g. Clear

asymmetry in growth rate was observed in two broods: in one (circular symbols in Figure 7), the larger chick (26.3 g) weighed more than twice its sibling (10.9 g) by day 10 (see also Figure 3c). The latter had disappeared by day 15.

Nocturnal focal watches conducted at six nests (of four females) showed that chick brooding and provisioning was undertaken solely by the female. In almost 25 hours of monitoring (mean watch length:  $113.6 \pm 17.3$  min,  $n = 13$ ), no male visits were observed, whereas 67 female visits were recorded, at a mean rate of  $3.04 \pm 0.80$  visits/hour (range: 1.20-4.94;  $n = 4$  females). Females spent on average  $7.7 \pm 1.3$  minutes (range: 0.1-46.0 min;  $n = 58$ ) at the nest during each visit, and  $11.8 \pm 1.3$  minutes (range: 1.5-59.9 min;  $n = 55$ ) away from the nest between visits. It was not possible to confirm whether chicks were provisioned on every visit. Time spent at the nest during nocturnal focal watches was negatively correlated with minimum ambient temperature (Spearman rank correlation:  $r_s = -0.81$ ,  $n = 13$ ,  $P < 0.005$ ). In 100% (10 of 10) of daytime checks during the chick period, the female was present at the nest site, either brooding or immediately adjacent to the chicks.

Females displayed a range of anti-predator behaviours whilst incubating or brooding. When initially approached, they relied on their cryptic plumage, crouching motionless with eyes closed to slits. If the intruder approached to within 0.5-2.0 m, they would shuffle forward into the adjacent clearing in preparation for take-off. On one occasion, a female incubating a single, recently laid egg performed a presumed threat display: drooping the wings slightly, puffing up the body



**FIGURE 7.** Growth rate of eight White-winged Nightjar chicks between hatching and 15 days of age. Each brood represented by different shape; open and closed symbols represent two chicks within same brood. Four chicks weighed on day 0 had masses of c. 5 g (square and diamond symbols).

feathers, raising and slightly splaying the tail, whilst rocking the body and tail from side-to-side. When eventually flushed (off eggs or chicks), females typically performed an injury-feigning distraction display, flying 5-10 m away from the nest with a low, laboured flight, before landing clumsily in the vegetation. If approached again, the female would fly off normally, although on most occasions she was subsequently found to have remained near the nest site.

At one week old, chicks were already beginning to lose their natal down and attain the juvenile plumage

pattern. After about 10 days, the developing flight feathers began to project from their feather sheaths. Although I could not confirm the exact age of fledging, extrapolation of observed growth rates suggests that chicks attain mean adult mass (*c.* 50 g) at *c.* 19 days. The sole surviving chick of one clutch present on day 18 could not be relocated on day 20.

Owing to uncertainty over the fate of most broods, I could not estimate fledging success or overall nesting success. I recorded two instances of predation (once of eggs, once of chicks; Table 5), but could not identify

TABLE 5. Summary of White-winged Nightjar nesting attempts during 1999 and 2000 breeding seasons.

Season	Female	First nesting attempt				Second nesting attempt			
		Date first egg laid	Incubation period	Hatching date	Chicks last seen at nest site	Date first egg laid	Incubation period	Hatching date	Chicks last seen at nest site
1999	F063	26 September	– <sup>a</sup>	–	–	25 October	19 days	13 November	1 December <sup>b†</sup>
1999	F066	25 September	19 days	14 October	25 October <sup>c†</sup>	21 November	19 days	10 December	14 December <sup>d</sup>
1999	F067	–	–	–	–	–	–	– <sup>e</sup>	10 December <sup>†</sup>
2000	F010	–	–	– <sup>f</sup>	18 October <sup>g†</sup>	12 November	19 days	1 December	14 December <sup>†</sup>
2000	F066	11 October	17 days	28 October	– <sup>h</sup>	13 November	19 days	2 December	17 December <sup>†</sup>

(a) Eggs taken by unknown predator within one week of laying.

(b) Smaller of two chicks disappeared during afternoon of 28 November; larger chick no longer present by 3 December.

(c) Nest not checked for five days; no sign of chicks on 31 October.

(d) Both chicks still present – no further fieldwork in 1999.

(e) Single chick discovered on 23 November; estimated by mass and stage of feather development as approximately 10 days old.

(f) Two chicks discovered on 13 October; estimated by mass and stage of feather development as approximately 10 days old.

(g) Female and chicks found to have moved to new site by 20 October; not seen subsequently.

(h) Chicks disappeared, presumably taken by a predator, within one week of hatching.

(†) Denotes chick(s) believed to have fledged successfully.

TABLE 6. Mean  $\pm$  SE values of topographical variables for White-winged Nightjar nest sites and an equal number of random sites.

Variable	Nest sites (n = 9)	Random sites (n = 9)	Significance <sup>a</sup>
Gradient (°)	5.6 $\pm$ 1.2	4.8 $\pm$ 0.9	$t_{16} = -0.52$ , ns
Altitude (m)	218 $\pm$ 5	217 $\pm$ 5	$t_{16} = -0.07$ , ns
Distance to nearest stream (m)	306 $\pm$ 61	319 $\pm$ 54	$t_{16} = 0.17$ , ns
Distance to nearest male display arena (m)	227 $\pm$ 49	208 $\pm$ 56	$t_{16} = -0.25$ , ns
Aspect – number of sites facing:			
NE (0-90°)	1 (11%)	0 (0%)	
SE (90-180°)	1 (11%)	1 (11%)	
SW (180-270°)	5 (56%)	6 (67%)	
NW (270-360°)	2 (22%)	2 (22%)	
Habitat – number of sites in:			
Campo cerrado	6 (67%)	8 (89%)	
Wet grassland	3 (33%)	1 (11%)	

(a) From unpaired t-tests.



the predator on either occasion. One female and her chicks were found to have moved to a new clearing, *c.* 10 m from the original nest site, when the chicks were about 10 days old. Assumptions about the fate of other broods, based solely on the disappearance of chicks from the original nest site, therefore seem inappropriate. Of 11 chicks ringed at the nest site, I did not recapture any (post-fledging) before the end of my fieldwork in June 2001. However, one chick ringed in October 2000 was subsequently recaptured as a yearling male in December 2001 (J. Mazar Barnett *in litt.*).

TABLE 7. Summary of morphometrics of 14 White-winged Nightjar eggs from seven clutches.

Measure	Mean $\pm$ SE	Range
Mass (g) <sup>a</sup>	6.7 $\pm$ 0.1	5.8-7.5
Length (mm)	27.7 $\pm$ 0.3	26.7-29.9
Maximum breadth (mm)	21.0 $\pm$ 0.1	19.8-21.7
Volume (cm <sup>3</sup> )	6.2 $\pm$ 0.1	5.4-7.1

(a) Mass provided only for eggs weighed within two days of laying (n = 10).

## DISCUSSION

During the breeding season, male White-winged Nightjars defended small territories on the upper slopes of low ridgelines in the southern sector of Aguará Ñu. The patterns of territory use and ownership I observed supported the suggestion that male territories are traditional (Clay *et al.* 2000). Territories were significantly aggregated within the survey area, with the primary display arenas of neighbouring males separated on average by distances of *c.* 250 m. Males played no part in the parental care of eggs or chicks, and females were only rarely observed near display arenas, with anecdotal evidence suggesting that they mainly visited around full moon when assessing males and seeking copulations. Nest sites were on average 227 m from the nearest display arena, with no evidence to suggest that they fell within the boundaries of male territories. Chick paternity analyses using the amplified fragment length polymorphism (AFLP) technique (Vos *et al.* 1995) suggested that the nearest territory-holding male was not always the father of a brood, and that one male sired the chicks of at least two different females during 1999 (K. Dasmahapatra *in litt.*).

The timing of White-winged Nightjar nesting attempts showed remarkable synchrony with the full moon. A relationship between nest initiation date and moon phase has been demonstrated for a number of

nightjar species (*e.g.* Jackson 1985, Mills 1986, Vilella 1995, Perrins & Crick 1996, Pichorim 2002), and authors typically emphasise the advantages of moonlight for foraging during the first two weeks of the nestling period. The modal incubation period of 19 days resulted in chicks hatching between the new moon and first quarter, and hence during a period of increasing moonlight. However, with male investment in reproduction apparently limited to genes, it might also be argued that females use nights with high moonlight to assess the quality of males before securing copulations (although these two considerations are not incompatible).

Male White-winged Nightjars displayed for a relatively prolonged period between late August and early January, broadly coinciding with the vocal activity of other nightjar species breeding at the study site (*e.g.* Common Pauraque *Nyctidromus albicollis*, Little Nightjar, Spot-tailed Nightjar *Hydropsalis maculicauda* and Rufous Nightjar *Antrostomus rufus*). The considerable variation in display rate within this period was likely due more to environmental conditions than to consistent differences between males. The usually rather short-lived high levels of activity observed when males first arrived at display arenas at dusk were perhaps analogous to the dawn peak of song activity noted for many diurnal birds. Following this initial burst, male display rate was best predicted by ambient levels of moonlight. Increases in vocal activity under conditions of increased moonlight have been noted for various nightjar species (*e.g.* Cooper 1981, Mills 1986, Wilson & Watts 2006), so it is not surprising that a similar relationship should exist for a species with such a strong visual component to its display. The “tik tik” call produced by males while in the vicinity of their display arenas seems likely also to play a role in mate attraction or territory defence.

My results support previous suggestions that the “tk” and “grrrrr” components of male display sounds are both mechanical, rather than vocal, in origin (Clay *et al.* 2000). Careful observation indicated that the “tk” sound was not produced by clapping of the wings below the body, as postulated by Clay *et al.* (2000), but probably by contact with the display mound. However, there was little doubt that the “grrrrr” sound was produced by the wings during the male’s near-vertical ascent from the display mound. Although not as highly modified as those of the Sickie-winged Nightjar *Eleothreptus anomalus* (which is known to produce mechanical wing sounds; Straneck & Viñas 1994), the rigid, curved outer primaries of definitive male White-winged Nightjars probably play a key role in generating the “grrrrr” (Clay *et al.* 2000, Pople 2003). The production of mechanical sounds is relatively rare in birds (Bostwick 2000), but its evolution is often associated with acrobatic, polygynous courtship displays (Prum 1998), as occur in the White-winged Nightjar system.

Overall, my results indicate that the population of White-winged Nightjars at Aguará Ñu employs a polygynous mating system. Although the breeding biology of most nightjar species remains poorly known, polygyny is apparently relatively uncommon in the Caprimulgidae, and has only been demonstrated convincingly for two other species: the Standard-winged Nightjar *Macrodipteryx longipennis* and Pennant-winged Nightjar *M. vexillarius* (Fry *et al.* 1988, Holyoak 2001, Jackson 2004). Male emancipation from parental care is an important prerequisite for any form of polygyny (Höglund & Alatalo 1995), but is unexpected in altricial bird species if fledging success is limited by the amount of food brought to the nestlings (Oring 1982). Snow & Snow (1979) proposed three ecological attributes that favour the evolution of male emancipation in altricial bird species: frugivory; the ability to regurgitate food; and roofed nests (in rainy season breeders). Nightjars are well known to regurgitate food for their chicks (*e.g.* Cramp 1985, Sick 1993, Cleere 1999), and this ability probably facilitates maximal provisioning efficiency per trip away from the nest. In addition, for species living in savanna habitats, such as the White-winged and Standard-winged Nightjars, the mass hatches of winged termites and ants that occur during summer rains (*e.g.* Jackson 2000, Pinheiro *et al.* 2002) could be analogous to the periodic super-abundance of food associated with frugivory.

Although the population of White-winged Nightjars at Aguará Ñu appeared to fulfil all four of the criteria stipulated by Bradbury (1981) for lek-mating species, the exact nature of the mating system remains uncertain. The inter-male distances I recorded far exceed those typical of so-called “classical” lekking species, but were within the range observed for other “exploded” or “dispersed” avian leks (*e.g.* Théry 1992, Alvarez Alonso 2000, Gray *et al.* 2009). Moreover, the question of whether males were aggregated for sexual reasons, or solely as a result of the patchy availability of suitable display habitat, remains unanswered. If the latter is true, and males were spaced regularly within the available habitat (*e.g.* Pruett-Jones & Pruett-Jones 1982), the study population might best be described as exhibiting a “landmark” mating system. This term has traditionally been reserved for insect species in which males aggregate on hilltops or in forest clearings (*e.g.* Alcock 1981), but is applicable to any taxon using a specialised habitat to provide encounter sites for mating (Höglund & Alatalo 1995). Although the evolutionary causes of aggregation in landmark species differ from those for classical lekking species, females of the former do also visit male aggregations primarily for the purpose of mating, and hence the phenomenon still fits the broad definition of lekking proposed by Höglund & Alatalo (1995).

My results have various implications for the conservation of the White-winged Nightjar and the

management of its habitats. The sex-ratio bias of adult captures is likely to have been an artefact of the greater conspicuousness of males (particularly during the breeding season), rather than a true reflection of a skewed population sex ratio. However the finding that the study population probably exhibits a polygynous, possibly even lekking, mating system does have potential consequences for reproductive skew and effective population size (Sutherland 1998). Furthermore, if male display arenas are located at traditional sites, these areas could be of special importance to the population, with limited possibilities for relocation if they are destroyed (Clay *et al.* 2000). As with most species of grassland bird at the study site (*pers. obs.*), the White-winged Nightjar nests between September and December, on the ground amongst campo cerrado or wet grassland vegetation. Any wildfires during the nesting period would have a major impact on breeding success, and extensive burns in the latter half of August could also disrupt nesting if vegetation did not regrow sufficiently before the onset of breeding activity. Wildfires are a regular occurrence at Aguará Ñu, particularly during the austral spring (*e.g.* August and September), so my findings add weight to recommendations elsewhere for more active fire management within the few protected areas where this globally threatened species is known to persist (*e.g.* Rodrigues *et al.* 1999, Capper *et al.* 2000, Pople 2003).

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